Spontaneous temporal coordination during tapping behavior in dyads: A comparative study in chimpanzees and humans

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Contents

Chapter 1

General Introduction

Interpersonal coordination in humans

Interpersonal coordination, including spatial and temporal coordination with others, is important in many species, and is seen in behaviors that range from the coordinated group behaviors of bird flocks and fish schools, to the social group behaviors of humans (e.g., in dancing). In humans, we further show interpersonal coordination even in a basic social unit, which is dyad. An ability to coordinate one's own actions with another is known to establish a smooth interaction, joint action and communication in humans (Bernieri & Rosenthal, 1991). Did humans evolve unique mechanisms for fine control over interpersonal coordination? Or is the human behavior more continuous with similar behaviors we can observe in apes and even monkeys? Studying humans from an evolutionary perspective is important to understand these questions.

In a classical work in the late 19th century, Triplett (1898) introduced the idea of social facilitation, which explains the acceleration or increase in intensity of many behaviors in the existence of others, including enhancements on many cognitive tasks in the case of humans (for review, Zajonc, 1965). Since these initial observations, many studies have focused on inter-individual influences on one's own performance. In more recent work, many studies have focused on more than two individuals at one time as a social unit, to understand how we humans adapt our behavior in a collective social space.

Interpersonal coordination, including spatial and/or temporal coordination, can occur not only when we planned the coordination but also emerge more spontaneously when there are no explicit joint plans or common knowledge between individuals (Knoblich et al., 2011). For instance, people coordinate themselves in space by

mimicking one another's mannerisms, including posture, body configuration or facial expression (Chartrand & Bargh, 1999), or pedestrians often temporally coordinate themselves by falling into the same walking patterns (van Ulzen et al., 2008). Experimental studies on spontaneous spatiotemporal coordination have further shown that the observed actions from others influence the execution of one's own actions even when the movement observation is task-irrelevant (Brass et al., 2001; Craighero et al., 2002; Heyes et al., 2005). Moreover, previous studies have found that it is difficult to resist an automatic coupling of one's movements with an interacting partner, even when the participants were actually instructed to ignore each other's movements (Schmidt & O'Brien, 1997; Killner et al. 2003; Issartel et al., 2007; Richardson et al., 2007; Yun et al., 2012). These findings from social psychology provide strong support for the hypothesis that there are automatic processes for the emergence of spatial and/or temporal coordination in humans.

Social function of interpersonal coordination in humans

Recently, interpersonal coordination, including spatial (e.g., mimicry) and temporal (e.g., interactional synchrony) coordination, gained much attention because it suggested an essential function in social interaction. When we are mimicked by or synchronized to others, we tend to show increased affiliation, rapport and feelings of empathy towards them (Chartrand & Bargh, 1999; Hove & Risen, 2009) and behave cooperatively with the partner (Wiltermuth & Heath, 2009) and prosocially in general (van Baaren et al., 2004). Developmental studies further demonstrated that the sensitivity to synchronized

movement in promoting prosocial behaviors develops quite early (Kirschner & Tomasello, 2010), emerging in infants as young as 14-months-old (Cirelli et al., 2014). Importantly, this early development of social coordination appears to be a component of healthy social functioning: studies in infants with autism spectrum disorders (ASD) revealed that movement abnormalities in spatiotemporal coordination are some of the earliest known precursors to a later diagnosis of ASD (Williams et al., 2001; Grossberg & Seidman, 2006), and are correlated with later deficits in empathic ability (Piek & Dyck, 2004). Although the underlying mechanisms whereby positive social consequences result from interpersonal coordination remain a topic of active investigation (c.f., blurring self-other boundaries, Paladino et al., 2010), an increasing number of studies indicate that spatial and/or temporal coordination plays an important role in maintaining harmonious social relationships among humans.

Evolutionary origins of interpersonal coordination in humans

There is one study showing that other highly social non-human primate species share an adaptive function of interpersonal coordination with humans. Paukner et al. (2009) reported that capuchin monkeys (*Cebus capucinus*), which are a highly social primate species, preferred humans who imitated their behaviors over non-imitators. Specifically, the results showed that the monkeys look longer at imitators, spend more time in proximity to imitators, and choose to interact more frequently with imitators in a token exchange task. Other studies (Nielsen et al., 2005; Paukner et al., 2005; Haun & Call, 2008), focusing just on the perceptual ability to discriminate whether they are being

imitated by human experimenter, also showed a consistent result in both great apes and macaques: both species increase their visual attention to imitators. These studies from non-human primates suggest that behaviors that are structurally and temporally contingent on one's own movement attract attention and facilitate interaction with others. Taken together, these findings suggest that spatiotemporal coordination may also play a positive social role in non-human primates during their actual interactions. However, it remains unclear whether non-human primates coordinate their behavior with other conspecific individuals in a similar manner as that shown with human experimenters.

Although they involve interaction with a human experimenter rather than with a conspecific, there are pioneering studies on spontaneous mimicry behaviors in non-human primates, reporting neonatal facial mimicry in chimpanzees (Myowa-Yamakoshi et al., 2004) and in monkeys (Ferrari et al., 2006). Moreover, there is evidence that those two species show contagious yawning (Anderson et al., 2004; Paukner & Anderson., 2006; Campbell et al., 2009). These studies, while focusing on simple specific behaviors, nonetheless show that humans are not unique in their ability to mimic others' facial expressions in social interaction, and suggest that automatic mimicry may be one evolutionary primitive component of social coordination in primates.

Studies on temporal coordination in non-human primates have mostly observed behaviors under a non-social context (Zarco et al., 2009; Hattori et al., 2013; 2015; Konoike et al., 2012). Only a few studies have recently been done under a social context (Kobayashi & Hashiya, 2009; Nagasaka et al. 2013; Fuhrmann et al., 2014), although field observations in chimpanzees have for some time documented coordinative

behaviors, for instance during territorial boundary patrols (Goodall et al., 1979; Watts & Mitani, 2001) or vocal chorusing (Arcadi, 1996; Gros-Louis & Mitani, 1998; Fedurek et al., 2013).

Nagasaka et al. (2013) first demonstrated that Japanese macaques (*Macaca fuscata*) can temporally coordinate their movements with their conspecific partner, even without explicit training. In the experiment, the monkeys were only required to produce repetitive left-to-right arm movements while facing their partner. Although the findings suggest that, like humans, macaques have an ability for temporal coordination with a partner, further evidence in non-human primates is needed. In particular, it has remained unclear which aspects of coordination may be similar between apes and humans, and which may differ and possibly be unique to humans. To address these important open questions, the current thesis targeted chimpanzees (*Pan troglodytes*) and directly compared them with humans under the same experimental setup. Similar to the methods in Nagasaka et al., (2013), the participants in dyads simultaneously produced repetitive left-to-right tapping movements with their conspecific partner. The similar experimental protocols for the first time permit a broader comparison of interpersonal coordination across monkeys, chimpanzees and humans.

Comparative cognitive study in chimpanzees

The comparative method is crucially important in exploring the evolutionary origins of human behavior and the human mind. Studies on chimpanzees (*Pan troglodytes*) are especially important because they are phylogenetically the closest living relative to

humans. Field studies have shown that chimpanzees form complex social groups in their natural habitat (Goodall, 1986; Matsuzawa et al., 2010; Nishida et al., 2010) and exhibit a number of higher cognitive abilities, including the skill to use tools (Whiten et al., 1999) and the social intelligence required to form coalitions and alliances (de Waal, 1982). All of these examples argue that we can find evolutionary precursors to human cognitive abilities in chimpanzees. However, to further quantify the similarity and dissimilarity of these cognitive abilities, and to eventually gain insight also into the physiological mechanisms behind them, it was necessary to design a comparative cognitive study that could be conducted under controlled experimental setup where humans and chimpanzees participate in exactly the same task, using the same apparatus, and following the same procedure (Matsuzawa et al., 2006). In this line of research, laboratory studies have been conducted and provided compelling evidence for cognitive abilities in chimpanzees that parallel many of those seen in humans (Tomasello & Call, 1997; Matsuzawa et al., 2006).

Scope of this thesis

The current thesis conducted a comparative study in chimpanzees and humans to help us better understand the evolutionary origins of temporal coordination in humans. We humans can rapidly and completely coordinate our movements in time with those of others, as can be seen in the dances or ritual behaviors of many ethnic groups. Did humans evolve unique mechanisms for fine control over temporal coordination? Or is the human behavior more continuous with similar behaviors we can observe in other

animals? A comparative cognitive study is one of the crucial methods required to understand these questions. The current thesis aimed to examine similarities and dissimilarities in temporal coordination between chimpanzees and humans, when they produce simultaneous tapping movements with a conspecific partner. Especially in Chapter 3, where both chimpanzees and humans were examined under the originally established face-to-face setup, I investigated not only temporal coordination itself, but also the characteristics of that coordination (harmony/directionality/modality/mode).

This thesis aims to address the following four questions. First, do chimpanzees also have an ability to temporally coordinate their behaviors with another chimpanzee? If they do, subsequent questions can be raised: does their coordination show perfect phase and tempo matching? Or do they coordinate their movements without exact synchronization, such as adapting their tempo to match, but no matching the phase onset of the movement? Second, if a dyad (either of two chimpanzees or of two humans) shows temporal coordination, which participants in the dyad contribute to it? This will be answered by examining directionality of the tapping tempo change in each participant. For instance, does one participant typically lead the tempo, and the other participant follows and adapts? Third, which type of sensory modality is used in detecting the tapping behavior of a partner? An effect of auditory and/or visual cues will be examined under two different experimental setups (the side-by-side setup in Chapter 2 and the face-to-face setup in Chapter 3). Finally, does the temporal coordination emerge quickly and completely or slowly and partially? Speed and strength of the temporal coordination will be compared between chimpanzees and humans.

The General Discussion (Chapter 4) will take up the findings from the current thesis and a prior study in macaques (Nagasaka et al., 2013) to provide a broader

172 comparison across humans, chimpanzees and macaques. Also, I will discuss how the
173 current analyses relate to the previous neurophysiological studies and comparative
174 cognitive studies from an evolutionary perspective. Finally, I will address what would
175 be an intriguing research question in future study.
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References

Anderson, J. R., Myowa–Yamakoshi, M., & Matsuzawa, T. (2004). Contagious yawning in chimpanzees. Proceedings of the Royal Society of London B: Biological Sciences, 271(Suppl 6), S468-S470.

Arcadi, A. C. (1996). Phrase structure of wild chimpanzee pant hoots: Patterns of production and interpopulation variability. American Journal of Primatology, 39(3), 159–178.

Bernieri, F. J., & Rosenthal, R. (1991). Interpersonal coordination: behavior matching and interactional synchrony. In Fundamentals of nonverbal behavior: studies in emotion & social interaction (pp. 401–432).

Brass, M., Bekkering, H., & Prinz, W. (2001). Movement observation affects movement execution in a simple response task. Acta Psychologica, 106(1-2), 3–22.

Campbell, M. W., Carter, J. D., Proctor, D., Eisenberg, M. L., & de Waal, F. B. (2009). Computer animations stimulate contagious yawning in chimpanzees. Proc Biol Sci, 276(1676), 4255–4259.

Chartrand, T. L., & Bargh, J. a. (1999). The chameleon effect: the perception-behavior link and social interaction. Journal of Personality and Social Psychology, 76(6), 893–910.

Cirelli, L. K., Einarson, K. M., & Trainor, L. J. (2014). Interpersonal synchrony increases prosocial behavior in infants. Developmental Science, 17(6), 1003–1011.

Craighero, L., Bello, A., Fadiga, L., & Rizzolatti, G. (2002). Hand action preparation influences the responses to hand pictures. Neuropsychologia, 40(5), 492-502.

de Waal, F. (1982). Chimpanzee politics: Power and sex among apes. London: Jonathan

Cape.

Fedurek, P., Machanda, Z. P., Schel, A. M., & Slocombe, K. E. (2013). Pant hoot chorusing and social bonds in male chimpanzees. Animal Behaviour, 86(1), 189–196.

Ferrari, P. F., Visalberghi, E., Paukner, A., Fogassi, L., Ruggiero, A., & Suomi, S. J. (2006). Neonatal imitation in rhesus macaques. PLoS Biology, 4(9), 1501–1508.

Fuhrmann, D., Ravignani, A., Marshall-Pescini, S., & Whiten, A. (2014). Synchrony and motor mimicking in chimpanzee observational learning. Scientific Reports, 4, 5283.

Goodall, J., Bandora, A., Bergmann, E., Busse, C., Matama, H., Mpongo, E., .. & Riss, D. (1979). Intercommunity interactions in the chimpanzee population of the Gombe National Park. *The great apes*, *5*, 13-53.

Gros-Louis, J., & Mitani, J. C. (1998). Chorusing and Call Convergence in Chimpanzees: Tests of Three Hypotheses. Behaviour, 135, 1041–1064.

Grossberg, S., & Seidman, D. (2006). Neural dynamics of autistic behaviors: cognitive, emotional, and timing substrates. Psychological Review, 113(3), 483–525.

Hattori, Y., Tomonaga, M., & Matsuzawa, T. (2013). Spontaneous synchronized tapping to an auditory rhythm in a chimpanzee. Scientific Reports, 3, 1566.

Hattori, Y., Tomonaga, M., & Matsuzawa, T. (2015). Distractor effect of auditory rhythms on self-paced tapping in chimpanzees and humans. PLoS ONE, 10(7).

Haun, D. B., & Call, J. (2008). Imitation recognition in great apes. Current Biology, 18(7), R288-R290.

Heyes, C., Bird, G., Johnson, H., & Haggard, P. (2005). Experience modulates

automatic imitation. Cognitive Brain Research, 22(2), 233-240.

Hove, M. J., & Risen, J. L. (2009). It's All in the Timing: Interpersonal Synchrony Increases Affiliation. Social Cognition, 27(6), 949–960.

Issartel, J., Marin, L., & Cadopi, M. (2007). Unintended interpersonal co-ordination: "can we march to the beat of our own drum?" Neuroscience Letters, 411(3), 174–179.

Kilner, J. M., Paulignan, Y., & Blakemore, S. J. (2003). An interference effect of observed biological movement on action. Current Biology, 13(6), 522–525.

Kirschner Sebastian, S., & Tomasello, M. (2010). Joint music making promotes prosocial behavior in 4-year-old children. Evolution and Human Behavior, 31(5), 354–364.

Knoblich, G., Butterfill, S., & Sebanz, N. (2011). Psychological research on joint action: theory and data. Psychology of Learning and Motivation-Advances in Research and Theory, 54, 59–101.

Kobayashi, H., & Kazuhide, H. (2009). Spontaneous synchrony by chimpanzees in response to humans' behavior. The Japanese Journal of Psychonomic Science, 27, 179–180.

Konoike, N., Mikami, A., & Miyachi, S. (2012). The influence of tempo upon the rhythmic motor control in macaque monkeys. Neuroscience research, 74(1), 64-67.

Matsuzawa, T., Humle, T., & Sugiyama, Y. (2010). The chimpanzees of Bossou and Nimba. Tokyo: Springer.

Myowa-Yamakoshi, M., Tomonaga, M., Tanaka, M., & Matsuzawa, T. (2004). Imitation in neonatal chimpanzees (Pan troglodytes). Developmental Science, 7(4), 437–

442.

Nagasaka, Y., Chao, Z. C., Hasegawa, N., Notoya, T., & Fujii, N. (2013). Spontaneous synchronization of arm motion between Japanese macaques. Scientific Reports, 3, 1151.

Nielsen, M., Collier-Baker, E., Davis, J. M., & Suddendorf, T. (2005). Imitation recognition in a captive chimpanzee (Pan troglodytes). Animal cognition, 8(1), 31-36.

Nishida, T., Zamma, K., Matsusaka, T., Inaba, A., & McGrew, W. C. (2010). *Chimpanzee behavior in the wild: an audio-visual encyclopedia*. Springer Science & Business Media.

Paladino, M.-P., Mazzurega, M., Pavani, F., & Schubert, T. W. (2010). Synchronous multisensory stimulation blurs self-other boundaries. Psychological Science : A Journal of the American Psychological Society / APS, 21(9), 1202–1207.

Paukner, A., Anderson, J. R., Borelli, E., Visalberghi, E., & Ferrari, P. F. (2005). Macaques (Macaca nemestrina) recognize when they are being imitated. Biology Letters, 1(2), 219-222.

Paukner, A., & Anderson, J. R. (2006). Video-induced yawning in stumptail macaques (Macaca arctoides). Biology Letters, 2(1), 36–8.

Piek, J. P., & Dyck, M. J. (2004). Sensory-motor deficits in children with developmental coordination disorder, attention deficit hyperactivity disorder and autistic disorder. Human movement science, 23(3), 475-488.

Richardson, M. J., Marsh, K. L., Isenhower, R. W., Goodman, J. R. L., & Schmidt, R. C. (2007). Rocking together: Dynamics of intentional and unintentional interpersonal coordination. Human Movement Science, 26(6), 867–891.

Schmidt, R. C., & O'Brien, B. (1997). Evaluating the dynamics of unintended interpersonal coordination. Ecological Psychology, 9(3), 189-206.

Tomasello, M., & Call, J. (1997). Primate cognition (Vol. 24, No. 3). Oxford University Press, USA.

van Baaren, R. B., Holland, R. W., Kawakami, K., & van Knippenberg, A. (2004). Mimicry and prosocial behavior. Psychological Science, 15(1), 71–74.

Watts, D. P., Mitani, J. C., & Watts, D. P. (2001). Boundary Patrols and Intergroup Encounters in Wild Chimpanzees. Behaviour, 138(3), 299–327.

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., … Boesch, C. (1999). Cultures in chimpanzees. Nature, 399(6737), 682–685.

Williams, J. H., Whiten, A., Suddendorf, T., & Perrett, D. I. (2001). Imitation, mirror neurons and autism. Neuroscience & Biobehavioral Reviews, 25(4), 287-295.

Wiltermuth, S. S., & Heath, C. (2009). Synchrony and cooperation. Psychological Science, 20(1), 1–5.

Yun, K., Watanabe, K., & Shimojo, S. (2012). Interpersonal body and neural synchronization as a marker of implicit social interaction. Scientific reports, 2.

Zajonc, R. (1965). Social facilitation. Science, 149(3681), 269–274.

Zarco, W., Merchant, H., Prado, L., & Mendez, J. C. (2009). Subsecond timing in primates: comparison of interval production between human subjects and rhesus monkeys. Journal of neurophysiology, 102(6), 3191-3202.

