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You are in sync with me

Cacioppo, S.; Zhou, H.; Monteleone, G.; Majka, E.a.; Quinn, Kimberly; Ball, A.b.; Norman, G.j.; Semin, G.r.; Cacioppo, J.t.

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You are in sync with me: Neural correlates of interpersonal synchrony with a partner

Stephanie Cacioppo, Haotian Zhou, George Monteleone, Elizabeth A. Majka, Kimberly A. Quinn, Aaron B. Ball, Gregory J. Norman, Gün. R. Semin, John T. Cacioppo

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You are in sync with me:

Neural correlates of interpersonal synchrony with a partner

Stephanie Cacioppo^{1,2}; Haotian Zhou³, George Monteleone¹; Elizabeth A. Majka³, Kimberly A. Quinn⁴, Aaron B. Ball¹, Gregory J. Norman³, Gün. R. Semin^{5,6}; John T. Cacioppo^{1,2,3}

1. Center for Cognitive and Social Neuroscience, HPEN laboratory, University of Chicago, 940 East 57th Street, Chicago, IL

2. Department of Psychiatry and Behavior Neuroscience, University of Chicago, A27 S. Maryland Avenue, Chicago, IL, 60637

3. Department of Psychology, University of Chicago, 5848 S. University Avenue, Chicago, IL, 60637

4. School of Psychology, University of Birmingham, Edgbaston, Birmingham, B15 2TT, United Kingdom; Department of Psychology, DePaul University, 2219 N. Kenmore Ave., Chicago, IL 60657

5. Faculty of Social and Behavioral Sciences, Utrecht University, Heidelberglaan 1, 3584 CS, Utrecht, Netherlands

6. Department of Psychology, Koç University, Istanbul, Turkey

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Running Title: Neural correlates of interpersonal synchrony

Corresponding Author: Dr. John T. Cacioppo, Ph.D. [\(Cacioppo@uchicago.edu\)](mailto:Cacioppo@uchicago.edu); The University of Chicago ; Department of Psychology, 5848 South University Avenue, Chicago, IL, 60637

Abstract

Interpersonal synchrony is characterized by a temporary alignment of periodic behaviors with another person. This process requires that at least one of the two individuals monitors and adjusts their movements to maintain alignment with the other individual (the referent). Interestingly, recent research on interpersonal synchrony has found that people who are motivated to befriend an unfamiliar social referent tend to automatically synchronize with their social referent, raising the possibility that synchrony may be employed as an affiliation tool. It is unknown, however, whether the opposite is true; that is, whether the person serving as the referent of interpersonal synchrony perceives synchrony with their partner or experiences affiliative feelings towards the partner.

To address this question, we performed a series of studies on interpersonal synchrony with a total of 103 participants. In all studies, participants served as the referent with no requirement to monitor or align their behavior with their partner. Unbeknownst to the participants, the timings of their "partner's" movements were actually determined by a computer program based on the participant's (i.e., referent's) behavior.

Overall, our behavioral results showed that the referent of a synchrony task expressed greater perceived synchrony and greater social affiliation toward a synchronous partner (i.e., one displaying low mean asynchrony and/or a narrow asynchrony range) than with an aynchronous partner (i.e., one displaying high mean asynchrony and/or high asynchrony range). Our neuroimaging study extended these results by demonstrating involvement of brain areas implicated in social cognition, embodied cognition, self–other expansion, and action observation as correlates of interpersonal synchrony (vs. asynchrony). These findings have practical implications for social interaction and theoretical implications for understanding interpersonal synchrony and social coordination.

Keywords: Social neuroscience; fMRI; Interpersonal synchrony; Dyads; Shared representations. **Highlights:**

- First fMRI study on social consequences of synchrony where the participant served as referent.
- Referents recruit brain areas involved in social and embodied cognition during synchrony.
- Referents expressed greater feelings of affiliation toward synchronous partners.

1. Introduction

Early studies of synchrony focused on the mechanisms underlying a person's ability to synchronize movements with some *referent*, such as a metronome (cf, Repp, 2005). Interpersonal synchrony, the alignment in time of the periodic movements of two or more individuals, has also been investigated because of its putative social consequences. Interpersonal synchrony promotes an array of positive interpersonal outcomes, such as affiliation (Hove and Risen 2009), liking (Miles, Nind, Henderson, Macrae, 2009), rapport (Vacharkulksemsuk and Fredrickson, 2012), and emotional support satisfaction (Jones and Wirtz, 2007). Interpersonal synchrony also leads to outcomes that extend beyond individuals to promote groups, including cooperation (Wiltermuth and Heath, 2009) and compassion (Valdesolo and DeSteno, 2011). Functionalist accounts of synchrony posit that the primary purpose of synchrony is to foster social bonds (Semin, 2007; Semin and Cacioppo, 2008) and strengthen the collective (McNeill, 1995; Ehrenreich, 2006 Haidt, Seder, Kesibir, 2008; Haidt, 2012). McNeill (1995) argued that synchrony played an important role in the ascension of our species, and previous investigations have documented motivational factors that promote interpersonal synchrony and various social consequences of synchrony (Bernieri, 1988; Cappella, 1997; Lakin and Chartrand, 2003; Hove and Risen, 2009; Marsh et al., 2009; Wiltermuth and Heath, 2009; Miles et al., 2010; Paladino et al., 2010; Valdesolo and DeSteno, 2011; Vacharkulksemsuk and Fredrickson, 2012).

The research to date has focused on a particular type of interpersonal synchrony, in which the participants share the goal of synchronizing (either directly with their fellow participants, or with some other cue that results in their synchronization with each other). Interpersonal synchrony can take other forms, however, and individuals may find themselves being the referents for others' synchronization goals without sharing those goals for themselves. In the

current research, we investigated experimentally whether being the *referent* for a partner who responds in a more or less synchronous fashion (rather than an intentional contributor to the synchrony produced by a partner) affects the referent's perceived synchrony with and affiliative response toward the partner. Second, we investigated the neural correlates of interpersonal synchrony (vs. asynchrony) in this referent.

1. 1. Three processes underlying the emergence of interpersonal synchrony

The temporal relation between the movements of two or more individuals determines the degree of interpersonal synchrony. However, the same state of synchrony may be the outcome of any of three distinct production processes, which we refer to as orchestration, reciprocal entrainment, and unilateral entrainment. In orchestration, synchrony is achieved when two or more individuals entrain their movements to an external pacesetter (e.g., the pacing sound of a metronome) that "directs" the shared movement pattern, much like a conductor leading scores of musicians. For example, Hove and Risen (2009) manipulated interpersonal synchrony by having participants tap to beats created by a metronome.

In reciprocal entrainment, synchrony is achieved through a give-and-take process in which individuals within a system (e.g., dyad) monitor each other and adjust their own movement in a mutual fashion. For example, Oullier and colleagues (2008) found that dyadic interpersonal synchrony reflected movements that were distinct from individuals' movements prior to the interaction, suggesting that participants shifted their movement in response to their partners' movement.

Finally, in unilateral entrainment, one individual within a dyad (the "synchronizer") unilaterally adjusts his or her movements to entrain to the movements of the other individual (the

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referent) within the dyad – an individual who moves periodically but does not adjust his or her movements in reciprocation to promote synchrony. Previous work has focused on interpersonal synchrony achieved through orchestration or reciprocal entrainment (e.g., Delaherche et al., 2012; Repp and Su, 2013). Our focus here is on the social effects and neural correlates of unilateral entrainment. In a pilot study (Study I) and Study II, we sought to establish the extent to which a referent, who is subjected to a partner who behaves in a relatively synchronous or asynchronous fashion, *perceives* the former partner's movements to be more synchronous than the latter partner's movements, and feels greater affiliation toward the former than latter partner. In other words, we sought to ascertain whether (or not) unilateral synchrony promoted a sense of liking and rapport, thereby extending previous investigations centered on assessing the relative movement of those with a heightened motivation to socially connect with a target (e.g., Miles et al., 2010, 2011). In Study III, we investigated the neural correlates of perceived synchrony in the referent.

1.2. Social functions of synchrony

Over the past decades, two main bodies of literature have developed to better understand interpersonal synchrony. The literature on sensorimotor synchronization (SMS) focuses on an *action* that leads to synchrony by means of temporary coordination with a predictable external event (the referent). Among the findings in this field are that error correction is required to maintain SMS (see review by Repp, 2005), and stability is greater for synchronous than asynchronous inter-limb (e.g., arm or leg) movements within an individual (e.g., Yamanishi et al., 1980; Kelso, 1984) and between individuals (e.g., Schmidt et al., 1990; Richardson et al.,

2005), with the result being an increased likelihood of entrainment (e.g., Engström et al., 1996; Schmidt and O'Brien, 1997).

A second literature focuses on the *social* functions of interpersonal synchrony. Hatfield, Cacioppo and Rapson (1993) hypothesized that interpersonal synchrony enhances the momentby-moment tracking of other people's feelings (even when individuals are not explicitly attending to this information), thereby promoting emotional alignment between interacting individuals. Relatedly, as described above, McNeill (1995) posited that synchrony contributes to group solidarity. Since the 1990s, a large number of studies have reinforced these hypotheses and showed that performing actions that are similar to, and coordinated with, those of an interacting partner enhances feelings of connectedness, affiliation, interpersonal rapport, and a blurring of self–other boundaries (Bernieri, 1988; Tickle-Dengen and Rosenthal, 1990; Bernieri et al., 1994; Cappella, 1997; Lakin and Chartrand, 2003; Hove and Risen, 2009; Miles et al., 2010, 2011; Paladino et al., 2010; Vacharkulksemsuk and Fredrickson, 2012), liking (e.g., Hove and Risen, 2009; Miles et al., 2009), perceived similarity and compassion (Valdesolo and DeStano, 2011), joint action (Valdesolo et al., 2010), cooperation and enhanced altruistic behavior (Wiltermuth and Heath, 2009; Valdesolo and DeSteno, 2011), better negotiation outcomes (Maddux, Mullen, and Galinsky, 2008), emotional empathy (Chartrand & Bargh, 1999; Sonnby-Borgström, 2002; Marzoli et al., 2011), person memory (Macrae et al., 2008; Miles et al., 2010), group cohesion (McNeil, 1995), and prosocial behavior (van Baaren, Holland, Steenaert, and van Knippenberg, 2003; van Baaren, Holland, Kawakami, van Knippenberg, 2004; Marsh et al., 2009; Valdesolo and DeStano, 2011; Müller, Maaskant, van Baaren, Dijksterhuis, 2012). In sum, interpersonal synchrony is a foundation for effective social interaction and enhanced sociality (Miles et al., 2009; Delaherche, et al., 2012; Lumsden et al.,

2012). Little is known, however, about the social consequences of synchrony by unilateral entrainment.

1.3. The neural correlates of interpersonal synchrony

There is an extensive body of research on the underlying brain mechanisms for sensorimotor synchronization with an external stimulus. Briefly, brain areas known to be involved in movement timing, temporal prediction, error correction and internal modeling of sensorimotor dynamics (such as the basal ganglia, cerebellum, and prefrontal regions; e.g., Strick et al., 1993; Rao et al., 1997; Salman, 2002; Krause et al., 2010; Bijsterbosch et al., 2011; cf. also reviews by Rao et al., 1997; Lewis et al., 2004; Repp, 2005) are activated during synchrony. This brain network highlights the importance of temporary coordination with a predictable external event (the referent) during synchrony. For instance, Lewis et al. (2004) investigated the neural correlates of rhythmic movement complexity to investigate error monitoring and correction. Among the brain regions that varied with movement complexity during sensorimotor synchronization (but not during similar self-paced movements) were the premotor cortex (PMC), supplementary motor cortex (SMA), and right dorsolateral prefrontal cortex (cf. Rao et al., 1997).