Chapter 2

Examination under side-by-side setup: an effect of auditory cues on temporal coordination in chimpanzees

Abstract

Humans often unconsciously coordinate behaviour with that of others in daily life. This interpersonal coordination, including mimicry and interactional synchrony, has been suggested to play a fundamental role in social interaction. If this coordinative behavior is socially adaptive, it may be shared with other highly social animal species. The current study targeted chimpanzees, which phylogenetically are the closest living relatives of humans and live in complex social groups, and examined whether interactional synchrony would emerge in pairs of chimpanzees when auditory information about a partner's movement was provided. A finger-tapping task was introduced via touch panels to elicit repetitive and rhythmic movement from each chimpanzee. We found that one of four chimpanzees produced significant changes in both tapping tempo and timing of the tapping relative to its partner's tap when auditory sounds were provided. Although the current results may have limitations in generalizing to chimpanzees as a species, we suggest that a finger-tapping task is one potential method to investigate interactional synchrony in chimpanzees under a laboratory setup.

Keywords: chimpanzees, temporal coordination, finger-tapping task, auditory interaction

Introduction

Humans often unconsciously coordinate their movements with those of others (Chartrand & Bargh, 1999). This interpersonal coordination includes two distinctive behaviours: mimicry and interactional synchrony (Bernieri & Rosenthal, 1991). Mimicry involves matching a type of behaviour, such as posture, body configuration, or facial expression, to another individual. Interactional synchrony, in contrast, is matching the timing of a movement, such as synchronous hand-clapping in a concert hall or stride-matching while walking with other individuals. Experimental studies have further shown that mimicry and interactional synchrony occur under automatic modulation in humans (Brass et al., 2001; Kilner et al., 2003; Richardson et al., 2007; Oullier et al., 2008; Watanabe, 2008).

Despite being common in humans, the function of interpersonal coordination remains a topic of investigation. Previous studies have shown that mimicry and interactional synchrony have positive social consequences in humans: when we are mimicked by or synchronized to others, we tend to show increased affiliation, rapport and feelings of empathy towards them (Chartrand & Bargh, 1999; Hove & Risen, 2009), and behave more prosocially in general (van Baaren et al., 2004). These findings suggest that interpersonal coordination, both mimicry and interactional synchrony, plays an important role in maintaining positive social relationships among humans.

Interestingly, one study showed that other highly social non-human primate species share an adaptive function of interpersonal coordination with humans (Paukner et al., 2009). Capuchin monkeys (*Cebus capucinus*), which are a highly social primate species, preferred humans who imitated their behaviours over non-imitators. This

finding suggests that mimicry may also play a positive social role in their actual interactions. However, it remains unclear whether non-human primates coordinate with conspecifics in a similar manner as that shown between capuchins and humans. Previous studies on mimicry have shown that non-human primates produce contagious yawning (Anderson et al., 2004; Paukner & Anderson, 2006) and neonatal facial mimicry (Tomonaga et al., 2003; Ferrari et al., 2006; Myowa-Yamakoshi et al., 2004), which suggest that humans are not unique in their ability to mimic other's facial expressions in a spontaneous manner.

Relative to the studies of mimicry, there are few studies of interactional synchrony in non-human primates. To date, two experimental studies have shown that mechanisms of spontaneous synchronization to external stimuli exist in non-human primates. Nagasaka, Chao, Hasegawa, Notoya & Fujii (2013) reported that Japanese macaques (*Macaca fuscata*) synchronized their arm movements with partner monkeys that were facing them. In a further test, they demonstrated that visual information of the other's movement was required to produce interactional synchrony, while auditory information of the other's movement had little influence. In contrast to the study of the macaques, Hattori, Tomonaga & Matsuzawa (2013) reported that a chimpanzee (*Pan troglodytes*) could synchronize to auditory sounds specifically when the sounds were isochronous and close to the chimpanzee's preferred tempo. These two studies indicate that chimpanzees and macaques may have different sensitivities to auditory information when producing synchronized movement (Merchant & Honing, 2014). However, little is known about whether chimpanzees are sensitive to auditory sounds of an irregular and fluctuating tempo that are produced by other conspecifics.

In the current study, we investigated whether interactional synchrony occurs in

pairs of chimpanzees (*Pan troglodytes*) when they are sitting side by side and auditory information about the other's movement is provided. Studies on chimpanzees are crucially important for understanding the evolutionary origins of interactional synchrony in humans, because they are phylogenetically the closest living relatives to humans. We introduced a finger-tapping task, which is extensively used for exploring sensorimotor synchronization in humans (Repp, 2005). The task was adapted to touch screen monitors, which facilitated repetitive and rhythmic tapping movements and enabled observation of interactional synchrony between chimpanzees in the current laboratory setup. The chimpanzees performed the task under two different auditory conditions: with and without auditory sounds.

Methods

Participants

Two pairs, each consisting of a mother chimpanzee and her biological offspring (33-year-old Chloe and her 13-year-old daughter, Cleo; and 30-year-old Pan and her 13-year-old daughter, Pal) participated in the experiment. Both offspring had been successfully raised by their mothers since they were born at the Primate Research Institute, Kyoto University (Matsuzawa et al., 2006). They lived together with nine other chimpanzees in an enriched outdoor compound with attached indoor residences (Matsuzawa, 2006). All experiments were voluntary, and subjects were never deprived of water or food. All chimpanzees had extensive experience with cognitive tasks using a touch screen (Tomonaga, 2001) and some of the experiments included auditory cues as a discriminative stimulus (Izumi & Kojima, 2004; Martinez & Matsuzawa, 2009;

Ludwig & Adachi, 2011). Studies on social interactions between chimpanzees have also been conducted under various experimental setups (Yamamoto & Tanaka, 2010; Martin et al., 2011; Yamamoto et al., 2012; Martin et al., 2013; Martin et al., 2014). The care and use of chimpanzees were carried out in accordance with the 3rd edition of the Guide for the Care and Use of Laboratory Primates issued by Kyoto University Primate Research Institute in 2010. The experimental protocol was approved by the Animal Welfare and Animal Care Committee of the same institute.

Apparatus

Experiments were conducted in an experimental booth (1.8 × 2.15 × 1.75 m) adjacent to the chimpanzees' indoor residences. Two interconnected 17-inch LCD monitors (1280 × 1024 pixels) with a touch panel were used, and were set approximately 80 cm apart on the same side of the wall of the booth. Two universal feeders delivered a food reward to each chimpanzee. Auditory stimuli were played through a built-in speaker of the monitor. All the equipment and experimental events were controlled by a computer located outside the experimental booth.

Procedure

A finger-tapping task was introduced to elicit repetitive and rhythmic tapping movements from each chimpanzee using a touch panel. Each trial began with the presentation of a Start button on the screen. After touching the button, the chimpanzees were required to touch a visual target (5.8 × 5.8 cm) that appeared on the left or the right side of the monitor. When the target that appeared was touched once, it disappeared with a short beep sound (55 ms, 1000 Hz, approximately 50 dB) and reappeared on the

other side with 0 ms delay. After the left and the right targets were tapped alternatively several times, a trial ended with a chime, and food rewards were delivered to the chimpanzees. The inter-trial interval was 2 seconds. Each chimpanzee was individually trained to conduct the task, starting with a single tap, and then the number of required taps increased up to between 25 and 35. This training phase continued until the chimpanzees cleared a criterion of tapping without a pause of more than 3 seconds during a trial.

During the test phase, the pairs of chimpanzees conducted a finger-tapping task simultaneously (Figure 2-1). Two experimental conditions were prepared: without-sound and with-sound condition. In the without-sound condition, a short beep sound corresponding to each chimpanzee's tapping event was absent so that the sounds would not interfere with the chimpanzees' own preferred rhythmic movement. In contrast, in the with-sound condition, each tap by the chimpanzees was accompanied by a short beep sound so that the auditory information corresponding to movement could be exchanged between chimpanzees.

<<Figure 1 around here>>

In the test phase, a yoked-control procedure was used to equate the time of a trial Start and Finish between the chimpanzees. Master and yoked subject were randomly assigned on a trial basis. However, the timing of visual target presentation was not controlled by the experimenter for both chimpanzees. The target reappeared with 0 ms delay when the previous target was touched. Both chimpanzees in a pair produced the tapping movement with their own-preferred tempo across the experiment.

438

439 **Experimental design and statistical analysis**

440 To examine whether the chimpanzees changed their tapping behavior depending on
441 condition, 30 trials were collected for each test condition from each chimpanzee. Each
442 trial required 25 to 35 tapping movements. Five trials were conducted per block and 6
443 blocks were obtained over four experimental days. ABA block design was employed to
444 randomize the order of the two test conditions. Either an ABA or a BAB schedule was
445 conducted in any given day.

446 In addition to an effect of conditions, we also examined an effect of trial
447 number because we predicted that tapping behavior would change depending on time.
448 We used generalized linear mixed model (implemented in SPSS Advanced Models
449 14.0J) for data analysis. The fixed effects were Conditions and Trials, and the random
450 effect was Blocks (nested in trials) (Verbeke & Molenbergs, 1997). No multiple
451 comparisons within-pairs or within-the four chimpanzee participants was conducted in
452 the analysis.

453

454 **Results**

455

456 We first examined the effect of auditory sounds on the chimpanzees' tapping movement.
457 If auditory sounds interfered with the chimpanzees' tapping movements, the tapping
458 behaviour in the with-sound condition would differ from the without-sound condition.
459 To test this hypothesis, the mean tapping interval, which is an inverse form of tempo,
460 was compared between the without-sound and with-sound conditions. Some of the
461 tapping intervals from a 'miss-touching' event were excluded from the data analysis.

Excluded data were less than 10% for each participant and for each condition. For the statistical analysis, an effect of trial was additionally examined to see how tapping intervals change as time progresses. We found that all four chimpanzees produced distinctive patterns of tapping intervals across trials in the with-sound condition compared to the without-sound condition. There was significant interaction between condition and trial: Chloe, $F(4, 1612) = 4.427$, $p = 0.001$; Cleo, $F(4, 1567) = 4.408$, $p = 0.002$; Pan, $F(4, 1401) = 5.087$, $p < 0.001$; Pal, $F(4, 1752) = 5.637$, $p < 0.001$ (Figure 2-2).

<< Figure 2-2 around here>>

Next, we tested whether these distinctive patterns of tapping intervals in the with-sound condition were a response to auditory sounds from the partner chimpanzee. If there was an effect of auditory sounds from the partner chimpanzee, a convergence of tapping intervals would occur between the chimpanzees. To examine this hypothesis, we calculated an absolute difference in tapping intervals between the paired chimpanzees for each trial (Figure 2-3). A median tapping interval was used as a value of central tendency per trial for each chimpanzee. We found that for one pair of chimpanzees, Chloe and Cleo, the mean absolute difference in tapping intervals between them was significantly smaller in the with-sound condition compared to the without-sound condition, $t(29) = 2.229$, $p = 0.03$, although it was not clear which chimpanzee significantly changed the tapping tempo toward their partner (see Figure 2-4). Another pair of chimpanzees, Pan and Pal, showed no significant changes between the without-sound and the with-sound condition, $t(29) = 0.407$, $p = 0.685$.

<< Figure 2-3 and 2-4 around here>>

Finally, we examined whether tapping movements would converge in time among pairs of chimpanzees. We calculated the asynchrony (Figure 2-5), which was defined as the minimal difference in timing from a partner's tap to a chimpanzee's own tap. Consistent with the analysis on tapping intervals, we examined this for an effect of condition and trial (Figure 2-6). We found that the mean asynchrony from Chloe, that is, the difference in timing between the pair when Chloe followed her partner Cleo's tap, became significantly smaller as the trial progressed in the with-sound condition. Chloe showed a significant interaction between condition and trial, $F(4, 1406) = 3.171$, $p = 0.013$. A post hoc analysis revealed a simple main effect of trials within the with-sound condition, $F(4, 1406) = 3.730$, $p = 0.005$. Multiple comparisons based on estimated marginal means with Sidak's correction further revealed that the mean asynchrony for the 5th trial was significantly smaller than the 1st and 3rd trials (1st vs. 5th, $p = 0.016$; 3rd vs. 5th, $p = 0.017$). In the other three chimpanzees, we found no significant interaction or main effect of the condition or of the trial on asynchrony.

<< Figure 2-5 and 2-6 around here>>

Discussion

In the current study, we investigated whether interactional synchrony would occur in pairs of chimpanzees when auditory information of the partner's movements was

provided. All four chimpanzees were affected by auditory sounds; however, a convergence of tapping intervals was found only in the pair of Chloe and Cleo. This suggests that auditory sounds from partners could affect a chimpanzee's own tapping tempo. Asynchrony analyses demonstrated that Chloe augmented her tapping movements to match those of her partner's, particularly as the trial progressed and when auditory sounds were provided. Although the synchronization shown by Chloe was relatively weak compared to that of humans, her behaviour was consistent with previous studies showing that both the tempo and timing of movements (represented by tapping intervals and asynchrony, respectively) change when humans synchronize to musical beats or with other individuals (Neda et al., 2000; Repp, 2005; Richardson et al., 2007; Merchant & Honing, 2014). Considered together, we demonstrated that at least one chimpanzee could produce interactional synchrony with auditory sounds from her partner.

None of the chimpanzees in the current experiment were trained to match their tapping behavior with the others. Thus, the behaviours seen in Chloe are consistent with previous studies demonstrating that non-human primates can produce spontaneous synchronization with external stimuli even without explicit training (Nagasaka et al., 2013; Hattori et al., 2013).

Although this study cannot discern whether the presence of the other (partner) chimpanzee is an important factor for the emergence of interactional synchrony, we suggest that Chloe's behaviour differed from the way in which chimpanzees coordinate with isochronous auditory sounds in non-social settings. Hattori, Tomonaga & Matsuzawa (2013) showed that a chimpanzee named Ai synchronized to isochronous auditory sounds that were close to her own preferred tempo, but not to distant or

534 random tempos. In contrast, Chloe synchronized with the auditory sounds of an
535 irregular and distant tempo. These differences imply that the presence of a partner might
536 facilitate interactional synchrony with a fluctuating tapping tempo generated by another
537 individual.

538 Previous studies on humans demonstrated that synchronous handclapping can
539 disappear and reappear several times during applause (Neda et al., 2000). However, in
540 non-human primates, the way in which interactional synchrony occurs and changes over
541 time has not yet been revealed. To our knowledge, this is the first study showing that a
542 chimpanzee coordinated her own rhythmic movement with the interacting partner in a
543 more synchronous manner as time progressed. To further confirm a gradual process in
544 interactional synchrony among chimpanzees, our future research will examine the
545 execution of tapping movements under a prolonged duration in a laboratory setting.

546 Despite our results, we admit that the current study may not allow us to
547 generalize to all chimpanzees because only one of four subjects showed a tendency
548 toward interactional synchrony with a partner. A long history of conducting independent
549 computer tasks (Matsuzawa et al., 2006; Tomonaga, 2001) while ignoring others might
550 have overshadowed the effect of auditory sounds in the current experimental setting.
551 Further study is needed under a new laboratory setup to exclude this plausible artefact.

552 In summary, the current study demonstrated that interactional synchrony can
553 occur between chimpanzees, as observed in a single chimpanzee that augmented her
554 tapping movements upon hearing auditory sounds to converge on her partner's
555 movements. Although the current study requires further evidence to suggest that
556 chimpanzees may have the capacity to modulate their behaviours to synchronize with
557 other conspecifics, it demonstrated that a finger-tapping task is one potential method for

558 investigating interactional synchrony under a laboratory setting. Compared to a recent
559 observational study showing that a chimpanzee synchronized a motor action with
560 another chimpanzee in the context of observational learning (Fuhrmann et al., 2014),
561 experimental studies such as the current one can clarify cognitive processes related to
562 behaviour, such as visual and auditory perception and attention, to understand the
563 underlying mechanisms of interpersonal coordination.

564 Future studies should consider social relationships to explore what social
565 factors may influence the intensity of interactional synchrony in chimpanzees and other
566 animals. Although the current study focused on mother-offspring pairs, field
567 observations have documented coordinated behaviours in male chimpanzees, such as
568 during territorial boundary patrols (Goodall et al., 1979; Watts & Mitani, 2001) and
569 vocal chorusing (Arcadi, 1996; Mitani & Gros-Louis, 1998; Fedurek et al., 2013). To
570 understand the adaptive significance of interactional synchrony and its relevance to
571 empathy (Preston & de Waal, 2002) in chimpanzees, our future study will also
572 investigate pairs of unrelated chimpanzees with a range of social relationships.
573

574 **References**

575 Anderson, J. R., Myowa–Yamakoshi, M., & Matsuzawa, T. (2004). Contagious yawning
576 in chimpanzees. Proceedings of the Royal Society of London B: Biological
577 Sciences, 271(Suppl 6), S468-S470.

578 Arcadi, A. C. (1996). Phrase structure of wild chimpanzee pant hoots: Patterns of
579 production and interpopulation variability. American Journal of Primatology,
580 39(3), 159–178.

581 Bernieri, F. J., & Rosenthal, R. (1991). Interpersonal coordination: behavior matching
582 and interactional synchrony. In Fundamentals of nonverbal behavior: studies in
583 emotion & social interaction (pp. 401–432).

584 Brass, M., Bekkering, H., & Prinz, W. (2001). Movement observation affects movement
585 execution in a simple response task. Acta Psychologica, 106(1-2), 3–22.

586 Chartrand, T. L., & Bargh, J. a. (1999). The chameleon effect: the perception-behavior
587 link and social interaction. Journal of Personality and Social Psychology, 76(6),
588 893–910.

589 Fedurek, P., Machanda, Z. P., Schel, A. M., & Slocombe, K. E. (2013). Pant hoot
590 chorusing and social bonds in male chimpanzees. Animal Behaviour, 86(1),
591 189–196.

592 Ferrari, P. F., Visalberghi, E., Paukner, A., Fogassi, L., Ruggiero, A., & Suomi, S. J.
593 (2006). Neonatal imitation in rhesus macaques. PLoS Biology, 4(9), 1501–
594 1508.

595 Fuhrmann, D., Ravignani, A., Marshall-Pescini, S., & Whiten, A. (2014). Synchrony
596 and motor mimicking in chimpanzee observational learning. Scientific Reports,
597 4, 5283.