The literature on the neural correlates of the perception and social consequences of interpersonal synchrony is smaller (Tognoli et al., 2007; Kelso et al., 2009; Konvalinka et al., 2010; Fairhurst et al., 2012). To date, the social consequences of behavioral interpersonal synchrony have been mostly documented following both the mimicry of discrete bodily movements (e.g., foot shaking, face touching; van Baaren, Holland, Steenaert, and van Knippenberg, 2003) and the synchronization of more continuous sequences of action (e.g.,

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postural movements, facial expressions, gestures; Bernieri, 1988; Cappella, 1997; for review cf. Miles et al., 2009). For instance, a meta-analysis of studies of a related social motor action imitation—indicates activation of parietal and frontal regions including the superior parietal lobule, inferior parietal lobule, and dorsal premotor cortex (Molenberghs et al., 2009). Guionnet et al. (2011) extended this work in an fMRI study of participants as they imitated or were imitated by another person. Results revealed activation in the primary sensorimotor cortex, premotor and supplementary motor areas, left inferior frontal gyrus, left IPL, and left insula, whether imitating or being imitated. In addition, activation was found in the dorsal anterior cingulate (dACC), pre-supplementary motor area (pre-SMA), and a rostral part of the dorsolateral prefrontal cortex (DLPFC) in all conditions except during instructed imitation. The contrast of imitating or being imitated revealed that being imitated by another person led to greater activation in the dACC, pre-SMA, and DLPFC, and the dorsal region of the left anterior insular cortex, whereas imitating led to greater activation in the visual cortex, medial frontal cortex, posterior cingulate gyrus, precuneus, bilateral IPL, para-hippocampus, and hippocampus than being imitated.

Many of these regions constitute the default mode network (DMN; Raichle et al., 2001; Fox et al., 2005), a network that is more active during self-referential, social, and affective processing (Raichle and Snyder, 2007; van Overwalle and Baetens, 2009). Fairhurst et al. (2012) performed an fMRI study of sensorimotor synchronization with a virtual partner using a finger-tapping paradigm in which the virtual partner varied in adaptivity, which also corresponded to differing degrees of coupling between the virtual partner and participant. Participants were instructed to synchronize with the virtual partner while also maintaining the initial tempo, thereby establishing the goals of maintaining the periodicity of the finger tapping

and minimizing the phase differences in the finger tapping task. Objective synchrony was operationalized in terms of phase relations, whereas the feeling of being synchronized was operationalized as (lower) perceived task difficulty. Regression analyses identified different networks whether the participants were objectively in synchrony with the virtual partner (positive correlation with increased midline activation of structures including the ventromedial prefrontal cortex, vmPFC; hippocampus, supplementary motor area, SMA; primary somatosensory cortex, S1 extending into primary motor cortex, M1; posterior cingulate; and precuneus) or subjective perception of synchrony (i.e., reduced task difficulty was correlated with greater activation of the right IFG, right anterior insula, posterior dmPFC, bilateral ventrolateral prefrontal cortex, superior frontal gyrus, and inferior parietal activity in the region of the temporo-parietal junction for perceived synchronization difficulty, and SMA, S1/M1, vmPFC and hippocampus; Fairhust et al., 2013).

Although this body of research is on the perception and social consequences of interpersonal synchrony (e.g., Tognoli et al., 2007; Kelso et al., 2009; Konvalinka et al., 2010; Fairhurst et al., 2012), these studies have focused primarily on the neural correlates of one's synchronizing their behavior with a referent. Little is known about the neural bases of interpersonal synchrony from the perspective of the referent. Thus, in the present study, we used fMRI to investigate how regional brain activity was modulated by differences in synchronous stimuli during a tapping-based interactive task compared to asynchronous stimuli with a synchronizer. Moreover, little is known about the neural regions that might be correlated with subjective perceptions of synchrony and corresponding feelings of affiliation between a referent and a synchronizer. Therefore, we also ran correlational analyses to explore this relationship (see Method section for details). To the best of our knowledge, this is the first empirical

investigation of the neural correlates of the participants' perception of interpersonal synchrony and their feelings of affiliation with a virtual co-acting partner when the participant is the referent (rather than the synchronizer).

2. General experimental procedures

2.1. Participants

All participants were native English speakers with normal or corrected-to-normal vision, and were not taking antidepressant medication. As ascertained by an anamnesis, none of the participants reported prior or current neurological or psychiatric disorders (e.g., traumatic brain injury with loss of consciousness, epilepsy, neurological impairment or degenerative neurological illness). All participants provided written informed consent to participate in the experiment, which was approved by the University of Chicago Health Sciences Institutional Review Board. All participants received monetary compensation for their participation.

2.2. General experimental task

The experimental task was presented to participants as a computer-mediated communication task that involved simple back-and-forth keyboard tapping between members of a dyad. Specifically, the task was described as an abstract simulation of cell-phone texting, where a beat (i.e., a single tap on the computer keyboard) replaced actual text—actions described as "*bexting*," short for beat-based texting (Figure 1).

Throughout the session, the message board at the top of the screen displayed various information and instructions about the task. Participants were informed that the circle labeled "I" was their own avatar, which would immediately pulse each time they would send a beat (i.e., pressed the keyboard once). The pulse was visually represented by a short animation of the

circle transforming into a square and then back into the circle. Participants were also told that the central server would pair them up with randomly selected fellow participant in the room, one of whom would be represented by an avatar labeled "A" or "B". It was emphasized to the participants that the specific avatar (i.e., "A" or "B") chosen to represent their partner on the screen was randomly determined after the partner was selected, thus bearing no relationship to the partner's true identity. Once the dyad was formed, participants' avatar and the partner's avatar entered the "*bexting*" zone represented by the rectangular box surrounding the two avatars (Figure 1).

The participant was told that their task was simply to generate a series of beats at a designated frequency (e.g., 1 beat/sec), regardless of their partner's beat frequency (i.e., unencumbered by any need to coordinate their beats with their partner's beats). Participants were also informed that the task of their partner was to respond to each one of their beats with another beat—with no time constraint to respond except that they had to send a beat back to each beat prior the occurrence of the referent's $n+1$ st beat. Although the participant served as the referent, no mention was made of this and no mention was made of synchrony. The two dyadic members bexted with each other for an extended period of time, called a bexting round (described below), which consisted of multiple equal-length trials separated by short breaks.