598 Goodall, J., Bandora, A., Bergmann, E., Busse, C., Matama, H., Mpongo, E., .. & Riss,
599 D. (1979). Intercommunity interactions in the chimpanzee population of the
600 Gombe National Park. *The great apes*, *5*, 13-53.
601 Gros-Louis, J., & Mitani, J. C. (1998). Chorusing and Call Convergence in
602 Chimpanzees: Tests of Three Hypotheses. Behaviour, 135, 1041–1064.
603 Hattori, Y., Tomonaga, M., & Matsuzawa, T. (2013). Spontaneous synchronized tapping
604 to an auditory rhythm in a chimpanzee. Scientific Reports, 3, 1566.
605 Hove, M. J., & Risen, J. L. (2009). It's All in the Timing: Interpersonal Synchrony
606 Increases Affiliation. Social Cognition, 27(6), 949–960.
607 Izumi, A., & Kojima, S. (2004). Matching vocalizations to vocalizing faces in a
608 chimpanzee (Pan troglodytes). Animal Cognition, 7, 179–184.
609 Kilner, J. M., Paulignan, Y., & Blakemore, S. J. (2003). An interference effect of
610 observed biological movement on action. Current Biology, 13(6), 522–525.
611 Ludwig, V. U., Adachi, I., & Matsuzawa, T. (2011). Visuoauditory mappings between
612 high luminance and high pitch are shared by chimpanzees (Pan troglodytes)
613 and humans. Proceedings of the National Academy of Sciences of the United
614 States of America, 108(51), 20661–5.
615 Martin, C. F., Bhui, R., Bossaerts, P., Matsuzawa, T., & Camerer, C. (2014).
616 Chimpanzee choice rates in competitive games match equilibrium game theory
617 predictions. Sci Rep, 4, 5182.
618 Martin, C. F., Biro, D., & Matsuzawa, T. (2014). The Arena System: a novel shared
619 touch-panel apparatus for the study of chimpanzee social interaction and
620 cognition. Behavior Research Methods, 46(3), 611–8.
621 Martin, C. F., Biro, D., & Matsuzawa, T. (2011). Chimpanzees' use of conspecific cues

622 in matching-to-sample tasks: Public information use in a fully automated
623 testing environment. Animal Cognition, 14(6), 893–902.
624 Martinez, L., & Matsuzawa, T. (2009). Auditory–visual intermodal matching based on
625 individual recognition in a chimpanzee (Pan troglodytes). Animal cognition,
626 12(1), 71-85.
627 Masters, J. C., & Couette, S. (2015). Characterizing cryptic species: A morphometric
628 analysis of craniodental characters in the dwarf galago genus Galagoides.
629 American Journal of Physical Anthropology, 158(2), 288–299.
630 Matsuzawa, T., Tomonaga, M., & Tanaka, M. (2006). Cognitive development in
631 chimpanzees. Springer, Tokyo.
632 Matsuzawa, T. (2006). Sociocognitive development in chimpanzees: A synthesis of
633 laboratory work and fieldwork. In Cognitive Development in Chimpanzees (pp.
634 3–33).
635 Merchant, H., & Honing, H. (2014). Are non-human primates capable of rhythmic
636 entrainment? Evidence for the gradual audiomotor evolution hypothesis.
637 Frontiers in neuroscience, 7.
638 Myowa-Yamakoshi, M., Tomonaga, M., Tanaka, M., & Matsuzawa, T. (2004). Imitation
639 in neonatal chimpanzees (Pan troglodytes). Developmental Science, 7(4), 437–
640 442.
641 Nagasaka, Y., Chao, Z. C., Hasegawa, N., Notoya, T., & Fujii, N. (2013). Spontaneous
642 synchronization of arm motion between Japanese macaques. Scientific Reports,
643 3, 1151.
644 Néda, Z., Ravasz, E., Brechet, Y., Vicsek, T., & Barabási, A.-L. (2000). Self-organizing
645 processes: The sound of manyhands clapping. Nature, 403(6772), 849–850.

Oullier, O., de Guzman, G. C., Jantzen, K. J., Lagarde, J., & Kelso, J. a S. (2008). Social coordination dynamics: measuring human bonding. Social Neuroscience, 3(2), 178–192.

Paukner, A., & Anderson, J. R. (2006). Video-induced yawning in stumptail macaques (Macaca arctoides). Biology Letters, 2(1), 36–8.

Paukner, A., Suomi, S. J., Visalberghi, E., & Ferrari, P. F. (2009). Capuchin monkeys display affiliation toward humans who imitate them. Science (New York, N.Y.), 325(5942), 880–883.

Preston, S. D., & De Waal, F. B. (2002). Empathy: Its ultimate and proximate bases. Behavioral and brain sciences, 25(01), 1-20.

Repp, B. H. (2005). Sensorimotor synchronization: a review of the tapping literature. Psychonomic Bulletin & Review, 12(6), 969–992.

Richardson, M. J., Marsh, K. L., Isenhower, R. W., Goodman, J. R. L., & Schmidt, R. C. (2007). Rocking together: Dynamics of intentional and unintentional interpersonal coordination. Human Movement Science, 26(6), 867–891.

Tomonaga, M. (2001). Investigating Visual Perception and Cognition in Chimpanzees (Pan troglodytes) through Visual Search and Related Tasks: from Basic to Complex Processes. Primate Origins of Human Cognition and Behavior , 55–86.

Tomonaga, M., Myowa-Yamakoshi, M., Hashiya, K. & Chatani, K. Neonatal imitation of facial expressions in nonhuman primates: comparisons among humans, chimpanzees, gibbon, macaques, and squirrel monkey. In M. Tomonaga, M. Tanaka, & T. Matsuzawa (Eds.), Cognitive and behavioral development of chimpanzees: comparative perspective (pp. 327–332). (Kyoto University Press

670 Kyoto, 2003) (in Japanese)
671 van Baaren, R. B., Holland, R. W., Kawakami, K., & van Knippenberg, A. (2004).
672 Mimicry and prosocial behavior. Psychological Science, 15(1), 71–74.
673 Verbeke, G. and Molenberghs, G., (Eds.). (1997). *Linear Mixed Models in Practice: A*
674 *SAS-Oriented Approach*. New York: Springer.
675 Watanabe, K. (2008). Behavioral speed contagion: Automatic modulation of movement
676 timing by observation of body movements. Cognition, 106(3), 1514–1524.
677 Watts, D. P., Mitani, J. C., & Watts, D. P. (2001). Boundary Patrols and Intergroup
678 Encounters in Wild Chimpanzees. Behaviour, 138(3), 299–327.
679 Yamamoto, S., Humle, T., & Tanaka, M. (2012). Chimpanzees' flexible targeted helping
680 based on an understanding of conspecifics' goals. Proceedings of the National
681 Academy of Sciences, 109(9), 3588-3592.
682 Yamamoto, S., & Tanaka, M. (2010). The influence of kin relationship and reciprocal
683 context on chimpanzees' other-regarding preferences. Animal Behaviour, 79(3),
684 595–602.
685

Figure 2-1. Chimpanzees (left: Chloe, right: Cleo) conducting a finger-tapping task.

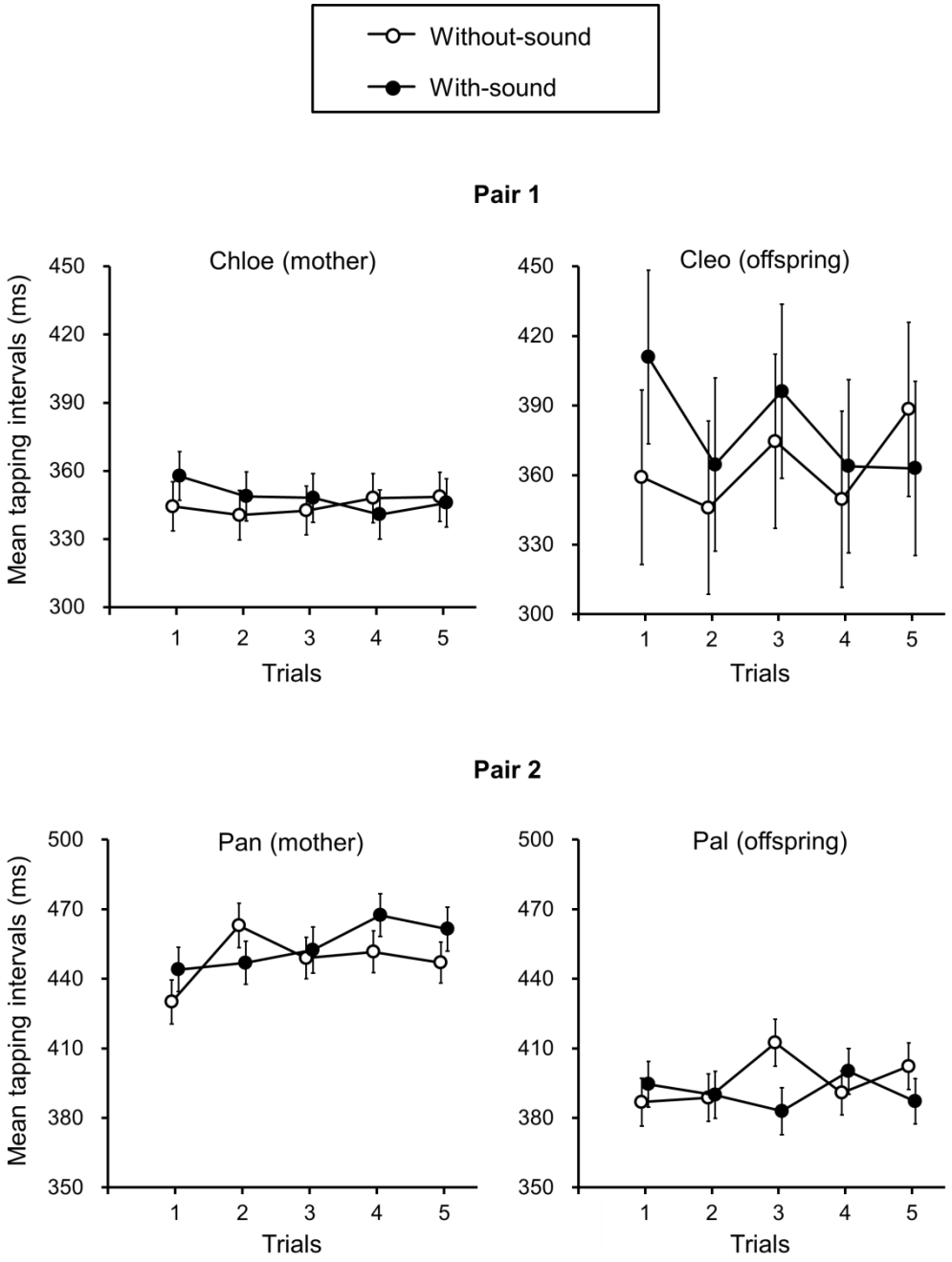

Figure 2-2. Mean tapping intervals across five trials under two auditory conditions for each chimpanzee. Error bars represent 95% confidence intervals of the mean.

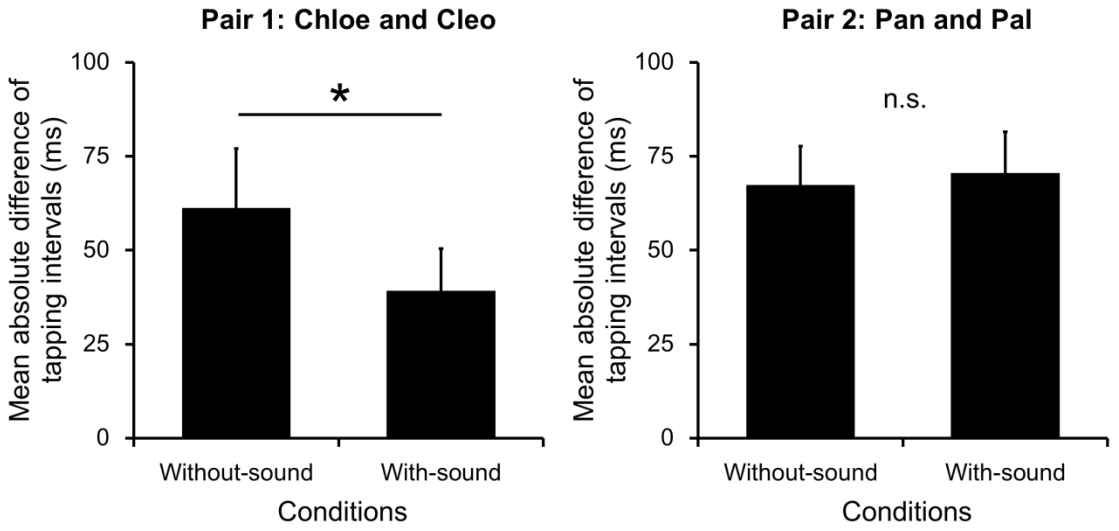

Figure 2-3. Mean absolute difference in tapping intervals under two auditory conditions for each pair of chimpanzees. Error bars represent 95% confidence intervals of the mean.

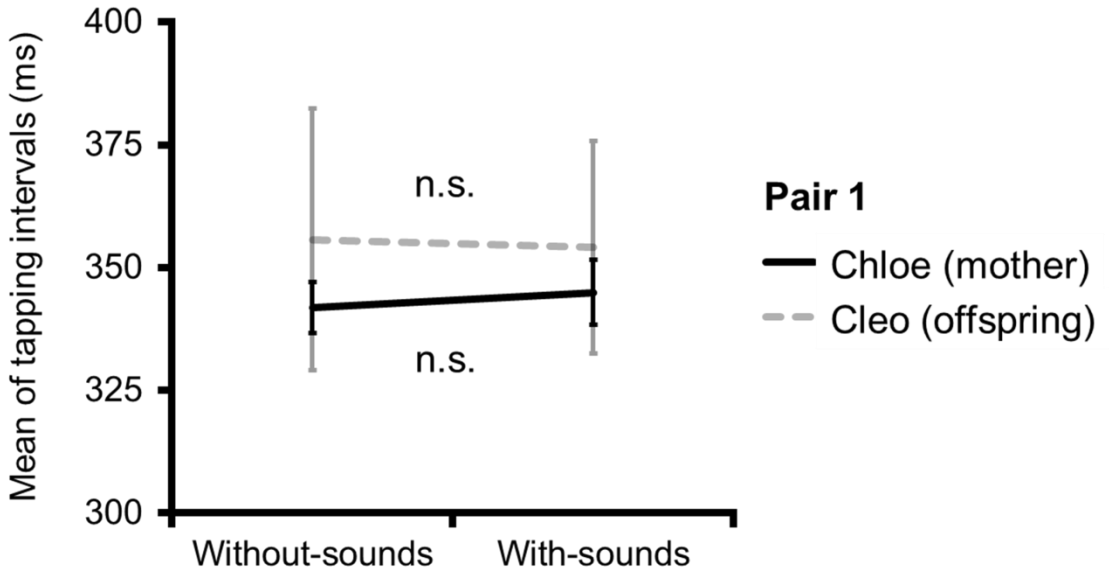

Figure 2-4. Mean tapping intervals depending on two auditory conditions in a pair of Chloe and Cleo. Error bars represent 95% confidence intervals of the mean.

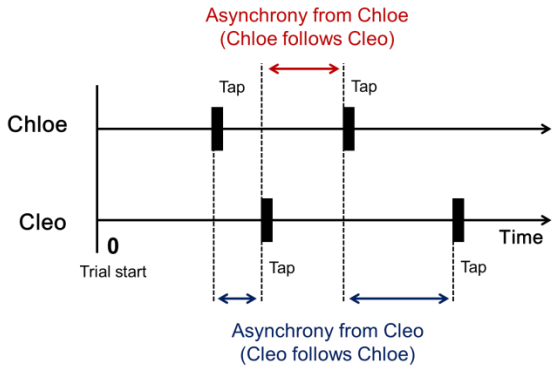

Figure 2-5. Schematic representation of asynchrony.

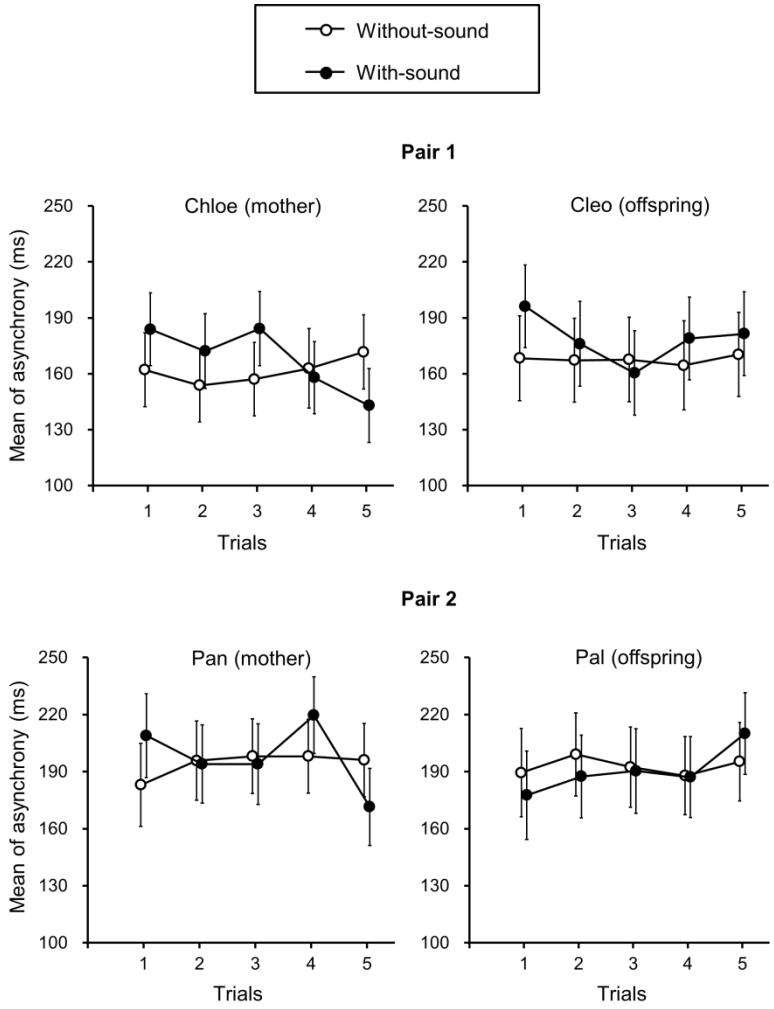

Figure 2-6. Mean asynchrony across five trials under two auditory conditions for each chimpanzee. Error bars represent 95% confidence intervals of the mean.

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Chapter 3

Examination under face-to-face setup

Chapter 3-1

An effect of auditory and visual cues on temporal coordination in chimpanzees and humans

Abstract

To establish a smooth interaction with others, an ability to match timing of the movement with those of others is important. While a number of studies addressed mechanisms of the synchronized behavior in humans, few studies have focused on non-human primates. To understand similarities and dissimilarities of the temporal coordination between humans and non-human primates, the current study examined chimpanzees and humans under the same experimental setup. A finger-tapping task was used to produce a repetitive tapping movement from each participant. The tapping tempo of each participant was measured in isolation before two participants in a pair produced simultaneous tapping movement while facing each other under auditory and visual interaction. Analysis of the tapping tempo difference between participants in a pair revealed that both chimpanzees and humans show a spontaneous tempo convergence as a response to the partner's tapping tempo. However, strength of the tempo adjustment toward the partner's tapping tempo was stronger in humans compared to chimpanzees. These results indicate that both species share an ability to adapt their tempo of the movement with another. However, they differ in that humans establish a shared tempo as soon as they interact but chimpanzees show it more slowly and partially.

Keywords: chimpanzees, humans, tempo convergence, multimodal interaction, kinship

Introduction

In nature, animals sometimes coordinate their movements in time. For example, animal species such as fish, birds or fireflies show beautiful synchrony when observed in large aggregations. On the other hand, some bird species (e.g., Western Grebes) show a unique pair-dance during a courtship. Such synchronized behavior also emerges in humans during social interaction, yet the evolutionary origins of interactional synchrony in humans remain a topic of investigation (cf., Ravignani et al., 2014).

Many experimental studies in humans have focused on dyads to precisely quantify the nature of interactional synchrony. Although the methodology varied across the studies, a consistent finding was obtained that we humans tend to synchronize the movement within milliseconds timescale with another when they exchange sensory information of the movement (Schmidt & O'Brien, 1997; Richardson et al., 2007; Oullier et al., 2008). An observational study from developmental perspectives also revealed that even neonate (2 days old) can change their movement contingently with adult speech (Condon & Sander, 1974). This spontaneous nature of interactional synchrony suggests that an ability to synchronize with others plays an important role in humans (*Homo sapiens*) during social interaction.

To understand evolutionary origins of interactional synchrony in humans, an increasing number of the studies focused on non-human primates. Nagasaka et al. (2013) reported that Japanese macaques (*Macaca fuscata*) spontaneously coordinate their arm movement with an interacting conspecific partner. In addition to this, an experimental study (Kobayashi & Hashiya, 2009) and a case study (Fuhrmann et al., 2014) showed that chimpanzees (*Pan troglodytes*) also possess an ability to coordinate

their movement with social partners. In this line of the studies, our previous study examined whether the chimpanzees would coordinate their movement with a conspecific partner when they simultaneously produce the tapping movement under an experimental setup where only auditory cues were available (Yu & Tomonaga, 2015). Although an effect of the auditory stimuli from the partner was weak, the findings demonstrated that the chimpanzees could spontaneously align a timing of the tapping movement with those of the partner's movement.

While a number of evidences reported that non-human primates, including macaques and chimpanzees, share an ability to spontaneously coordinate with another social partner with humans, there are few studies comparing humans and non-human animals under the same methodology. Direct comparison is essential for investigating similarities and dissimilarities between humans and non-human primates. In this study, chimpanzees (Experiment 1) and humans (Experiment 2) were examined under the same experimental setup with the same experimental task.

Experiment 1

In our previous study in chimpanzees (Yu & Tomonaga, 2015), a finger-tapping task was conducted under side-by-side setup where only auditory information of the partner's movement was available. Results showed that only one among two tested pairs made a spontaneous tapping tempo change toward tempo convergence and phase match when they tapped together. Despite of this result, it was difficult to generalize the findings in chimpanzees because of the weak occurrence. I assumed that an effect of auditory cues might have been overshadowed by a long history of conducting

independent tasks while ignoring others in the current setup (cf., Matsuzawa, Tomonaga & Tanaka, 2006). In other words, they were habituated to external stimuli which may interfere with their own tasks. To facilitate an interaction between the chimpanzees, I established a new experimental setup called face-to-face setup. The chimpanzees were re-tested under this face-to-face setup where visual cues in addition to auditory cues of the partner's movement were available.

Methods

Participants

Four pairs, consisting of five female chimpanzees (*Pan troglodytes*) at the Primate Research Institute, Kyoto University, Japan, participated in the experiment. Among the pairs, two pairs were mother and her biological offspring chimpanzees (34-year-old mother [Chloe] and her 14-year-old offspring [Cleo]; 31-year-old mother [Pan] and her 14-year-old offspring [Pal]) who also joined our previous experiment (see Chapter 2; Yu & Tomonaga, 2015). Another two pairs were from non-kin relationship (37-year-old female [Pen] named Pendensa paired with Chloe and Cleo, respectively). They lived together with seven other chimpanzees in an enriched outdoor compound with attached indoor residences (Matsuzawa, 2006). All the chimpanzees have had extensive experience with perceptual and cognitive studies (Tomonaga, 2001; Matsuzawa, 2003; Matsuzawa et al., 2006), including social cognition tests under various social contexts (Myowa-Yamakoshi & Matsuzawa, 1999; Hirata & Matsuzawa, 2001; Yamamoto et al., 2012; Martin et al. 2014). Three chimpanzees (Chloe, Cleo and Pal) among the participants had an experience in conducting a finger-tapping task under non-social

distractive auditory rhythms (including unpublished data, see Hattori et al. 2013; 2015).

Apparatus

LED push buttons (Fuji Electric, 2 × 2 cm) were used to produce a finger tapping movement from each chimpanzee. The two buttons were aligned horizontally 12.5 cm apart in a transparent acrylic panel (45 × 45 cm). The distance between the two acrylic panels that pairs of chimpanzees faced from each other was approximately 24 cm. Auditory feedback corresponding to each chimpanzee's tapping event was played by a speaker placed in the ceiling of the experimental booth. An automated universal feeder was used to deliver a food reward to each chimpanzee. All the equipment and experimental events were controlled by a computer located outside the experimental booth.

Task

Each trial began with illumination of two push buttons. The chimpanzees were required to tap either one of the two buttons. When one of the buttons was pressed once, its light turned-off with an auditory feedback (boing sound, 200 ms, and approximately 70 dB). The chimpanzees were again required to tap the remaining lighted-up push button. When this button was also pressed once, its light turned-off with the auditory feedback and another button in the other side illuminated with 0ms delay. After pressing alternatively illuminating two buttons for several times, a trial ended with a positive auditory reinforcement and a piece of fruit was delivered to the chimpanzees. The inter-trial interval was 2 seconds.

Procedure

The chimpanzees were first trained individually to habituate to the task, since the current study used a different apparatus from the previous one (Yu & Tomonaga 2015). The training phase started with a single tap and then the number of required taps increased up to between 20 to 40 taps. After the chimpanzees cleared the criteria of tapping without a pause greater than 5 seconds, they moved to the test phase. In test phase, two experimental conditions were prepared: alone condition and paired condition. In the alone condition, the chimpanzees conducted the task individually as they did in the training phase (Figure 3-1-1a). In contrast, in the paired condition, pairs of the chimpanzees conducted the task simultaneously while facing each other through a transparent acrylic panel (Figure 3-1-1b). During the paired condition, the timing of a trial Start and Finish was equal between the two chimpanzees. The chimpanzee who was designated to finish a trial with producing alternative tapping from 20 to 40 times was randomly changed in every six trials. The auditory feedback corresponding to each tapping event differed in pitch between the two chimpanzees of a pair. These two distinctive auditory feedbacks were assigned to each chimpanzee from the training phase, respectively.

<<Figure 3-1-1 around here >>

Two pairs of mother and offspring chimpanzees were tested first under ABABA experimental design. Each block (A: alone condition; B: paired condition) was conducted for three consecutive experimental days. Each experimental day was consisted of 30 trials. In total, 270 trials and 180 trials were presented to each

chimpanzee in the alone condition and the paired condition, respectively. After this experiment completely finished, Pen and Cleo were tested. Finally, Pen and Chloe were tested. These two pairs from non-kin relationship were tested under AB design. Again, each block was conducted for three consecutive experimental days, and each day was consisted of 30 trials. In total, 90 trials were presented for each test condition to each chimpanzee.

Results

Tapping intervals that were not from alternative left and right tapping movement were excluded from the analysis. The tapping intervals less than 100 ms or greater than 2 sec were omitted as outliers. Excluded data were less than 6% of the total taps for each participant and for each condition. Median tapping intervals of each trial was used as the dependent variable. In the analysis of the paired condition, data of the median tapping intervals were excluded from both participants in a pair if either one of the chimpanzees showed less than 3 data points of the tapping interval in a trial.

We first examined a possibility of the order effects in the current data. If the order effects exist, the tapping intervals of the chimpanzees tested under ABABA design (Chloe, Cleo, Pan and Pal) would sequentially increase or decrease as the condition alternates between A (alone condition) and B (paired condition). One-way ANOVA and Post hoc comparisons using the Tukey HSD test showed no sign of the consecutive order effects in these four chimpanzees (see Figure 3-1-2 and Table 3-1-1). In the case of Pen who was tested only under AB design, we examined the order effects in three experimental days for each condition. If the order effects exist, the tapping intervals

across three experimental days would sequentially increase or decrease in each condition. The statistical tests revealed no sign of the order effects neither in Pen (see Figure 3-1-3 and Table 3-1-2 in Supplementary Information). The current results indicated that there are no order effects which may confound an effect of the currently prepared two test conditions (alone and paired condition) on the chimpanzees' spontaneous tapping tempo.

<< Figure 3-1-2 and 3-1-3, Table 3-1-1 and 3-1-2 around here>>

After this confirmation, we examined the changes of the tapping tempo depending on condition for each chimpanzee in all four tested pairs (Figure 3-1-4; see also Table 3-1-3). Two sample *t*-tests assuming unequal variance revealed a significant difference in the tapping intervals for a following chimpanzees: [Cleo] with Chloe, $t(262) = 7.52$, $p < 0.001$, $d = 0.77$; [Pan] with Pal, $t(346) = 5.19$, $p < 0.001$, $d = 0.52$; [Pal] with Pan, $t(263) = 6.93$, $p < 0.001$, $d = 0.72$; [Cleo] with Pen, $t(177) = 2.26$, $p = 0.025$, $d = 0.34$; [Pen] with Cleo, $t(165) = 5.36$, $p < 0.001$, $d = 0.80$; [Chloe] with Pen, $t(172) = 5.80$, $p < 0.001$, $d = 0.87$. On the other hand, their partner chimpanzees in two pairs showed no difference: [Chloe] with Cleo, $t(418) = 0.81$, $p = 0.419$, $d = 0.08$; [Pen] with Chloe, $t(151) = 1.05$, $p = 0.296$, $d = 0.16$. Since the current sample size was large, we referred effect size to interpret the results from each chimpanzee. We found that [Cleo] with Pen showed a small effect size ($d = 0.34$), while the effect size for the other chimpanzees who showed the significant difference in their tapping tempo exceeded Cohen's convention for a moderate effect ($d = .50$). In case of [Pan] with Pal, we found that the tapping tempo in the fifth block (the 3rd alone condition) resulted the

883 significant difference between the two test conditions (see Figure 3-1-2b and Table
884 3-1-1b). Further video analysis revealed that postures in the fifth block (mostly, stood
885 with three limbs) differed from the other blocks (sat upright), suggesting that a change
886 of the posture during the experiment confounded a result of the tapping tempo of [Pan].
887 In sum, the current results showed a similar pattern in that only one chimpanzee in each
888 pair significantly changed their tapping tempo in a direction of the partner's tapping
889 tempo in the paired condition.
890
891 <<Figure 3-1-4 and Table 3-1-3 around here>>
892
893 Here we note that an analysis of the closest tap-to-tap timing difference
894 between two participants (i.e., asynchrony) and its positional information was not
895 conducted due to experimental artifact in the current setup. Following studies with
896 video analysis may facilitate further understanding on how spatial and temporal
897 coordination would occur in chimpanzees with high resolution in time.
898
899 **Discussion**
900
901 The present study aimed to investigate whether spontaneous temporal coordination
902 would occur in pairs of chimpanzees when they simultaneously produce the tapping
903 movement under auditory and visual interaction. An analysis of the tapping intervals in
904 the paired condition in comparison with the alone condition indicated that only one
905 chimpanzee in each pair significantly changed the tapping tempo toward their partner's
906 tapping tempo while the partner chimpanzees showed no significant changes in

907 response to their partner's tapping tempo. This finding suggests that the chimpanzees
908 show unequal response when they produce distinctive tapping movements from each
909 other.

910 Compared to our previous study (Yu & Tomonaga, 2015), which was conducted
911 under side-by-side setup where only auditory stimuli were provided, the chimpanzees in
912 the current study were more significantly influenced by the partner's tapping tempo. I
913 assume that visual cues in addition to auditory cues in the current face-to-face setup
914 facilitated an interaction between the chimpanzees in a pair. However, it is yet difficult
915 to clarify an effect of auditory and visual cues on their spontaneous tapping tempo
916 changes respectively because both stimuli were introduced at the same time when the
917 chimpanzees simultaneously produced the tapping movement. A following study is
918 needed to examine this question.

919 All four tested pairs showed unidirectional coordination, even though there was
920 no explicit training to do so. Similar unidirectional coordination in pairs of chimpanzees
921 has also been reported in a different social context. In a cooperative task which requires
922 simultaneous rope pulling by two chimpanzees for getting food, unidirectional attention
923 and waiting response by one chimpanzee was consistently observed across studies
924 (Chalmeau, 1994; Hirata & Fuwa, 2007). Although a required cognitive abilities and
925 underlying mechanisms of the current study may be different from the cooperative task,
926 the findings indicate that chimpanzees rarely coordinate their movement mutually with
927 another in their social interactions.

928 The chimpanzees from kin and non-kin relationship showed a different pattern
929 in that *who* changes the tapping tempo toward the partner. We assume that relatively
930 *slow* tapping individuals are likely to change their movement to coordinate with *fast*

931 tapping partners, which was also observed in our following study in humans under the
932 same experimental setup with the current chimpanzees (Experiment 2). However, in
933 case of mother and her offspring chimpanzees, it seems that fast tapping tempo is not
934 facilitated because they showed that *fast* tapping offspring chimpanzees changed the
935 movement toward their *slow* tapping mothers. Further discussion will be described in
936 General discussion.

937 The current experiment clarified an introductive process of interactional
938 synchrony by demonstrating unidirectional adaptation in tempo in pairs of chimpanzees.
939 Further studies in chimpanzees using our method will help to understand evolutionary
940 origins of interactional synchrony in humans.

941

942 **Experiment 2**

943

944 To directly compare between chimpanzees and humans, I examined four pairs of adult
945 humans under the same experimental setup with the chimpanzees. Previous studies in
946 human dyads revealed that how difficult it is to resist a movement coupling with an
947 interacting partner and what is the most stable form of the temporal coordination
948 between humans (Schmidt & O'Brien, 1997; Issartel et al., 2007; Richardson et al.,
949 2007). Findings from these studies indicate that we humans not only have an ability to
950 sustain coordinative movement but also have automatic modulations to establish smooth
951 interaction with others. However, little is known about spontaneous and dynamical
952 processes toward temporal coordination when humans simultaneously produce rhythmic
953 movement with another under multisensory interaction. At the moment, few studies
954 reported spontaneous nature of interactional synchrony in humans (Oullier et al., 2008;

for group synchrony, see Néda et al., 2000). We believe that quantitative and qualitative analysis for the transitional process of temporal coordination will help to understand social interaction that is unique in humans.

In social psychology, social facilitation is a well-known phenomenon that fast movement becomes dominant behavior when individuals simultaneously engage in a simple motor activity in full view of each other (Tripplett, 1898; Zajonc, 1965). Since we introduced a simple task that requires repetitive left and right tapping movement, there was a possibility to have an effect of social facilitation in the current study.

Methods

Participants

Eight graduate students from Kyoto University Primate Research Institute participated in the experiment (mean age = 23.3±1.0 years), and they were grouped into 4 experimental pairs (hereafter, H1, H2, H3, and H4). The pairs were consisted of two male pairs and two female pairs. They were all acquainted with each other. The research protocol was reviewed and approved by the Human Ethics Committee, Primate Research Institute, Kyoto University.

Apparatus

LED push buttons (Fuji Electric, 2 × 2 cm) were used to produce a finger tapping movement from each participant. The two buttons were aligned horizontally 12.5 cm apart in a transparent acrylic panel (45 × 45 cm). The distance between the two acrylic panels that pairs of the participants faced from each other was approximately 24 cm. All

auditory stimuli, including auditory feedback corresponding to each participant's tapping event, were played by a speaker placed in the ceiling of the experimental booth. All the equipment and experimental events were controlled by a computer located outside the experimental booth.

Procedure

All the participants visited the laboratory for two consecutive days. In the first day, each participant came alone and performed a finger-tapping task (alone condition). Before the experiment, verbal instruction was given to the participants that the task requires alternative tapping movement from 15 to 30 times for each trial. They were also instructed to produce the tapping movement with preferred hand with their comfortable tempo which could maintain for whole day. In the next day, a pair of the participants visited the laboratory together (paired condition). They were informed that the experiment will be exactly the same with the previous day except that two participants will simultaneously perform the task this time. They were asked not to have a conversation during the task. After the end of the experiment, the participants were debriefed and any additional questions were answered.

The participants were informed beforehand that the experiment will last for 30 minutes for each experimental day. Three blocks of 30 trials (90 trials) were performed per day with a short break between blocks.

Results

Tapping intervals, which is an inverse form of tempo, was calculated for the alternative

tapping movement. Few very short (<100 ms) or long (>2 s) tapping intervals were removed as outliers (less than 0.5% of the total taps for each participant). Median tapping intervals of each trial was used as the dependent variable. The data from the alone condition showed that the participants tend to gradually stabilize their tapping tempo as a trial progress (see Figure 3-1-5). To eliminate this order effect, data from the last third block (30 trials) from each condition was used only for the analysis.

<<Figure 3-1-5 around here>>

The tapping intervals depending on condition were examined for each participant in four tested pairs (Figure 3-1-6; see also Table 3-1-4). Two sample *t*-tests assuming unequal variance revealed that, except for one participant (H1B, $t(54) = 1.86$, $p = 0.068$, $d = 0.48$), all the other seven participants showed a significant change in the tapping tempo depending on condition (H1A, $t(57) = 47.87$, $p < 0.001$, $d = 12.36$; H2A, $t(47) = 7.27$, $p < 0.001$, $d = 1.88$; H2B, $t(47) = 18.73$, $p < 0.001$, $d = 4.84$; H3A, $t(56) = 89.63$, $p < 0.001$, $d = 23.14$; H3B, $t(33) = 17.18$, $p < 0.001$, $d = 4.44$; H4A, $t(54) = 6.29$, $p < 0.001$, $d = 1.62$; H4B, $t(54) = 26.49$, $p < 0.001$, $d = 6.84$). A pattern of the tapping tempo change indicated that the participants tend to produce faster tapping tempo in the paired condition in comparison with the alone condition, except for the relatively fast tapping individual in H2. The current result also demonstrated that the tempo difference between participants in a pair became smaller in the paired condition in comparison with the alone condition, indicating that tempo convergence occurred when the participants produced the tapping movement simultaneously with the partner under auditory and visual interaction.