At the end of a bexting round, the participants reported their impression of their partner by answering a short questionnaire displayed on the message board. After completing the questionnaire, participants were led to believe that the server would form a new pairing between themselves and another randomly selected fellow participant and that a new bexting round would then ensue. This made it possible to manipulate partner synchrony using a within-subjects design, which is especially important if the paradigm is also to be used to investigate the neural

correlates of perceived interpersonal synchrony. Due to the presence of at least three other fellow participants, the use of cubicles, rubber keyboards to ensure key presses could not be heard, and the supposedly random pairing scheme implemented by the central server, it was impossible for the participants to map their ostensible partners to any particular individual in the room. As a result, the only reliable information about a given partner accessible to the participants was the timings of that partner's beat series. Objective synchronicity by definition is contingent on the alignment of timing per se, so this feature of the paradigm allowed us to examine whether timing information was sufficient to influence perceived synchrony and social affilition.

2.3. General manipulation of unilateral entrainment

The participant and their partner correspond, respectively, to the referent and synchronizer involved in unilateral entrainment. Unbeknownst to the participants, the "partner's" beat series were generated by a computer program, which made it possible to experimentally manipulate the degree to which the partner's beats were entrained to the referent's beats. More precisely, the partner's beat latency (i.e., the interval between the referent's beat and the partner's beat) was sampled from a uniform distribution with predetermined mean and range (described below). Because prior research has manipulated synchrony using latency ranges varying between 0 and 90 degrees, beat latencies in the present research were manipulated within the same range. By manipulating the means and range of the distribution of partner's response latency, different levels of synchrony could be produced. This feature ensured that the variation in synchrony was determined solely by the unilateral

entrainment on the part of the ostensible synchronizer rather than through mutual entrainment or orchestration.

3. Study I (Pilot study)

Because the present experimental tapping task differs from existing paradigms, we first conducted a pilot study to test whether the cover story for the tapping task was believable and whether the task instructions were easy for participants to understand.

3.1. Participants

Forty-seven community residents (19 women) participated in this pilot study. Participants ranged from 19 to 52 years of age $(M = 25.10, SD = 7.19)$. No participants were excluded from the analyses. Data collection started at a beginning of an academic quarter and stopped at the end of that academic quarter.

3.2. Experimental procedure

Participants were tested in groups of four in the same testing room. This procedure was used to ensure that participants did not know with whom they would be bexting during any given task period. Each participant was seated in a separate cubicle, which was equipped with one computer. Participants were free to adjust the position of their chairs to their utmost comfort level. Participants were told that all the four computers in the room were connected to a central server. Each bexting round consisted of six 12-second trials. The asynchrony (i.e., response latency) distributions of the partners were experimentally manipulated such that the interaction with one partner was more synchronous than the other. Specifically, the mean asynchrony and

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asynchrony range were 220 ms and ± 110 ms for the low-synchronous partner and 110 ms and ± 10 ms for the high-synchronous partner. The order in which participants bexted with a synchronous or asynchronous partner was counterbalanced across participants. The bexting program was coded in Adobe ActionScript 3 and ran through Adobe Flash Player.

Participants' instruction was the following: "Using the spacebar, tap at a slow rate (approximately 1 beat per 2 sec) [a moderate rate (approximatley 1 beat per sec)/ a fast rate (approximately 2 beats per second)]". In each experimental block, all three suggested tempos for beat generation appeared twice (thus six trials in total), with the order randomly determined. The variation of the suggested tempos was to investigate generalizability.

At the end of each tapping experimental block, participants answered six items concerning the degree of social affiliation they felt toward the ostensible partner in that tapping experimental block. Specifically, participants were to indicate on a seven-point scale anchored by 1 (*not at all*) and 7 (*very much*), (1) How much rapport they felt with the partner, (2) How much they trusted the partner, (3) How much they liked the partner, (4) How much they would like to work with the partner, (5) How much they would like to confide in the partner, and (6) how close they felt to the partner. These six items showed high internal consistency across both conditions (*α*s > .92) and were thus averaged to yield a *social affiliation* score*.*

Embedded among these affiliation items was a *perceived synchrony* item, which asked participants to indicate how synchronized they were with the partner on the same seven-point scale (How synchronized was the communication between you and Partner A?). The inclusion of this measure was motivated primarily by one main consideration. Although our experimental manipulation objectively created two levels of synchrony, it was unclear whether participants would subjectively map the difference in their experiences with the two partners on the

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dimension of synchronicity. Given the apparent non-rhythmic nature of the synchronizer's task, the participants might have parsed the partner's behaviors into a series of independent local events (i.e., whether the partner responded in time on a given trial) instead of integrating these local events across the temporal span of the tapping experimental block. Thus, the participants might not perceive the synchronizer as engaging in periodic movement and thereby might not construe their interaction in terms of synchronicity. JSC

3.3. Results

3.3.1. Participants' feedback about the task instruction

Results from this pilot study revealed that none of the participants reported being confused regarding the task instruction. Furthermore, none of the participants suspected that their partners were actually a computer program rather than two of their fellow participants.

3.3.2.Participants' behavioral performance

To determine whether the participants' performance was influenced by the experimental manipulation, their performance was subjected to a 2 (Partner's type: low synchrony or high synchrony) x 2 (Order) x 2 (Gender) x 3 (Tapping pace: 2/sec, 1/sec, .5/sec) mixed ANOVA. Neither the main effect of synchrony manipulation nor any of the interactive effects involving synchrony manipulation was significant. Of all the interactive effects, the one with the largest effect size was the interaction between synchrony manipulation and tapping pace $(F(2,86) = 1.72)$, $p = .02$, η^2 _{partial} = .04). As for the main effect of synchrony manipulation, we found no evidence of our manipulation influencing tap-to-tap variability $(F(1,46) = 0.24, p = .63, \eta^2_{\text{partial}} = .01)$.

3.3.3. Participants' perceived synchrony

The perceived synchrony scores were subjected to a 2 (Partner's type: low synchrony or high synchrony) x 2 (Order) x 2 (Gender) mixed ANOVA. No significant results involving gender, order or tapping were observed, so we collapsed across these factors. Results showed that participants rated their interaction with the high-synchronous partner as being more synchronized ($M = 5.91$, $SD = 1.47$) than their interaction with the low-synchronous (i.e., asynchronous) partner ($M = 5.13$, $SD = 1.81$; $F(1, 46) = 6.45$, $p = .02$, η^2 _{partial}= .03; Table 1).