<< Figure 3-1-6 and Table 3-1-4 around here >>

Discussion

In the current study, a finger-tapping experiment was conducted in pairs of humans under the same experimental setup with the chimpanzees. In this setup, auditory and visual information of the partner's movement were available. Results showed that no pair could maintain their original tapping tempo when they simultaneously produce the tapping movement with their facing partner. This result was consistent with Oullier et al. (2008), reporting that pairs of adult humans voluntarily changed their movement as soon as they exchange information of the partner's movement. Although the current study focused only on tempo of the movement due to experimental artifact, it added further evidence that humans show spontaneous and dynamical changes when they produce rhythmic movement with another under multisensory interaction.

There was a general tendency that *faster* tapping tempo was facilitated when human participants tapped together than they tapped alone. This result resembles a phenomenon called social facilitation (Tripplett, 1898; Zajonc, 1965), showing that the presence of others increases the speed of simple task performance. A meta-analysis of the effects of the presence of others on the task performance revealed that subject anxiety seemed to be related with speed of the performance, while individual's physiological arousal increases only if the individual is performing a complex task (Bond & Titus, 1983). Considering that facing each other without any verbal communication occurs rarely in our daily interaction, it may have elicited some extent

of anxiety from the participants in the current experiment. Thus, it is plausible that social facilitation was induced as the fundamental forms of inter-individual influence in the current setup.

More importantly, we demonstrated that tempo convergence occurs in human participants under the current experimental setup. All four tested pairs showed a significant decrease in the tempo difference between participants when they tapped together. The observed tempo convergence was achieved by a significant tempo changes by the relatively slow tapping individual in each pair. This suggests that the tempo adaptation occurred unequally between participants, and the relative slow tappers in each pair were more sensitive to their fast tapping partner's movement. This was somewhat different with the findings from Oullier et al. (2008), which also examined spontaneous nature of the movement coordination in dyads facing each other. They reported that most of the participants in a pair changed their tempo of the movement in a direction to their partner's tempo. In other words, they found that the tempo convergence occurred mutually between the participants. I speculate that several variables, including a trajectory of the movement and amplitude of the sensory information exchange, may result in types (whether mutual or unilateral) of the movement coordination in humans.

General discussion

The current study aimed to investigate similarity and dissimilarity between chimpanzees and humans on spontaneous temporal coordination when they interact with another conspecific partner. To directly compare between two species, they were tested under

the same experimental setup, so called face-to-face setup. In this setup, both auditory and visual information of the partner's movement were available from each other. A finger-tapping task which is extensively used for exploring sensorimotor synchronization in humans (Repp, 2005) was introduced to produce repetitive and rhythmic tapping movement from each participant. The current study established an experimental method for examining temporal coordination in both chimpanzees and humans. Although the current study did not examine whether synchronous tapping occurs during the interaction due to experimental artifact, analysis of the tapping tempo demonstrated an introductive process of the temporal coordination in both species.

In Experiment 1, four pairs consisting of five female chimpanzees were examined. Two pairs were mother and her biological offspring chimpanzees and the other two pairs were from non-kin relationship. Results showed that only one chimpanzee in each pair significantly changed the tapping tempo toward their partner's tapping tempo when they tapped together under auditory and visual interaction. In Experiment 2, four pairs consisting of eight adult humans were examined under the same experimental setup with the chimpanzees. Results showed that fast tapping tempo was socially facilitated and the tempo convergence emerged when humans in a pair exchange auditory and visual information of the tapping movement with another. Overall, the Experiment 1 and 2 revealed similarities and dissimilarities between chimpanzees and humans on their spontaneous tempo convergence. Detailed findings will be described in following subsections.

Finding 1: unidirectional tempo convergence occurs in chimpanzees and humans

The results showed that chimpanzees and humans are similar in that they show unequal

response when they produce simultaneous tapping movement with their conspecific partner under auditory and visual interaction. In other words, both species showed that only one individual in each pair significantly changed the tapping tempo toward their partner's tapping tempo.

In humans, the tempo convergence occurred by significant tapping tempo changes of the relatively slow tapping individuals in each pair because there was a general tendency that fast tapping tempo was socially facilitated in the current setup. As I mentioned earlier, it is plausible that the current face-to-face setup and the experimental procedure elicited some extent of subject anxiety when the human participants conduct the task simultaneously with another. Similar pattern of the tempo convergence was observed in the chimpanzees from non-kin relationship, showing that relatively slow tapping individuals changed the tapping tempo toward their fast tapping partner's tempo. Although these chimpanzees in a pair were familiar with each other because they live together in one social group (c.f., Matsuzawa, 2006), they have little experience in visiting the experimental booth together and conduct the task while facing each other (c.f., Yamamoto et al., 2009; Yamamoto & Tanaka, 2010). Therefore, it is plausible that a level of anxiety also increased in these chimpanzees so that the similar pattern of the tempo convergence with those of human participants was observed.

On the other hand, in the chimpanzees from kin-relationship (mother and her biological offspring), fast tapping tempo was not socially facilitated. Rather, relatively fast tapping individuals changed the tapping tempo toward their slow tapping partner. This result indicates that anxiety level was not increased when they conducted the task simultaneously. Previous studies in humans reported that there is the calming influence of affiliation (Schachter, 1959). Considering that the current mother and offspring

chimpanzees have high affiliation and they often visit the experimental booth together, less anxious level than any other kinds of social relationship may have led to the distinctive pattern of tempo convergence in the current experiment in these chimpanzees.

Interestingly, both offspring chimpanzees showed the tapping tempo change toward their slow tapping mother chimpanzees. Although the current experiment was not an explicit learning context, this result is consistent with a field research in wild chimpanzees reporting that young chimpanzees observe their mother or older individuals when they are to learn a use of tools (Biro et al., 2003). During the experiment, I found that one offspring chimpanzee (Cleo) often observes her mother conducting the task in proximate distance (see Figure 3-1-7) but the opposite rarely occurred. These results indicate that offspring chimpanzees have disposition to attend their mother's movement regardless of social context.

<< Figure 3-1-7 around here >>

Finding 2: strength of the tempo convergence differs between chimpanzees and humans

Although both chimpanzees and humans showed the tempo convergence, strength of the convergence differed between those two species. Figure 3-1-8 represents a difference of the tapping intervals between two participants ([slow tapper]－[fast tapper]) depending on condition for four tested pairs from both chimpanzees and humans. The result shows that humans tend to produce significant decrease in the tempo difference in the paired condition in comparison with the chimpanzees, regardless of their initial tapping

difference in the alone condition. This indicates that the tempo convergence occurs precisely and quickly in humans, while it occurs partially and slowly in chimpanzees.

Previous studies in chimpanzees and humans reported that they share an ability to match tapping onset especially when tempo of the auditory stimuli is similar to their own preferred tapping tempo (Hattori et al., 2013; 2015). Although the current study did not analyze each participant's tapping onset in relation with those of the partner's due to experimental artifact, the current result indicates that species differences may exist also in the occurrence of synchronous tapping between chimpanzees and humans.

<< Figure 3-1-8 around here >>

In summary, the current study demonstrated that there are similarity and dissimilarity between chimpanzees and humans on an introductive process of spontaneous temporal coordination. When they simultaneously produce rhythmic tapping movement with conspecific partner under auditory and visual interaction, both chimpanzees and humans showed unidirectional tempo convergence but its strength of the occurrence was stronger in humans compared to chimpanzees. In chimpanzees, a different pattern of the tempo convergence was observed between kin (mother and offspring) and non-kin relationship. The current study clearly suggests that direct comparison under the same methodology is important to understand what is uniquely human.

References

Chalmeau, R. (1994). Do chimpanzees cooperate in a learning task? Primates, 35(3), 385–392.

Chartrand, T. L., & Bargh, J. a. (1999). The chameleon effect: the perception-behavior link and social interaction. Journal of Personality and Social Psychology, 76(6), 893–910.

Cirelli, L. K., Einarson, K. M., & Trainor, L. J. (2014). Interpersonal synchrony increases prosocial behavior in infants. Developmental Science, 17(6), 1003–1011.

Condon, W. S., & Sander, L. W. (1974). Neonate movement is synchronized with adult speech: Interactional participation and language acquisition. Science, 183(4120), 99-101.

Delaherche, E., Chetouani, M., Mahdhaoui, A., Saint-Georges, C., Viaux, S., & Cohen, D. (2012). Interpersonal synchrony: A survey of evaluation methods across disciplines. IEEE Transactions on Affective Computing.

Fuhrmann, D., Ravignani, A., Marshall-Pescini, S., & Whiten, A. (2014). Synchrony and motor mimicking in chimpanzee observational learning. Scientific Reports, 4, 5283.

Hattori, Y., Tomonaga, M., & Matsuzawa, T. (2015). Distractor effect of auditory rhythms on self-paced tapping in chimpanzees and humans. PLoS ONE, 10(7).

Hirata, S., & Fuwa, K. (2007). Chimpanzees (Pan troglodytes) learn to act with other individuals in a cooperative task. Primates, 48(1), 13–21.

Hirata, S., & Matsuzawa, T. (2001). Tactics to obtain a hidden food item in chimpanzee pairs (Pan troglodytes). Animal Cognition, 4(3-4), 285–295.

Hove, M. J., & Risen, J. L. (2009). It's All in the Timing: Interpersonal Synchrony Increases Affiliation. Social Cognition, 27(6), 949–960.

Issartel, J., Marin, L., & Cadopi, M. (2007). Unintended interpersonal co-ordination: "can we march to the beat of our own drum?" Neuroscience Letters, 411(3), 174–179.

Kobayashi, H., & Kazuhide, H. (2009). No TitleSpontaneous synchrony by chimpanzees in response to humans' behavior. The Japanese Journal of Psychonomic Science, 27, 179–180.

Lakin, J. L., & Chartrand, T. L. (2003). Using nonconscious behavioral mimicry to create affiliation and rapport. Psychological Science, 14(4), 334–339.

Martin, C. F., Bhui, R., Bossaerts, P., Matsuzawa, T., & Camerer, C. (2014). Chimpanzee choice rates in competitive games match equilibrium game theory predictions. Sci Rep, 4, 5182.

Matsuzawa, T. (2003). The Ai project: historical and ecological contexts. Animal cognition, 6(4), 199-211.

Matsuzawa, T., Tomonaga, M., & Tanaka, M. (2006). Cognitive development in chimpanzees. Springer, Tokyo.

Matsuzawa, T. (2006). Sociocognitive development in chimpanzees: a synthesis of laboratory work and fieldwork. In Cognitive development in chimpanzees (pp. 3-33). Springer Tokyo.

Miles, L. K., Griffiths, J. L., Richardson, M. J., & Macrae, C. N. (2010). Too late to coordinate: Contextual influences on behavioral synchrony. European Journal of Social Psychology, 40(1), 52–60.

Myowa-Yamakoshi, M., & Matsuzawa, T. (1999). Factors influencing imitation of

manipulatory actions in chimpanzees (Pan troglodytes). Journal of Comparative Psychology, 113(2), 128–136.

Nagasaka, Y., Chao, Z. C., Hasegawa, N., Notoya, T., & Fujii, N. (2013). Spontaneous synchronization of arm motion between Japanese macaques. Scientific Reports, 3, 1151.

Néda, Z., Ravasz, E., Brechet, Y., Vicsek, T., & Barabási, A.-L. (2000). Self-organizing processes: The sound of manyhands clapping. Nature, 403(6772), 849–850.

Oullier, O., de Guzman, G. C., Jantzen, K. J., Lagarde, J., & Kelso, J. a S. (2008). Social coordination dynamics: measuring human bonding. Social Neuroscience, 3(2), 178–192.

Ravignani, A., Bowling, D. L., & Fitch, W. T. (2014). Chorusing, synchrony, and the evolutionary functions of rhythm. Frontiers in Psychology, 5.

Richardson, M. J., Marsh, K. L., Isenhower, R. W., Goodman, J. R. L., & Schmidt, R. C. (2007). Rocking together: Dynamics of intentional and unintentional interpersonal coordination. Human Movement Science, 26(6), 867–891.

Schachter, S. (1959). The psychology of affiliation: Experimental studies of the sources of gregariousness. Stanford University Press.

Schmidt, R. C., & O'Brien, B. (1997). Evaluating the dynamics of unintended interpersonal coordination. Ecological Psychology, 9(3), 189-206.

Tomonaga, M. (2001). Investigating Visual Perception and Cognition in Chimpanzees (Pan troglodytes) through Visual Search and Related Tasks: from Basic to Complex Processes. Primate Origins of Human Cognition and Behavior , 55–86.

Triplett, N. (1898). The dynamogenic factors in pacemaking and competition. American

Journal of Psychology, 9(4), 507–533.

van Baaren, R. B., Holland, R. W., Kawakami, K., & van Knippenberg, A. (2004). Mimicry and prosocial behavior. Psychological Science, 15(1), 71–74.

Yamamoto, S., Humle, T., & Tanaka, M. (2012). Chimpanzees' flexible targeted helping based on an understanding of conspecifics' goals. Proceedings of the National Academy of Sciences, 109(9), 3588-3592.

Yu, L., & Tomonaga, M. (2015). Interactional synchrony in chimpanzees: Examination through a finger-tapping experiment. Scientific Reports, 5, 10218.

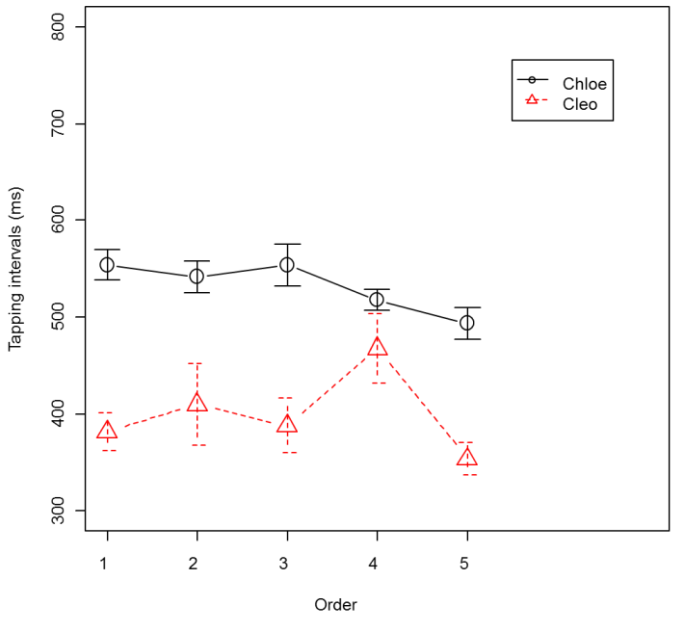
Yu, L., & Tomonaga, M. (2016). Unidirectional adaptation in tempo in pairs of chimpanzees during simultaneous tapping movement: an examination under face-to-face setup. Primates, 57, 181–185.

(a) (b)

Figure 3-1-1. A chimpanzee conducting a finger-tapping task under the face-to-face setup. (a) Tapping in the alone condition. (b) Tapping in the paired condition.

Figure 3-1-2. A change of the tapping intervals under ABABA design. Mean of the tapping intervals from each chimpanzee in a pair of mother and offspring chimpanzees. (a) Chloe (mother) and Cleo (offspring) and (b) Pan (mother) and Pal (offspring). Order 1, 3 and 5 represents A (alone condition), while order 2 and 4 represents B (paired condition). Error bars indicate 95% confidence intervals of the mean.

(a)



(b)

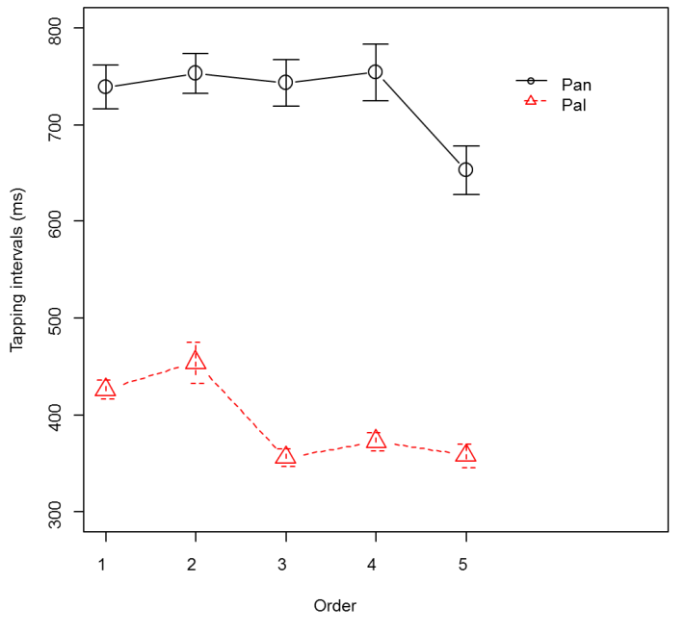
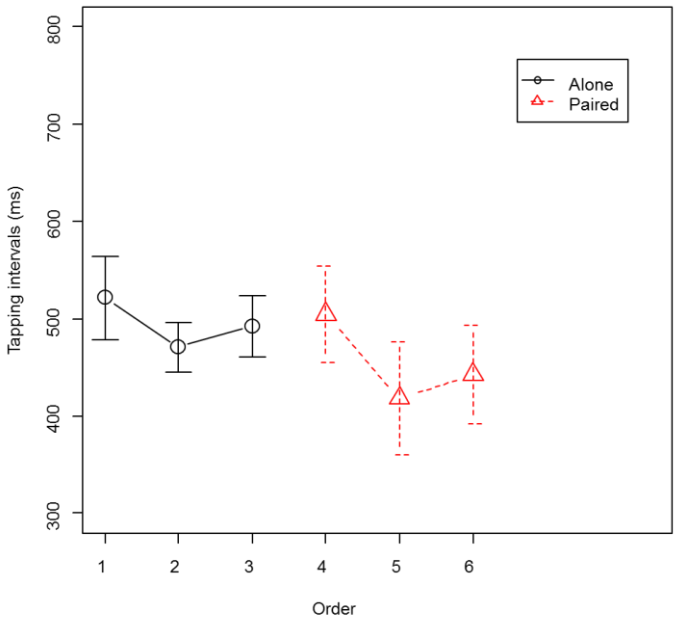


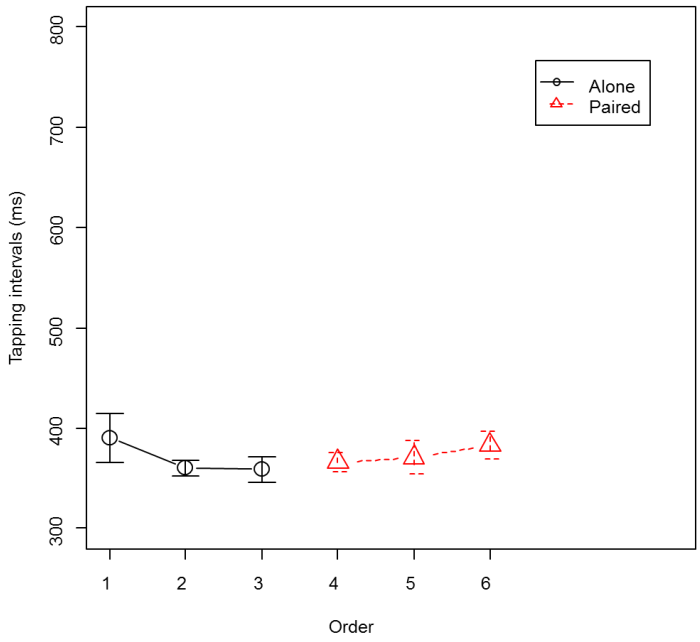
Figure 3-1-3. A change of the tapping intervals under AB design. Mean of the tapping intervals from [Pen] when paired with a non-kin conspecific partner (a) Cleo and (b) Chloe. Order represents each experimental day. Error bars indicate 95% confidence intervals of the mean.