3.3.4. Participants' social affiliation

The social affiliation scores were also subjected to a 2 (Partner type: low synchrony or high synchrony) x 2 (Order) x 2 (Gender) mixed ANOVA. No effects involving gender, order were found, so we collapsed across these factors. Results showed that participants felt greater social affiliation with the high-synchronous partner $(M = 4.91, SD = 1.59)$ than the lowsynchronous (asynchronous) partner ($M = 4.54$, $SD = 1.67$; $F(1, 46) = 4.32$, $p = .004$, η^2 partial = .02; Table 2).

3.4. Interim Conclusion

The results from this pilot study suggest that the tapping task is a viable paradigm for studying interpersonal synchrony achieved through unilateral entrainment. The cover story is believable and the instructions are easy to understand. The difference in perceived synchrony across the two conditions suggests that participants were influenced by interpersonal synchrony achieved through unilateral entrainment even though the participants played no role in the

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production of the synchrony¹ and the synchrony was unrelated to their task performance. We nevertheless found a significant effect on perceived synchrony and a stronger affiliative response toward the synchronous than asynchronous partner. This suggests the effects of interpersonal synchrony are not dependent on the synchrony being task-relevant or to the participant actually contributing to the observed synchrony. $56x$

4. Study II (Behavioral study)

4.1. Participants

Forty community residents (20 women) participated in this behavioral study. Participants ranged in age from 19 to 43 years ($M = 23.9$, $SD = 6.87$) and were tested in a similar setting as the pilot study. No participants were excluded in the analyses. Data collection stopped at the end of an academic quarter.

4.2. Experimental procedure

A similar procedure to that used in the pilot study (Study I) was used in Study II. Each participant played one tapping experimental block with each of four ostensible partners. Each experimental block consisted of eight 12-second trials followed by the series of questions on perceived synchrony and affiliation. The suggested tapping tempo for the referent (i.e., the participant) was kept the same throughout the experimental session at one beat per second. The asynchronies of the four ostensible partners were sampled respectively from four uniform distributions with unique mean-range combinations obtained by crossing two levels of asynchrony mean (120 ms versus 220 ms) with two levels of response latency ranges $(\pm 10 \text{ ms})$

. The computer algorithm used to manipulate the degree of synchrony ensured that the experimental manipulation of synchrony was orthogonal to the participant's beat series.

versus ± 110 ms). The order in which participants bexted with the four partners was manipulated using a Latin Square design, yielding 10 different orders. As in the pilot study, the six items measuring social affiliation exhibited a high level of internal consistency across all four conditions (α s > .97) and hence were combined. CRAN

4.3. Results

4.3.1. Participants' behavioral performance

A 2 (Mean response latency: 120 ms or 220 ms) x 2 (Response latency range: ±10 ms or ± 110 ms) x 2 (Gender) ANOVA was performed to determine whether the participant's (i.e., referent's) responses were influenced by their partner's behavior. No significant differences involving gender were observed, so we collapsed across this factor. The ANOVA revealed no significant interaction ($F(1,39) = 0.002$, $p = .97$, η^2 _{partial} = 0), and no main effect for mean response latency $(F(1,39) = 0.006, p = .94, \eta^2_{partial} = 0)$. The response latency range manipulation, however, did affect the referents' tap-to-tap variability. Specifically, participants' tap-to-tap variability was smaller when interacting with narrow-ranges partners $(+)$ 10 ms) than with broad-range partners $(+ 110 \text{ ms})$ ($Ms = 14.29 \text{ ms}$ and 82.34 ms, respectively; $F(1,39)$) $=162.1, p < .001, \eta^2$ partial = .81).

4.3.2. Participants' perceived synchrony

The perceived synchrony ratings were subjected to a 2 (Mean response latency: 120 ms or 220 ms) x 2 (Response latency range: ± 10 ms or ± 110 ms) x 2 (Gender) ANOVA. No significant differences involving gender were observed, so we collapsed across this factor. Results indicated that both main effects were significant. Partners who responded with short

(120 ms) mean lags were rated as being more synchronized $(M = 5.10)$ than partners who responded with long (220 ms) mean lags ($M = 4.59$; $F(1, 39) = 3.79$, $p = .06$, η^2 _{partial} = .09; Table 3), and partners with narrow $(± 10 \text{ ms})$ ranges were rated as being more synchronized than partners with broad (\pm 110 ms) ranges (*M*s = 5.20 and 4.59, respectively; *F*(1, 39) = 8.21, *p* = .007, η^2 partial = .17; Table 3). The two-way interaction was not significant *(F*(1, 39) = 0.02, *p* = .88, η^2 partial = .01). $\mathcal{S}^{\mathbf{C}}$

4.3.3. Participants' social affiliation

The social affiliation scores were subject to a 2 (Mean response latency: 120 ms or 220 ms) x 2 (Response latency range: ± 10 ms or ± 110 ms) x 2 (Gender) ANOVA. No tests involving gender were significant, so we also collapsed across this factor. The main effects for both aspects of partner's timing were significant: The participants expressed more social affiliation with the partners characterized by mean response latencies of 120 ms rather than 220 ms (*Ms* = 4.53 and 4.06, respectively; $F(1, 39) = 5.02$, $p = .03$, η^2 _{partial} = .10; Table 4), and with partners characterized by 10 ms than 110 ms response latency ranges (*M*s = 4.61 and 3.98, respectively; $F(1, 39) = 9.54$, $p = .01$, η^2 _{partial} = .20; Table 4). The two-way interaction did not reach significance $(F(1, 39) = 0.65, p = .42, \eta^2$ partial = .02).

4.4. Interim Conclusion

Participants serving as referents in the current study perceived partners as more synchronous when they showed relatively short response latencies (i.e., relatively small phase shifts) and when the variability of these response latencies was relatively small. Furthermore, and as in the pilot study, the mean response latency manipulation of interpersonal synchrony did

not influence the referents' tap-to-tap variability. Although the range (variability) of response latencies did affect the referents' tap-to-tap variability, the participants' tapping responses were not correlated with the perceived synchrony $(r(40) = -0.22, p = .17)$ or affiliative responses toward the partner $(r(40) = -0.25, p = .12)$, suggesting that the social affiliation effect cannot be explained by the effect of the experimental manipulation on the referents' tapping behavior. These findings are generally consistent with prior research (Miles et al., 2009) in which observers perceived higher levels of rapport between members of a dyad when the mean temporal difference between their strides while they were walking decreased.

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5. Study III (Neuroimaging study)

5.1. Participants

A total of 16 volunteers (7 women) were recruited via e-mail and subsequently screened and qualified with a follow-up telephone interview. All participants were right-handed, ranging from 19–25 years old ($M = 21.44$, $SD = 1.63$), and were healthy with no medical history of neurological, psychiatric or psychological disorders as ascertained by an anamnesis. Data from three volunteers out of the 16 could not be included in the analyses because the volunteers did not complete entirely the task as they were too slow and took too long during the instruction periods in between bexting rounds. The design was self-paced, and those subjects appeared to have trouble with the task and did not complete it before the set scanning time was complete (the scanner had a finite period in which it could run for each scan). The final fMRI results, thus, include 13 subjects.

5.2. Experimental procedure

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A similar procedure to the one described in the above behavioral study was used in this neuroimaging study. The main difference was that stimuli were presented while the participants were lying down in the scanner. Visual stimuli were projected from a PC located in the experimenter room to a back projection screen located in the scanner room. Stimuli were viewed using binocular goggles mounted on the head coil approximately 2 inches above the participants' eyes.

The entire task consisted of five blocks. Four of the experimental blocks involved the participant tapping at 1 Hz with an ostensible partner, and one block involved the participant tapping at 1 Hz with no partner (self-pacing). This latter block was included in order to evaluate participants' motor movements per se. Each experimental block consisted of eight 12-second trials. The order of the experimental conditions was varied across participants using a Latin Square design. Button-press responses were made with the index finger on an fMRI-compatible response box. As in the behavioral studies, a tap of the button during an experimental block caused the "I" avatar to pulse momentarily from a circle to a square, and the partner's response beat was depicted likewise.

After each one of the four experimental tapping blocks, the participants were also asked to answer the series of questions on perceived synchrony and affiliation with their ostensible partner. As in the previous two behavioral studies described above, these seven questions included one question about perceived synchronization and six questions about affiliation with their partner. Answers to the other six questions were again averaged into one composite index of interpersonal affiliation because of the high Cronbach alpha (> .8). Answers were navigated using the middle finger (moving to the left, selecting lower values) and ring finger (moving to the right, selecting higher values), and the answer selection was done using the index finger.

Before performing the actual behavioral experimental task, the participants and confederates (research assistants who did not participate in the study) performed a practice block in which they were asked to interact with a computer (rather than with a human). In contrast to the actual experimental task, the computer's response during practice lacked variability and had a constant inter-beat interval of 100 ms. This was intended to not only allow participants to familiarize themselves with the task, but also to enhance their perception that the beats they would then see during the experimental task were actually generated by a human partner. Following the practice block, the participant was prepared for fMRI scanning, where they performed the experimental task. A

5.3. Magnetic resonance imaging recordings

Imaging was performed on a 3-T Philips Achieva Quasar Dual 16 Ch scanner with quadrature head coil used for spin excitation and signal reception. High-resolution volumetric T1-weighted spoiled gradient-recalled (SPGR) images were obtained for each participant in one hundred eighty-one 1.0-mm sagittal slices with 8° flip angle and 24 cm field of view (FOV) for use as anatomical images. Functional images were acquired using an echo-planar acquisition with Z-Shimming with 32×4 -mm coronal slices with an inter-slice gap of 0.5 mm spanning the whole brain (TR = 2 sec, TE = 30 ms, flip angle = 80° , FOV = 22 cm, 64 x 64 matrix size, fat suppressed).

5.4. Functional image processing and analyses

Image pre-processing and analyses were performed using Analysis of Functional NeuroImages software (AFNI version AFNI_2011_12_21_1014, Medical College of

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Wisconsin). For each subject, motion detection and correction were undertaken using a sixparameter, rigid-body transformation. Functional images were co-registered and spatially smoothed using a 5-mm full width at half maximum Gaussian filter. Individual-subject analyses were conducted using the general linear model to generate estimates of blood oxygenation leveldependent (BOLD) signal on a voxelwise basis (Ward, 2002). Stimulus timing vectors for each of the four experimental conditions were convolved with a gamma-variate waveform using the AFNI program Waver, and the resulting model was fit voxelwise to preprocessed time-series data with a linear least-squares model using the AFNI program 3dDeconvolve, generating a map consisting of beta coefficients (fit values) at each voxel for each modeled condition--short lag / synchronous variance; long lag / synchronous variance; short lag / asynchronous variance; and long lag / asynchronous variance --as well as a baseline coefficient. Output from the deconvolution analysis for each subject was scaled voxelwise to percent signal change from baseline, and each subject's data were spatially transformed to Talairach and Tournoux (1988) stereotaxic coordinate space and interpolated to 3 mm^3 isometric voxels for group analysis.

Our fMRI analysis aimed to identify how regional brain activity was modulated by differences in synchronous stimuli during a tapping-based interactive task compared to asynchronous stimuli with a synchronizer. To this purpose, we first identified the brain regions sensitive to differences in synchrony and asynchrony using a voxelwise 2 (task/response period) x 2 (small/large range) x 2 (small/large lag) factorial ANOVA. Then, to assess the relationship of these regions to corresponding perceptions of synchrony and feelings of social affiliation, we correlated BOLD activity in each identified cluster with each respective behavioral measure. The self-pacing blocks were modeled in the fMRI GLM and were not treated as residuals. In

terms of our contrasts, they were treated as regressors of non-interest. The cluster threshold was at $p < .01$ corrected to alpha $< .05$.

Finally, because little is also known about the overall network of neural regions that might be correlated with subjective perceptions of synchrony and corresponding feelings of social affiliation between a referent and a synchronizer, we ran voxelwise correlation analyses in the same respect. To further elucidate what was driving voxelwise correlation effects, BOLD activity within voxelwise correlation regions was assessed according to a median split of behavioral measures. Voxelwise fMRI analyses were performed at the group level, the results of which were corrected for multiple comparisons using a Monte Carlo simulation to determine minimum cluster sizes corresponding to an alpha value of .05 for voxelwise threshold of $p < .01$ (729 µl) for the ANOVA analysis (Nichols, 2012). An additional corrected voxelwise threshold of $p < .025$ (1080 µl), was also used for the BOLD:behavior analysis, as $p < .01$ yielded no results for BOLD:Affiliation and limited results for BOLD:Synchrony.