1253

(a)



(b)



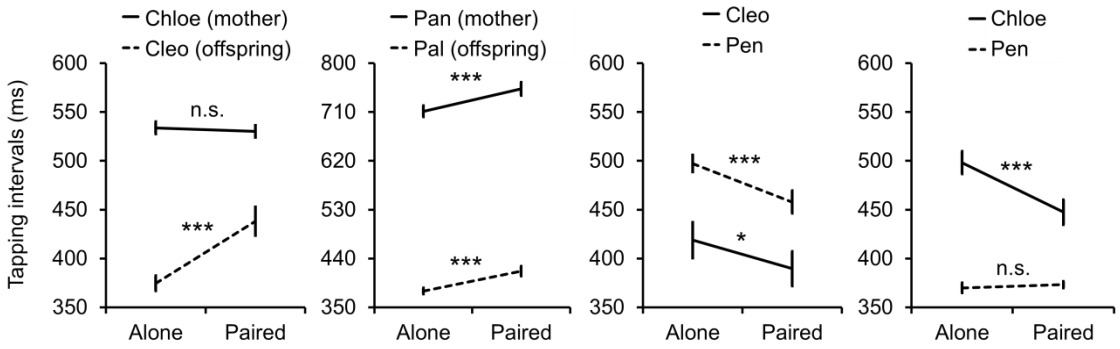


Figure 3-1-4. Mean of the tapping intervals under two test conditions for each chimpanzee in four pairs. Left two pairs are from mother and offspring chimpanzees. Right two pairs are from non-kin relationship chimpanzees. Error bars indicate 95% confidence intervals of the mean.

1254

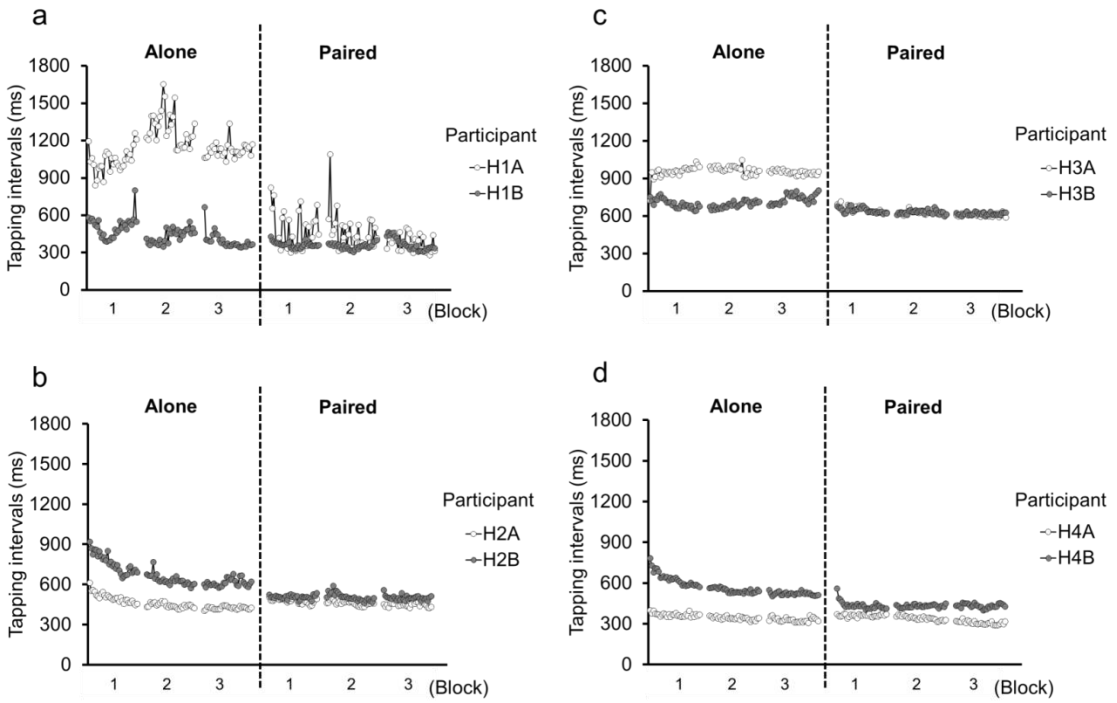


Figure 3-1-5. Median tapping intervals of each trial across three blocks in the alone and the paired conditions. (a)-(d) represents the data for each participant in four human pairs.

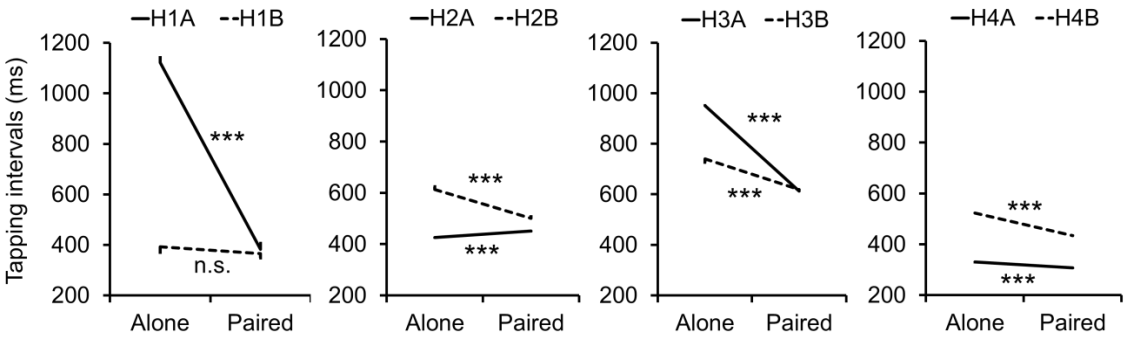


Figure 3-1-6. Mean of the tapping intervals under two test conditions for each human participants in four pairs. Error bars indicate 95% confidence intervals of the mean.

Figure 3-1-7. Offspring chimpanzee (Cleo) is observing her mother (Chloe) conducting the tapping task in close distance.

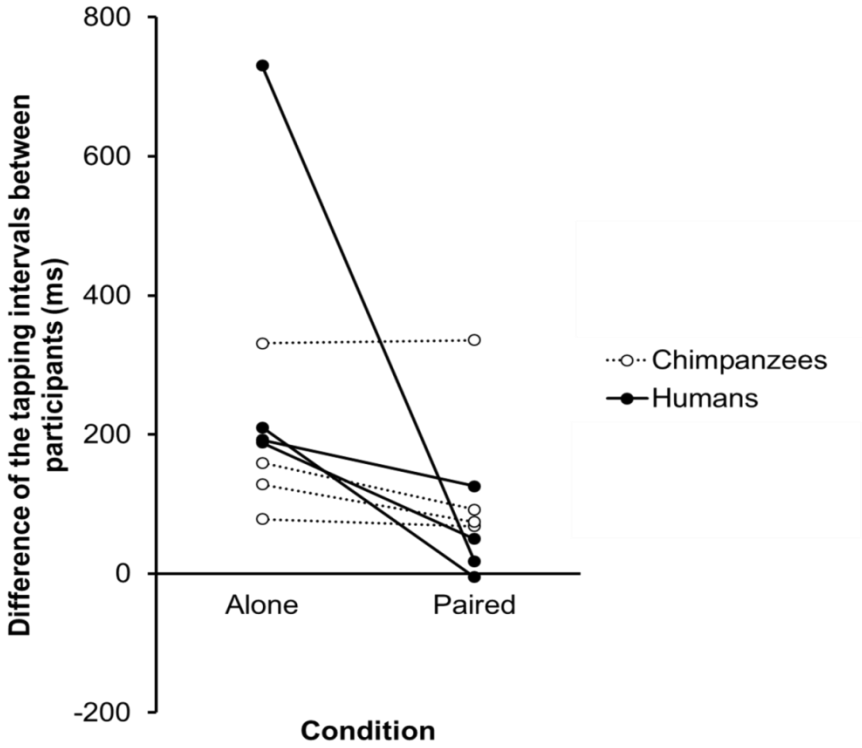


Figure 3-1-8. Each dot represents a difference of the mean tapping intervals between two participants in each pair for each condition. The dots connected by lines represent data from the same pairs. Negative values in the paired condition represent that relatively slow tapping individual in the alone condition became faster tapper than a partner in the paired condition.

Table 3-1-1
Post hoc comparisons using the Tukey HSD test to examine a possibility of the order effects. Results from a pair of mother and offspring chimpanzees. (a) Chloe and Cleo and (b) Pan and Pal.

(a)

	Chloe			Cleo		
Comparison	Estimate	*t* value	*p* value	Estimate	*t* value	*p* value
2 vs 1	-12.03	-1.10	0.81	28.41	1.43	0.61
3 vs 1	-0.17	-0.02	1.00	6.79	0.34	1.00
4 vs 1	-36.43	-3.32	0.0119 *	86.17	4.33	<0.001 ***
5 vs 1	-60.43	-5.51	<0.001 ***	-27.83	-1.40	0.63
3 vs 2	11.85	1.08	0.82	-21.62	-1.09	0.81
4 vs 2	-24.40	-2.23	0.18	57.77	2.90	0.03852 *
5 vs 2	-48.40	-4.42	<0.001 ***	-56.24	-2.83	0.04696 *
4 vs 3	-36.25	-3.31	0.0125 *	79.38	3.99	0.00151 **
5 vs 3	-60.26	-5.50	<0.001 ***	-34.62	-1.74	0.42
5 vs 4	-24.00	-2.19	0.20	-114.01	-5.73	<0.001 ***

(b)

	Pan			Pal		
Comparison	Estimate	*t* value	*p* value	Estimate	*t* value	*p* value
2 vs 1	14.50	0.91	0.89	28.17	3.22	0.0163 *
3 vs 1	4.95	0.31	1.00	-70.13	-8.01	<0.001 ***
4 vs 1	15.75	0.97	0.87	-53.37	-5.99	<0.001 ***
5 vs 1	-85.19	-5.32	<0.001 ***	-68.04	-7.78	<0.001 ***
3 vs 2	-9.55	-0.60	0.98	-98.30	-11.23	<0.001 ***
4 vs 2	1.25	0.08	1.00	-81.54	-9.16	<0.001 ***
5 vs 2	-99.68	-6.23	<0.001 ***	-96.21	-10.99	<0.001 ***
4 vs 3	10.80	0.66	0.96	16.76	1.88	0.34
5 vs 3	-90.14	-5.63	<0.001 ***	2.09	0.24	1.00
5 vs 4	-100.94	-6.20	<0.001 ***	-14.67	-1.65	0.47

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

Table 3-1-2
Post hoc comparisons using the Tukey HSD test to examine a possibility of the order effects. Results from [Pen] when paired with (a) Cleo and (b) Chloe.

(a)

	Alone			Paired with Cleo		
Comparison	Estimate	*t* value	*p* value	Estimate	*t* value	*p* value
2 vs 1	-50.38	-2.94	0.0308 *	-86.48	-3.23	0.0183 *
3 vs 1	-28.88	-1.69	0.25	-62.03	-2.32	0.09
3 vs 2	21.50	1.26	0.44	24.45	0.91	0.64

(b)

	Alone			Paired with Chloe		
Comparison	Estimate	*t* value	*p* value	Estimate	*t* value	*p* value
2 vs 1	-29.817	-3.502	0.0113 *	5.14	0.739	0.7457
3 vs 1	-31.65	-3.717	0.0077 **	16.817	2.418	0.0772
3 vs 2	-1.833	-0.215	0.9748	11.677	1.679	0.2527

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

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Table 3-1-3
Statistical data (Mean (SD)) of the tapping intervals depending on condition for each participant in four chimpanzee pairs.

Condition	Chloe	Cleo	Pan	Pal	Cleo	Pen	Chloe	Pen
Alone	533.81 (53.06)	374.56 (64.52)	711.43 (84.46)	380.05 (45.21)	418.78 (88.00)	497.29 (41.83)	498.21 (55.58)	369.93 (24.72)
Paired	530.15 (41.29)	438.18 (97.71)	752.78 (75.26)	416.84 (56.18)	389.57 (85.22)	457.89 (55.73)	447.40 (60.75)	373.19 (15.66)

Table 3-1-4
Statistical data (Mean (SD)) of the tapping intervals depending on condition for each participant in four human pairs.

	H1		H2		H3		H4	
Condition	A	B	A	B	A	B	A	B
Alone	1123.18 (56.15)	392.63 (62.89)	425.42 (10.01)	613.48 (28.26)	950.53 (15.81)	740.45 (37.48)	330.1 (15.45)	522.27 (11.33)
Paired	383.2 (63.56)	365.65 (48.57)	451.27 (16.70)	501.17 (16.73)	613.28 (13.22)	618.43 (10.40)	307.62 (12.04)	433.43 (14.46)

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Chapter 3-2

An effect of visual cues in addition to moderate auditory cues on temporal coordination in chimpanzees and humans

Abstract

While our previous studies demonstrated that chimpanzees share an ability to produce spontaneous temporal coordination with humans, it remains unclear especially how visual cues of the partner's movement influence on the emergence of tempo convergence. To examine this question, the current study conducted a stepwise analysis. Three conditions were prepared for both chimpanzees and humans: baseline, paired-invisible and paired-visible condition. In the baseline, the participants produced the tapping movement alone and their own preferred tapping tempo was measured. In the other two test conditions, pairs of the participants produced the tapping movement simultaneously with their conspecific partner. Only moderate auditory cues of the partner's movement were available in the paired-invisible condition, while visual cues in addition to the auditory cues were available in the paired-visible condition. Spontaneous tapping tempo changes occurred significantly between the baseline and the paired-invisible condition, while there was little between the two paired conditions. The observed tempo changes in the paired-invisible were toward harmonic tempo with the partner in both chimpanzees and humans. These results indicate that not visual but auditory cues play a critical role in the tempo convergence in both chimpanzees and humans in the current experimental setup.

Keywords: auditory and visual cues, harmony, chimpanzees, humans

Introduction

Our previous two studies revealed that chimpanzees and humans share an ability to produce spontaneous temporal coordination to some extent when they interact with another conspecific individual. The experiment under the side-by-side setup demonstrated that chimpanzees have an ability to match their tapping movement with auditory cues from the partner's movement (Yu & Tomonaga, 2015). The next experiment that was retested under the face-to-face setup where auditory and visual cues of the partner's movement were available showed that temporal coordination was enhanced in the chimpanzees (Yu & Tomonaga, 2016). These findings indicate that auditory cues can solely facilitate an interaction between the chimpanzees but additional visual cues enhance the influence of the partner's movement. However, it remains unclear how additional visual cues play a role in spontaneous temporal coordination in the chimpanzees because Yu & Tomonaga (2016) lacks stepwise experimental design. The current study aimed to examine an effect of visual cues of the partner's movement on one's own spontaneous tapping movement in chimpanzees. Humans were also examined to directly compare with the findings from the chimpanzees.

Methods

Participants

Two pairs of chimpanzees (*Pan troglodytes*) and humans (*Homo sapiens*) participated, respectively. All the participants were adult females. Among the chimpanzee pairs, one was from mother and her biological offspring (34-year-old mother [Chloe] and her

14-year-old daughter [Cleo]) who joined all of our previous experiments (Yu & Tomonaga, 2015; 2016). They also have an experience in conducting a finger-tapping task under non-social distractive auditory stimuli (unpublished data, see also Hattori et al., 2013; Hattori et al., 2015). Another pair was from non-kin relationship (37-year-old female [Pen] named Pendensa and 38-year-old female [Mari]). They all lived together with seven other chimpanzees in an enriched outdoor compound with attached indoor residences in the Primate Research Institute, Kyoto University, Japan (Matsuzawa, 2006). All the chimpanzees have had extensive experience with perceptual and cognitive studies (Tomonaga, 2001; Matsuzawa, 2003; Matsuzawa et al., 2006).

In humans, two 24-year-old graduate students from Kyoto University Primate Research Institute (H1X and H2Y) were paired with 60-year-old (H1Y) and 46-year-old (H2X) staff members of the institute, respectively. They were all acquainted with each other. The research protocol was reviewed and approved by the Human Ethics Committee, Primate Research Institute, Kyoto University.

Apparatus

LED push buttons (Fuji Electric, 2 × 2 cm) were used to produce a finger tapping movement from each participant. The two buttons were aligned horizontally 12.5 cm apart in a transparent acrylic panel (45 × 45 cm). The distance between the two acrylic panels that pairs of the participants faced from each other was approximately 24 cm. An automated universal feeder was used to deliver a food reward to each chimpanzee. All the equipment and experimental events were controlled by a computer located outside the experimental booth.

Task

Each trial began with illumination of two push buttons. The participants were required to tap either one of the two buttons. When one of the buttons was pressed once, its light turned-off and the participants were again required to tap the remaining lighted-up push button. When this button was also pressed once, its light turned-off and another button in the other side illuminated with 0 ms delay. A trial ended after pressing alternatively illuminating two buttons from 25 to 45 times. The chimpanzees received a piece of fruit in the end of trials. The inter-trial interval was 2 seconds.

Conditions

Two conditions were prepared for visibility control: Paired-invisible (Pi) and Paired-visible (Pv). In the paired-invisible (Pi) condition, black-colored paper was placed between two acrylic panels so that visual cues of the partner's movement can be blocked from each other (Figure 3-2-1a). In the paired-visible (Pv) condition, on the other hand, the black occluder was removed and visual cues of the partner's movement was available between participants (Figure 3-2-1b).