Difference scores (Synchrony minus Asynchrony) of BOLD signal and the corresponding behavioral data were also calculated for each subject, and these values were entered into a grouplevel, whole-brain voxelwise Pearson correlation to identify regions in which differential BOLD activity in response to the stimulus conditions was associated with the same contrast patterns in the behavioral responses.

5.5. Results

5.5.1. Behavioral results

The participants' ratings of perceived synchrony and affiliative responses were subjected to a 2 (Mean response latency: 120 ms or 220 ms) x 2 (Response latency range: ± 10 ms or ± 110

ms) x 2 (Gender) ANOVA. A gender effect was observed in this sample for ratings of perceived synchrony ($M_{\text{male}} = 5.25$, $M_{\text{female}} = 3.50$, $F(1,11) = 7.08$, $p = .02$, $p2 = .39$), and a marginal effect was observed for ratings of social affiliation ($M_{\text{male}} = 4.98$, $M_{\text{female}} = 3.59$, $F(1,11) = 4.40$, $p =$.06, η 2 = .29). However, neither gender effects showed a significant interaction with mean response latency or latency range, so we collapsed across the gender factor. Analyses revealed that participants perceived greater interpersonal synchrony $(M_{+/10ms} = 5.19, M_{+/110ms} = 3.42,$ *F*(1,12) =13.45, *p* = .004, η 2 = .40) and greater social affiliation ($M_{+/10ms}$ = 4.74, $M_{+/110ms}$ = 3.72, $F(1,12) = 7.46$, $p = .02$, $p2 = .16$) when the response latency range was small than large. No other tests approached statistical significance. No behavioral interaction effects were statistically significant for measures of perceived synchrony (Gender x Mean response latency: $F(1,11) =$.011, $p = .92$, $\eta^2 = .0001$; Gender x Response latency range, $F(1,11) = 4.04$, $p = .07$, $\eta^2 = .05$; Mean response latency x Var: $F(1,11) = 2.07$, $p = .18$, $\eta^2 = .01$; Gender x Mean response latency x Response latency range: $F(1,11) = 1.15$, $p = .31$, $\eta^2 = .007$) or for feelings of social affiliation. No behavioral interaction effects were statistically significant for measures of perceived synchrony (Gender x Mean response latency: $F(1,11) = 3.17$, $p = .10$, $\eta^2 = .011$; Gender x Response latency range: $F(1,11) = 2.99$, $p = .11$, $\eta^2 = .04$; Mean response latency x Response latency range: $F(1,11) = .43$, $p = .52$, $\eta^2 = .002$; Gender x Mean response latency x Response latency range: $F(1,11) = .06$, $p = .81$, $\eta^2 = .0002$).

5.5.2. Functional neuroimaging results

Synchrony vs. Asynchrony contrast

Based on the above results we collapsed across the Mean Response Latency factor to investigate the neural effects of variations in a partner's perceived synchrony with one's

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responding. Figure 2 and Table 5 display the main effects for Response Latency Range during the experimental tapping task. The synchrony minus asynchrony contrast revealed a significant main effect of synchrony, which was characterized by a greater response in three brain regions: i) left inferior parietal lobule (IPL) extending to the angular gyrus, portions of the left ii) parahippocampal gyrus extending to the amygdala and iii) the ventro-medial prefrontal cortex (vMPFC) and anterior cingulate cortex (ACC; Table 5). No significant results were found for which asynchronous stimuli elicited a larger BOLD response than synchronous stimuli.

Correlation analyses

Correlational analyses were first performed between the participants' ratings and each of the three areas depicted in Figure 2. The BOLD differential synchrony scores (dBOLD for synchrony minus asynchrony) in the vmPFC was the only region to be significantly correlated with the comparable difference in the ratings of perceived synchrony, $t(11) = 2.84$; $p = 0.016$; *R* $= 0.65$, and feelings of social affiliation, $t(11) = 2.44$, $p = 0.03$; $R = 0.59$; Figure 3).

Next, whole-brain voxelwise correlation analyses were performed between the dBOLD and the corresponding differences between conditions in perceived synchrony. Results revealed a positive correlation in the right cerebellar tonsil, and negative correlations in the right anterior prefrontal cortex/lateral prefrontal cortex (BA 46), left dMPFC, right lingual gyrus and right middle occipital gyrus (Figure 4 A & B; Table 6). To better understand this effect, we calculated a median split of our groups based on the rating difference and then analyzed the percent signal change of the synchronous and asynchronous conditions separately for the two groups (see Figure 4C).

Similar negative correlations were observed for the feelings of affiliation in the right lingual gyrus, and right inferior parietal lobule (Figure 5A $\&$ B, Table 7). We again calculated a median split and analyzed the percent signal change of the synchronous and asynchronous conditions separately for the two groups (Figure 5C).

6. Discussion

In the present series of three studies, we first sought to experimentally investigate an individual's *social perceptions of* a partner who responds in a more or less synchronous fashion in a unilateral entrainment paradigm. Behavioral results across all three studies revealed that synchrony by the partner enhanced a participant's ratings of perceived interpersonal synchrony of and social affiliation with the partner. Specifically, the participants felt greater synchrony toward a synchronous partner than with an asynchronous partner. These results indicate that neither the perception of interpersonal synchrony nor the affiliative consequences of synchrony are contingent on an individual's behavioral intentions or explicit goal to synchronize. In all three studies, referent participants felt more social affiliation with partners who responded synchronously rather than asynchronously, even though all partners (actually, a programmed series of responses) performed the assigned experimental task equally well.