<< Figure 3-2-1 around here>>

Procedure

Both chimpanzees and humans were tested under the same experimental schedule. To measure one's own preferred tapping tempo, both species firstly conducted the tapping task independently. This baseline (BL) was conducted for two consecutive days. Each day consisted of 5 blocks of six trials, and each trial required the participants to tap from

25 to 45 taps. After the participants cleared the baseline, they conducted the task simultaneously with their conspecific partner. The two test conditions were conducted with ABBA schedule (A: Paired-visible condition, B: Paired-invisible condition). Either one condition was conducted in a day for two consecutive days. Thus, each condition was performed for 4 experimental days in total. Same with the baseline, each experimental day consisted of 5 blocks of six trials and each trial required from 25 to 45 taps. The timing of a trial Start and Finish was equal between two participants in a pair during the two test conditions. In every each block, either one of the participants in a pair was randomly designated to finish a trial with producing alternative tapping from 25 to 45 times. Throughout the experiment, there was a mechanical click sound (approximately 50 dB) from the button pressing.

Analysis

Tapping intervals, which is an inverse form of tempo, was calculated only from an alternative tapping movement. Few very short (<100 ms) or long (>2 s) tapping intervals were removed as outliers. The tapping intervals were averaged for each block (n=10 for baseline; n=20 for Pi and Pv, respectively).

Two sample *t*-tests assuming unequal variance were conducted in stepwise. Firstly, the tapping intervals between baseline (BL) and Paired-invisible (Pi) were compared to confirm an effect of auditory cues of the partner's movement. Next, the Paired-invisible (Pi) and Paired-visible (Pv) conditions were compared to examine an effect of additional visual cues of the partner's movement. No Bonferroni or Holm correction was conducted because the current comparisons were planned independently.

Results

The mean of tapping intervals during three conditions, including baseline (BL), the paired-invisible (Pi) and paired-visible (Pv), were examined for each participant in both pairs of chimpanzees and humans (Figure 3-2-2). Comparisons between the BL and Pi revealed that all the participants, except for one chimpanzee (Cleo, $t(24) = 1.88$, $p = 0.072$), show a significant difference in their tapping intervals between the two conditions (Chloe, $t(27) = 3.80$, $p < 0.001$; Pen, $t(17) = 11.05$, $p < 0.001$; Mari, $t(27) = 4.65$, $p < 0.001$; H1X, $t(27) = 18.93$, $p < 0.001$; H1Y, $t(14) = 13.10$, $p < 0.001$; H2X, $t(14) = 3.54$, $p = 0.003$; H2Y, $t(27) = 5.71$, $p < 0.001$). Comparisons between the Pi and Pv revealed that 5 out of 8 participants show no significant difference between the conditions (Cleo, $t(31) = 1.04$, $p = 3.02$; Pen, $t(35) = 0.19$, $p = 0.848$; H1X, $t(30) = 0.78$, $p = 0.439$; H1Y, $t(26) = 0.42$, $p = 0.68$; H2X, $t(37) = 0.32$, $p = 0.747$). The other 3 participants showed a similar pattern in that they produced faster tapping tempo in the Pv in comparison with the Pi condition (Chloe, $t(35) = 2.15$, $p = 0.038$; Mari, $t(37) = 3.3$, $p = 0.002$; H2Y, $t(37) = 4.22$, $p < 0.001$). These findings suggest that auditory cues of the partner's movement were more influential than additive visual cues on spontaneous tapping movement in both chimpanzees and humans.

<< Figure 3-2-2 around here>>

To examine in what direction did the tapping tempo changes occur in relation to the partner's tapping tempo, the ratio of the mean tapping intervals between participants in a pair was calculated (relatively slow tapping individual's tapping

interval was divided by the fast tapping individual's tapping intervals for each pair, see Figure 3-2-3). In comparison with BL, both chimpanzees and humans showed the ratio which is close to 1:1 or 2:1 in the Pi condition. Comparisons between the Pi and Pv condition showed that the ratio in the Pv slightly deviated from that of the Pi condition. This result indicated that the tapping tempo changes occurred toward two different types of the tempo convergence in both chimpanzees and humans when they produce simultaneous tapping movement with their conspecific partner under multisensory cues.

<< Figure 3-2-3 around here>>

Discussion

The current study investigated the causal effect of multimodal cues of the partner's movement on spontaneous tempo convergence in both chimpanzees and humans. The current findings demonstrated that visual cues have little effect on the tempo convergence but auditory cues play a critical role in the convergence in both chimpanzees and humans. This finding supports our previous study (Yu & Tomonaga, 2015), reporting that one chimpanzee spontaneously showed the tapping alignment to her partner's tapping movement under the side-by-side setup where only auditory cues of the partner's movement were available. This result is also consistent with the previous studies in humans (Repp & Penel, 2002; 2004), reporting that humans are more strongly attracted to auditory than to visual rhythms. Taken together, the current experiment demonstrated that chimpanzees are similar with humans in terms of that auditory cues are sufficient to facilitate tempo convergence when the participants

simultaneously produce rhythmic movement with their conspecific partner.

The ratio of the tapping intervals between participants indicated that the tempo convergence fall into either 1:1 or 2:1 match. Previous studies in humans reported that polyrhythms (such as 3:2 or 5:3) are less stable than simple rhythms in which one frequency is an integer multiple of the other (such as 1:1, 2:1 or 3:1), often resulting in transitions to simple rhythms (Fraisse, 1982; Treffner & Turvey, 1993). This also suggests that chimpanzees share a stable form of the movement coordination with humans.

In summary, the current study with stepwise analysis demonstrated that auditory cues are sufficient in facilitating tempo convergence in both chimpanzees and humans. The current study also found that harmonic tempo convergence occurs in addition to perfect tempo matching in chimpanzee pairs like in human pairs.

References

Fraisse, P. (1982). Rhythm and tempo. The psychology of music, 1, 149-180.

Hattori, Y., Tomonaga, M., & Matsuzawa, T. (2013). Spontaneous synchronized tapping to an auditory rhythm in a chimpanzee. Scientific Reports, 3, 1566.

Hattori, Y., Tomonaga, M., & Matsuzawa, T. (2015). Distractor effect of auditory rhythms on self-paced tapping in chimpanzees and humans. PLoS ONE, 10(7).

Matsuzawa, T. (2003). The Ai project: historical and ecological contexts. Animal cognition, 6(4), 199-211.

Matsuzawa, T., Tomonaga, M., & Tanaka, M. (2006). Cognitive development in chimpanzees. Springer, Tokyo.

Matsuzawa, T. (2006). Sociocognitive development in chimpanzees: a synthesis of laboratory work and fieldwork. In Cognitive development in chimpanzees (pp. 3-33). Springer Tokyo.

Repp, B. H. (2005). Sensorimotor synchronization: a review of the tapping literature. Psychonomic Bulletin & Review, 12(6), 969–992.

Repp, B. H., & Penel, A. (2004). Rhythmic movement is attracted more strongly to auditory than to visual rhythms. Psychological Research, 68(4), 252–270.

Repp, B. H., & Penel, A. (2002). Auditory dominance in temporal processing: new evidence from synchronization with simultaneous visual and auditory sequences. Journal of Experimental Psychology. Human Perception and Performance, 28(5), 1085–1099.

Tomonaga, M. (2001). Investigating Visual Perception and Cognition in Chimpanzees (Pan troglodytes) through Visual Search and Related Tasks: from Basic to Complex Processes. Primate Origins of Human Cognition and Behavior , 55–

86.

Treffner, P. J., & Turvey, M. T. (1993). Resonance constraints on rhythmic movement. Journal of Experimental Psychology: Human Perception and Performance, 19(6), 1221–1237.

Yu, L., & Tomonaga, M. (2015). Interactional synchrony in chimpanzees: Examination through a finger-tapping experiment. Scientific Reports, 5, 10218.

Yu, L., & Tomonaga, M. (2016). Unidirectional adaptation in tempo in pairs of chimpanzees during simultaneous tapping movement: an examination under face-to-face setup. Primates, 57, 181-185.

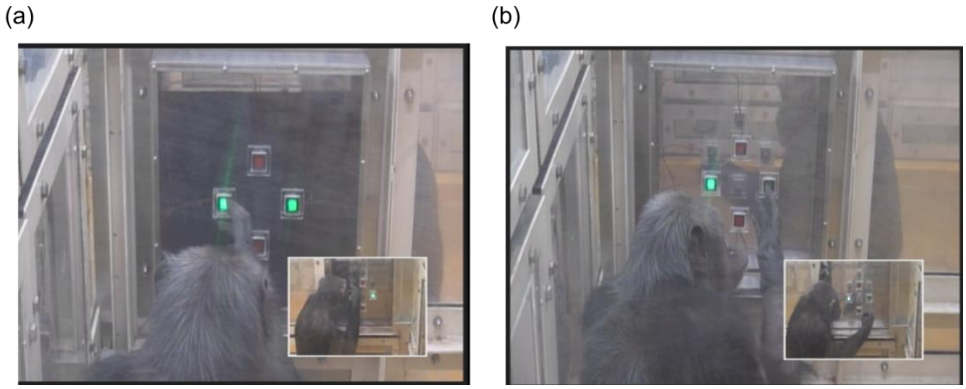

Figure 3-2-1. A pair of the chimpanzees (Chloe and Cleo) conducting the finger-tapping task under two test conditions. (a) Tapping in the Paired-invisible condition where the occluder prevents visual cues of the partner's movement. (b) Tapping in the Paired-visible condition where the tapping movement is visible from each other.

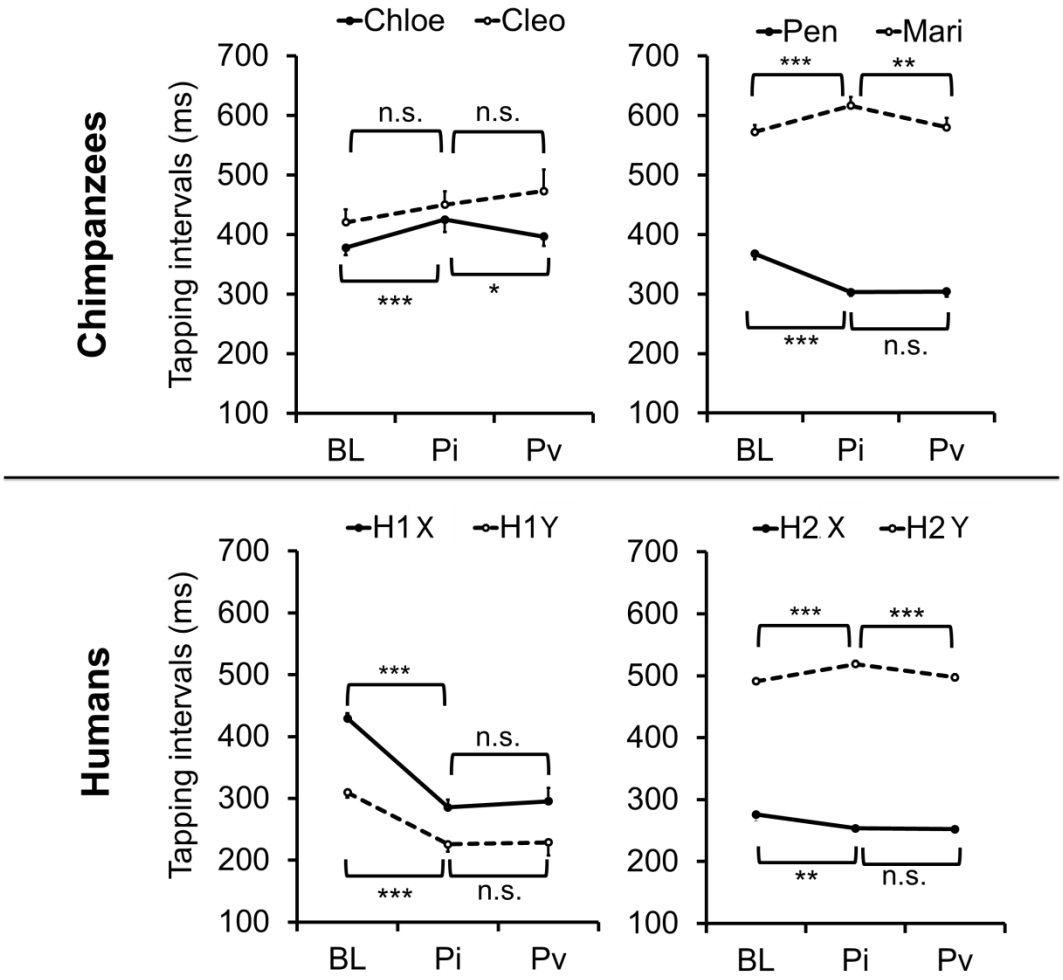

Figure 3-2-2. Mean of the tapping intervals under three conditions (baseline, Paired-invisible and Paired-visible) for each participant in each pair in chimpanzees and humans. Error bars indicate 95% confidence intervals of the mean.

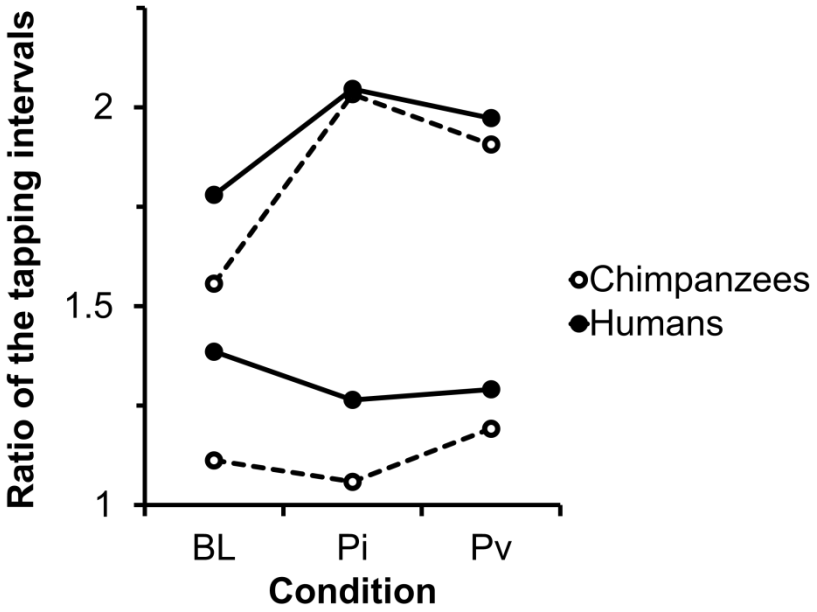

Figure 3-2-3. Each dot represents a ratio of the mean tapping intervals between two participants in each pair for each condition. The dots connected by lines represent data from the same pairs.

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Chapter 4

General Discussion

Summary

Temporal coordination is important in many species, and is seen in behaviors that range from the coordinated group behaviors of bird flocks and fish schools, to the social group behaviors of humans (e.g., in dancing). To understand evolutionary origins of temporal coordination in humans, the current study established a novel experimental method for examining spontaneous temporal coordination in chimpanzees and humans under a social context. Moreover, to understand the causal effect of multimodal cues on the emergence of temporal coordination in both species, an effect of auditory and/or visual cues of the partner's movement was examined under the experimental setup. A finger-tapping task which is extensively used for exploring sensorimotor synchronization in humans (Repp, 2005) was introduced to produce repetitive and rhythmic movement from each participant.

In Chapter 2, two pairs of chimpanzee mothers and their biological offspring were examined under the side-by-side setup where only auditory cues of the partner's movement were available. Results indicated that chimpanzees can use auditory cues from their partner for temporal coordination (Yu & Tomonaga, 2015). However, it was difficult to generalize the findings to all chimpanzees, because only one out of four chimpanzees showed both significant tapping tempo convergence and the tapping alignment toward her partner. One possibility to explain the failure of the three chimpanzees to show temporal coordination may have been their training history (cf., Matsuzawa, Tomonaga & Tanaka, 2006). Specifically, the chimpanzees may have learned to ignore other chimpanzees while performing various tasks, and this may have resulted in them also ignoring a partner chimpanzee in the present study. To clarify the

spontaneous emergence of temporal coordination in chimpanzees, retest was needed under a more interactive experimental setting.

To facilitate an interaction between chimpanzees, I established a new experimental setup, called the face-to-face setup, where both auditory and visual cues of the partner's movement were available (instead of only auditory, as in the prior study). In Chapter 3-1, I examined both chimpanzees (four pairs, including the two mother-offspring pairs who participated in the previous study, as well as two new non-kin pairs) and humans (four non-kin pairs). Results indicated that chimpanzees and humans are similar in that they show unidirectional adaptation in tempo when they simultaneously produce tapping movements with a partner under auditory and visual interaction. Interestingly, the participants from non-kin relationships in both chimpanzees and humans tended to converge toward the faster tapping tempo, whereas the four chimpanzees from mother and offspring pairs showed no such effect. Instead, offspring chimpanzees changed their tempo towards that of their relatively slow tapping mother.

In addition to the similarities seen between chimpanzees and humans, the current study revealed a notable difference between two species: whereas tempo convergence occurs rapidly and completely in humans, it is slow and partial in chimpanzees. These findings suggest that chimpanzees and humans share modulations when producing their own rhythmic movement under multimodal interaction with their partner. However, an ability to precisely coordinate the movement in time with their partner may have evolved gradually after the human lineage separated from that of chimpanzees.

The findings from Chapter 3-1 support the hypothesis that auditory cues by

themselves are sufficient to facilitate coordinated interaction between the chimpanzees (see Chapter 2). However, it remained unclear whether visual cues might also have an effect. In Chapter 3-2, I examined an effect of visual cues in addition to moderate auditory cues of the partner's movement, under the same face-to-face setup in both chimpanzees and humans. Results showed that auditory cues are sufficient for temporal coordination in both chimpanzees and humans, whereas visual cues in addition to the auditory cues have weak additional effect. For clarification, here I note that this does not yet prove that the visual cues do nothing. It could just be that humans and chimpanzees rely on auditory cues, when bimodal cues are available. I assume that if there are only visual cues, with no auditory cues, they would have some effect on temporal coordination in both species (c.f., Schmidt & O'Brien, 1997; Richardson et al., 2007; Oullier et al., 2008). In my study, there was no clear evidence of any interspecies difference between chimpanzees and humans with respect to sensory modality in temporal coordination.

Overall, the current comparative study in chimpanzees and humans demonstrated that chimpanzees have the ability to temporally coordinate their rhythmic movement with those of a partner, an ability they share with humans. The results also show that both species can use auditory cues in perceiving their conspecific partner's rhythmic movement. Although experimental artifacts prevented an analysis of possible phase matching, I found clear evidence in both species for a spontaneous change in tempo that led to increased temporal coordination. Taken together, the current studies for the first time provide valuable new evidence that chimpanzees and humans share a common ability for temporal coordination. This provides an important complement to prior publications of temporal coordination in non-human primates, which had so far

been limited to chimpanzees (Hattori et al., 2013; 2015) examined under a non-social context or monkeys (Nagasaka et al., 2013) without direct comparisons between species in the same study.

Comparisons between humans, chimpanzees and macaques

Although the current study examined only chimpanzees and humans, findings from a prior study in macaques (Nagasaka et al., 2013) were included in my analyses to provide a broader comparison. As mentioned earlier, Nagasaka et al. (2013) first demonstrated that Japanese macaques (*Macaca fuscata*) can spontaneously coordinate their movements in time with a conspecific partner, when they produce repetitive left-to-right arm movements while facing each other. They used push buttons for producing the rhythmic movement from each monkey and provided auditory feedbacks for each tapping event. In sum, their experimental protocol is similar to the current study (especially, Chapter 3) in three respects: 1) the participants produce sinusoidal arm movement with their preferred tempo, 2) the participants in the dyad were facing each other so that visual cues of a partner's movements were available, 3) auditory feedback corresponding to each tapping movement were provided so that auditory cues of a partner's movements were available.

Table 4-1 shows a summary of the findings on the following questions: First, do non-human primates have an ability to temporally coordinate their behaviors with a conspecific partner as humans do? Second, which type of sensory modality is used in detecting the behavior of a partner? Third, does their coordination show perfect phase

and tempo matching or not? Fourth, if a dyad shows temporal coordination, especially 1:1 tempo matching, which participants in the dyad contribute to it?

<< Table 4-1 around here>>

As indicated in the top row of Table 4-1, the broadest summary supported by my findings is that the ability to temporally coordinate behaviors with a conspecific partner is shared in common across humans, chimpanzees and macaques. Moreover, the findings showed that auditory cues are sufficient in facilitating spontaneous temporal coordination in both chimpanzees and humans, whereas visual cues appear to be more important in macaques (see row 2 and 3 of Table 4-1). It is important to note that the comparisons across the species with respect to sensory modality are not precisely comparable. Whereas Nagasaka et al. (2013) tested a purely visual condition that had no auditory components at all, my conditions in humans and chimpanzees all had some auditory component, even when they were mostly focused on the visual modality (such as the mere sound of the button click). Thus, my studies cannot yet exclude the possibility that humans and chimpanzees could also use purely visual cues. What is clear across studies in the three different species is that humans and chimpanzees can use a stimulus that is only auditory, with no visual component, whereas this is not sufficient to produce coordination in macaques. In summary, while the control conditions are not exactly alike, the findings suggest that macaques use mostly visual information for temporal coordination, whereas humans and chimpanzees tend to rely mostly on auditory information.

These cross-species effects of sensory modality in interpersonal coordination

are also consistent with the previous studies examined under a non-social context, reporting that macaques have a large bias toward visual rather than auditory cues to drive their tapping behavior (Zarco et al., 2009), whereas chimpanzees are capable to spontaneously synchronize their movement with an auditory rhythm as are humans (Hattori et al., 2013; 2015). Thus, it seems that the sensory modality for processing temporal information is consistent in each species regardless of whether the stimuli are social or nonsocial. It will be interesting to further understand qualitative and quantitative species differences in their response toward social and non-social stimuli (c.f., Kilner et al., 2003), because there is a large body of evidence showing that the brain processes biological and non-biological movement differently in macaques (Oram & Perrett, 1994) and in humans (Frith & Frith, 1999; Allison et al., 2000; Grossman et al., 2000; Grezes et al., 2001).

Since temporal coordination consists of two components (phase match and tempo match), I examined those components separately. Although the current study could not provide clear results of the phase matching because of experimental artifacts (Chapter 3), previous studies in humans have shown that we have a strong tendency to synchronize the movement with those of others, as soon as there is exchange of sensory information about the movements (Schmidt & O'Brien, 1997; Neda et al., 2000; Issartel et al., 2007; Richardson et al., 2007; Oullier et al., 2008). In macaques, Nagasaka et al. (2013) showed that they spontaneously produce synchronized movements that are in-phase, which is similar to what is observed in humans. Although there is no clear evidence yet in chimpanzees, these prior findings in monkeys and humans would strongly predict that phase matching would also be seen in chimpanzees, even without explicit training or verbal instruction. Further comparative work is clearly needed, but I

speculate that there are no species differences in terms of the emergence of phase matching across humans, chimpanzees and macaques.

My findings on tempo matching are a main focus of this comparative study. The broad finding is that there is a gradation of tempo matching abilities, from humans, to chimpanzees, to macaques. A particular strength of my studies is that tempo matching abilities can be further decomposed into the ability to show harmonic tempo matching, and how rapidly and completely a 1:1 tempo match convergence is achieved. These distinct components provide further evidence for a gradation across the three species. If we look at chimpanzees and humans in their tempo matching, both species showed a change in their spontaneous tapping tempo toward a 1:1 tempo match with a partner when there were both auditory and visual cues (see Chapter 3-1). Interestingly, however, both species also showed a 2:1 match in addition to a 1:1 match, when the amplitude of the auditory cues was smaller (see Chapter 3-2). Although no differences emerge here in tempo matching between chimpanzees and humans, a difference does emerge when we look at how this tempo convergence developed. In humans, it is rapid and complete, whereas in chimpanzees it is slow and partial. The spontaneous tendency of tempo convergence is the same in the two species, but how they get there is different.

If I now compare my results with those from macaques (from Nagasaka et al., 2013), we see a qualitative continuation of the development of tempo convergence. For 1:1 tempo matching, the convergence is strong and salient in humans, moderate in chimpanzees, and weak in macaques. In the study of Nagasaka et al. (2013), emergence of 1:1 match was observed in only one out of three tested pairs. In addition, macaques show a further difference from both chimpanzees and humans, in that their harmonic tempo matching extends to a 4:1 matching. If we thus put together the harmonic tempo

matching abilities, and the qualitative nature of the development of the tempo convergence, we see a gradient across all three species that supports evolutionary continuity of temporal coordination.

It is worth further comment on the findings of harmonic tempo matching. Louder sound tended to produce higher 1:1 tempo convergence in both chimpanzees and humans. This finding suggests an intriguing psychological mechanism that should be studied further in future experiments—sound amplitude is effectively converted into speed in the behavior. One possible candidate psychological mechanism that could explain this effect might be a shared state of higher arousal, caused by louder sounds, and resulting in faster movements.

When both chimpanzees and humans show a significant tapping tempo change toward 1:1 match, the participants from non-kin relationships in both chimpanzees and humans showed a social facilitation of fast tapping tempo, whereas the four chimpanzees from mother and offspring pairs showed no such effect. Instead, offspring chimpanzees changed their tempo toward that of their relatively slow tapping mother.

Interspecies differences in temporal coordination and the relation to neural connectivity

Although both chimpanzees and humans showed temporal matching, there were clear differences in the strength of the tempo convergence between the two species, as I just discussed above. Also, further comparison with data from macaques revealed that monkeys show even weaker tempo convergence in comparison with humans and chimpanzees. These findings suggest some specific hypotheses about what might be different in the brains of these species that accounts for the behavioral differences. For

example, it could be that auditory or visual perception is less good in chimpanzees than in humans, or that motor control is generally worse in chimpanzees than in humans. There is little evidence, however, to support these two hypotheses. Instead, a more plausible hypothesis is that the strength of a link between perceiving a partner's movement and producing one's own movement is different across three primate species.

This last hypothesis has some preliminary support. Recently, Merchant & Honing (2014) proposed a hypothesis that interspecies differences in audio-motor connectivity are related to an ability to entrain to external cues in humans, chimpanzees and macaques. They referred a diffusion tensor imaging study which examined the arcuate fasciculus (Rilling et al., 2008) to support their claim. The arcuate fasciculus is a white-matter fiber track that links lateral temporal cortex with frontal cortex via a dorsal projection. This pathway is known to be critical in human language, especially spoken language (c.f., speech). Rilling et al. (2008) demonstrated that humans show massive reciprocal connections between frontal and parietal-temporal cortex via the arcuate fasciculus, whereas macaques show weaker and chimpanzees show an intermediate level of connectivity. It is possible that an uninterrupted and continuous arcuate pathway enables rapid information exchange between sensory and motor regions, which could be required for the rapid and precise tempo convergence seen in humans.

Here I note that the current tapping movement produced by each participant is a voluntary and smooth movement. Therefore, additional brain areas that function to control voluntary movements, such as the basal ganglia and cerebellum, will also be involved in the currently observed temporal coordination. The evidence from the arcuate fasciculus will be only a small part of the story. Further studies, such as comparison of the fiber tracks that connect these additional brain regions as well, may

facilitate our understanding on a gradual increase in the rate and accuracy of tempo convergence across the three species.

Lastly, it is important to note that the current study demonstrated that chimpanzees show different responses toward a conspecific partner from the way in which they coordinate with non-social auditory rhythms. Whereas they synchronized to isochronous auditory rhythms only that were close to one's own preferred tapping tempo (Hattori et al., 2013; 2015), the chimpanzees in a dyad coordinated to irregular and dissimilar tempo generated by a conspecific partner (Yu & Tomonaga, 2015; 2016). This different response toward social and non-social cues has been also reported in humans and macaques. In humans, for example, Kilner et al. (2003) investigated whether the participants' trajectory of the movement would be interfered when they observe other's movement while producing their own movement. They found that the participants show significantly high variability of the movement trajectory when they observe a human partner's movement rather than robot's movement. In macaques, Nagasaka et al. (2013) demonstrated that the monkeys in a dyad show spontaneous in-phase coordination when they simultaneously produce the tapping movement while facing each other. This finding was surprising because it has been known that monkeys hardly show phase matching, although they can be trained to show tempo matching with non-social rhythmic cues (Zarco et al., 2009; Konoike et al., 2012). Taken together, these behavioral evidences from the three primate species suggest that a social partner facilitates more flexible movement coordination in comparison with the non-social cues. In other words, recognition of a social partner seems to give a positive effect on a link between perception and motor control. A further study with neuroimaging techniques may help us to understand the brain areas and networks that are responsible for the

temporal coordination during social interaction in primate species.

Temporal coordination and its social function

Despite being shared in common across macaques, chimpanzees and humans, the function of temporal coordination remains a topic of investigation. Previous studies, which examined implicit recognition of imitation by measuring an increased attention toward an imitator, reported that great apes and macaques share ability with human infants to implicitly recognize the movement that is structurally and temporally contingent on their own movement (Nielsen et al., 2005; Paukner et al., 2005; Haun & Call, 2008). I assume that humans, who produce the most salient temporal coordination among the three primate species, should also have a strong tendency to attend to their partner, which may facilitate social interaction in natural settings. In other words, I speculate that temporal coordination functions in a similar way with spontaneous facial mimicry in humans (Sato & Yoshikawa, 2007), suggesting that both temporal and spatial coordination is not a form of intra-individual processing but is inter-individual communication. The evidence for this speculation would include many social behaviors commonly observed in humans, such as rhythmic group behaviors during rituals and dancing. However, this still leaves unknown the possible function of temporal coordination in the non-human primate species.

Future direction:

Explore the developmental basis of temporal coordination in humans

The current study demonstrated that offspring chimpanzees change their behavior toward their mother chimpanzee. Although the current experiments do not include a social context of learning, this result was consistent with the finding from a field study (Biro et al., 2003), reporting that young chimpanzees observe their mother or older individuals when they are trying to learn the use of tools. The result was also consistent with the style of social learning in chimpanzees which is known as "education by master-apprenticeship" (Matsuzawa, 2002; Matsuzawa et al., 2008), whereby mothers serve as the model for their young to learn through observation, but the mothers do not actively teach them.

In humans, on the other hand, active teaching is a unique feature of human education, so called pedagogy that has been hypothesized to be a uniquely human adaptation enabling culture (Csibra & Gergely, 2011). Although human infants already develop the ability to synchronize their body movement with adult speech when they are only 2 days old (Condon & Sander, 1974), mothers have a strong tendency to produce child-directed speech (i.e., motherese) to their young. Moreover, when the infant reaches an age to voluntarily manipulate an object with their hands, mothers often provide some objects for them and mold their infant's hand to support their movement. Therefore, I would expect to find an opposite pattern of temporal coordination in human mother-infant pairs from what I found in chimpanzees. That is, if tested in the same experiment as I described here, human mothers would quickly and entirely change their tempo to match that of their infant.

The ontogenetic analysis of the development of interpersonal coordination is crucial to clarify not only when they learn but also why and how only humans could have fostered the capacity to coordinate their movements so precisely in time and space

with those of others. The current experimental method, which enables measurement of the behavioral changes within milliseconds timescale and can be used across a range of different species, should also be suitable for the future studies within human infants.

References

Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: role of the STS region. Trends in cognitive sciences, 4(7), 267-278.

Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C., & Matsuzawa, T. (2003). Cultural innovation and transmission of tool use in wild chimpanzees: Evidence from field experiments. Animal Cognition, 6(4), 213–223.

Condon, W. S., & Sander, L. W. (1974). Neonate movement is synchronized with adult speech: interactional participation and language acquisition. Science (New York, N.Y.), 183(1951), 99–101.

Csibra, G., & Gergely, G. (2011). Natural pedagogy as evolutionary adaptation. Philosophical Transactions of the Royal Society of London B: Biological Sciences, 366(1567), 1149-1157.

Frith, C. D., & Frith, U. (1999). Interacting minds--a biological basis. Science (New York, N.Y.), 286(5445), 1692–1695.

Grèzes, J., Fonlupt, P., Bertenthal, B., Delon-Martin, C., Segebarth, C., & Decety, J. (2001). Does perception of biological motion rely on specific brain regions? NeuroImage, 13(5), 775–85.

Grossman, E. D., Donnelly, M., Price, R., Pickens, D., Morgan, V., Neighbor, G., & Blake, R. (2000). Brain areas involved in perception of biological motion. Journal of Cognitive Neuroscience, 12(5), 711–20.

Hattori, Y., Tomonaga, M., & Matsuzawa, T. (2013). Spontaneous synchronized tapping to an auditory rhythm in a chimpanzee. Scientific Reports, 3, 1566.

Hattori, Y., Tomonaga, M., & Matsuzawa, T. (2015). Distractor effect of auditory rhythms on self-paced tapping in chimpanzees and humans. PLoS ONE, 10(7).

Haun, D. B., & Call, J. (2008). Imitation recognition in great apes. Current Biology, 18(7), R288-R290.

Issartel, J., Marin, L., & Cadopi, M. (2007). Unintended interpersonal co-ordination: "can we march to the beat of our own drum?" Neuroscience Letters, 411(3), 174–179.

Kilner, J. M., Paulignan, Y., & Blakemore, S. J. (2003). An interference effect of observed biological movement on action. Current Biology, 13(6), 522-525.

Matsuzawa, T. (2002). Chimpanzee Ai and her son Ayumu: An episode of education by master-apprenticeship. *The Cognitive Animal: Empirical and Theoretical Perspectives on Animal Cognition*, 189-195.

Matsuzawa, T., Tomonaga, M., & Tanaka, M. (2006). Cognitive development in chimpanzees. Springer, Tokyo.

Matsuzawa, T., Biro, D., Humle, T., Inoue-Nakamura, N., Tonooka, R., & Yamakoshi, G. (2008). Emergence of culture in wild chimpanzees: education by master-apprenticeship. In Primate origins of human cognition and behavior (pp. 557-574). Springer Japan.

Merchant, H., & Honing, H. (2014). Are non-human primates capable of rhythmic entrainment? Evidence for the gradual audiomotor evolution hypothesis. Frontiers in neuroscience, 7.

Nagasaka, Y., Chao, Z. C., Hasegawa, N., Notoya, T., & Fujii, N. (2013). Spontaneous synchronization of arm motion between Japanese macaques. Scientific Reports, 3, 1151.

Néda, Z., Ravasz, E., Brechet, Y., Vicsek, T., & Barabási, A.-L. (2000). Self-organizing processes: The sound of manyhands clapping. Nature, 403(6772), 849–850.

Nielsen, M., Collier-Baker, E., Davis, J. M., & Suddendorf, T. (2005). Imitation recognition in a captive chimpanzee (Pan troglodytes). Animal cognition, 8(1), 31-36.

Oram, M. W., & Perrett, D. I. (1994). Responses of Anterior Superior Temporal Polysensory (STPa) Neurons to "Biological Motion" Stimuli. Journal of Cognitive Neuroscience, 6(2), 99–116.

Oullier, O., de Guzman, G. C., Jantzen, K. J., Lagarde, J., & Kelso, J. a S. (2008). Social coordination dynamics: measuring human bonding. Social Neuroscience, 3(2), 178–192.

Paukner, A., Anderson, J. R., Borelli, E., Visalberghi, E., & Ferrari, P. F. (2005). Macaques (Macaca nemestrina) recognize when they are being imitated. Biology Letters, 1(2), 219-222.

Petrides, M., & Pandya, D. N. (2009). Distinct parietal and temporal pathways to the homologues of Broca's area in the monkey. PLoS Biol, 7(8), e1000170.

Repp, B. H. (2005). Sensorimotor synchronization: a review of the tapping literature. Psychonomic Bulletin & Review, 12(6), 969–992.

Richardson, M. J., Marsh, K. L., Isenhower, R. W., Goodman, J. R. L., & Schmidt, R. C. (2007). Rocking together: Dynamics of intentional and unintentional interpersonal coordination. Human Movement Science, 26(6), 867–891.

Rilling, J. K., Glasser, M. F., Preuss, T. M., Ma, X., Zhao, T., Hu, X., & Behrens, T. E. J. (2008). The evolution of the arcuate fasciculus revealed with comparative DTI. Nature Neuroscience, 11(4), 426–428.

Sato, W., & Yoshikawa, S. (2007). Spontaneous facial mimicry in response to dynamic facial expressions. Cognition, 104(1), 1-18.

Schmidt, R. C., & O'Brien, B. (1997). Evaluating the dynamics of unintended interpersonal coordination. Ecological Psychology, 9(3), 189-206.

Yu, L., & Tomonaga, M. (2015). Interactional synchrony in chimpanzees: Examination through a finger-tapping experiment. Scientific Reports, 5, 10218.

Yu, L., & Tomonaga, M. (2016). Unidirectional adaptation in tempo in pairs of chimpanzees during simultaneous tapping movement: an examination under face-to-face setup. Primates, 57, 181-185.

	Humans (Current study)	Chimpanzees (Current study)	Macaques (Nagasaka et al., 2013)
Temporal coordination	Yes	Yes	Yes
Auditory cues	○	○	×
Visual cues	△	△	○
Phase match	NA	NA	In-phase
Harmonic Tempo match	1:1 to 2:1	1:1 to 2:1	1:1 to 4:1
1:1 tempo convergence	Salient	Moderate	Weak
Mode of tempo convergence	Rapid and complete	Slow and partial	NA
Target of tempo convergence	Fast tapper	Fast tapper/ Mother	NA

NA: Not available

Table 4-1. Comparisons between three primate species on spontaneous temporal coordination under a social context

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