The current findings suggest that interpersonal synchrony achieved through unilateral entrainment may produce the same array of social consequences as has been found previously in studies using orchestration or reciprocal synchrony paradigms (cf. Bernieri, 1988, Tickle-Dengen and Rosenthal, 1990; Hatfield et al., 1993; Bernieri et al., 1994, Cappella, 1997; Lakin and Chartrand, 2003; Hove and Risen, 2009; Miles et al., 2009, 2010, 2011; Paladino et al., 2010; Vacharkulksemsuk and Fredrickson, 2012) or in studies using mimicry (e.g., van Baaren,

Holland, Steenaert, and van Knippenberg, 2003; Maddux, Mullen, and Galinsky, 2008; van Baaren, Janssen, Chartrand and Dijksterhuis, 2009; Stel et al., 2010; Muller, Maaskant, van Baaren, and Dijsterhuis, 2012). One possible interpretation for such social consequences may rely on the automatic (or nonconscious) human tendency to act in synchrony with others even when they are not aware of it. Like mimicry, interpersonal synchrony increases the social connection felt between individuals through an automatic process of "mimicry" that is described in the literature as a "by-product in interaction" (e.g., Chartrand and Bargh, 1999; van Baaren et al., 2009). This process is in line with a large body of evidence suggesting that the affiliative effects are not dependent on an individual's awareness of the interpersonal synchrony (e.g., see review by Hatfield et al., 1994; Cacioppo and Cacioppo, 2012). Another possible interpretation, which is related to the latter, is an interaction between feelings of liking and the activation of shared motor representations between the self and the other in several tasks, as it has been reported in interpersonal somatic mimicry (Sonnby-Borgström, 2002; Marzoli et al., 2011). Although interpersonal synchrony refers to the coordination of movement that occurs between individuals and interpersonal mimicry refers to the similarity in form of the actions between individuals, they both feature similarities in the temporal alignment of the actions and in their social consequences (Semin and Cacioppo, 2009; Cacioppo and Cacioppo, 2012). As illustrated by the social cognition model (from Semin and Cacioppo, 2009), synchronization and mimicry are "time-locked to the observed stimulus." Like mimicry, interpersonal synchrony also increases the social connection felt between individuals.

Our fMRI results extend these behavioral results by revealing the recruitment of brain areas involved in social cognition, embodied cognition, self—other information processing, and action observation as correlates of interpersonal synchrony (vs. asynchrony). More precisely, the

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synchrony minus asynchrony contrast revealed greater response in three brain regions: i) left IPL (BA 40) extending to the angular gyrus, ii) portions of the left parahippocampal gyrus (BA 38) extending to the amygdala; and iii) the ventro-medial prefrontal cortex (vmPFC; BA 32) extending to the anterior cingulate cortex. No significant results were found for which asynchronous stimuli elicited a larger BOLD response than synchronous stimuli.

The recruitment of BA 40 is consistent with previous studies showing the recruitment of this brain region while participants integrate visuo-motor information during observation and evaluation of actions (Grafton et al., 1996; Rizzolatti and Craighero, 2004; Desmurget et al., 2009; Grafton, 2009; Ortigue et al., 2009, 2010) and perception of elementary mechanical causality events (Blakemore et al., 2001). This action observation brain system is also known to sustain embodied cognitive mechanisms, meta-representation of the bodily self, detection of movements of others, self–other expansion, monitoring of others' intentions, perspective taking, and perception of a synchrony between visual and proprioceptive feedbacks, as well as observed and imagined actions (e.g., inferior parietal lobule; Grafton et al., 1996; Shimada et al., 2005; Rizzolatti and Sinigaglia, 2007; Ortigue et al., 2009; van Overwalle and Baetens, 2009; Fairhust et al., 2013). The recruitment of this brain network is in line with theories of embodied cognition and simulation, which suggest that people may understand actions of others, without any inferential reasoning, through a direct matching process that occurs via an automatic mapping between observed and performed actions, and via the reactivation of the bodily states that were originally active during past self-related experiences (Grafton, 2009; Niedenthal, 2007; Niedenthal, et al., 2005; Rizzolatti and Craighero, 2004; Rizzolatti, et al., 2001). Although embodied mechanisms are not a pre-requisite to act, connect or understand others, embodied behaviors offer new ways to investigate social perception, cognition, and behavior (e.g., Semin

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and Smith, 2002; Semin and Cacioppo, 2009; Cacioppo and Cacioppo, 2012). In line with Aron and Aron's (1986) self-expansion model which posits that others toward whom one feels a close social bond can be incorporated into the representation of one's self, and the relational model of communal sharing and cognitive interdependence (see Fiske, 2004; Smith, 2007; IJzerman and Semin, 2010; [Cacioppo and Cacioppo, 2012).

Differences in activation were also found in the parahippocampal area— a region shown previously to be involved in temporal discrimination and interval comparison (Harrington et al., 2002), and learning of adaptive events (Fairhust et al., 2013; Grossberg, 2013). These findings are in line with adaptive resonance theory, a cognitive and neural theory of how the brain automatically learns to identify, categorize, and predict events in a changing world (Grossberg, 2013).

Finally, several investigators have found the ventral part of the medial PFC is relatively activated when processing information about the self or similar others, whereas the dorsal part of the medial PFC is relatively activated when processing information about others (Mitchell et al., 2005; Amodio and Frith, 2006; Keysers and Gazzola, 2007; Epley et al., 2009). Consistent with synchrony increasing the perception of similarity, Fairhust et al. (2013) found greater activity in the vmPFC region when participants were in relative synchrony with a virtual partner. We also found greater activity in the vmPFC in the synchronous than asynchronous condition, and correlational analyses further revealed that the greater the difference in the BOLD signal in the vmPFC between the synchronous and asynchronous conditions, the greater the corresponding difference in the ratings of perceived synchrony and affiliation.

Correlational analyses involving the dmPFC showed the opposite pattern, as might be expected if interpersonal synchrony increases self—other overlap or egocentric information

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processing about the partner. To further investigate this result, a median split was performed to create two groups of participants, those who rated the synchronous partner as much more synchronous than they rated the asynchronous partner, and those who rated the synchronous and asynchronous partner relatively similarly on perceived synchrony. Analyses of the dmPFC showed the lowest levels of activation when the participants who most distinguished between the conditions were performing with a synchronous partner and the highest levels of activation when the participants who distinguished most between the conditions were performing with an asynchronous partner. This pattern was reversed and weaker in participants who perceived relatively little difference in synchrony between their synchronous and asynchronous partners.

In sum, the analyses of the mPFC regions suggest that the participants, who most distinguished between the synchronous and asynchronous partners, thought about the synchronous partner as being more similar to themselves and thought about the asynchronous partner as being more dissimilar to themselves, than the participants who less distinguished between the synchronous and asynchronous partners. When a synchronous, relative to an asynchronous, partner is assimilated to the self, it is the asynchronous partner who requires the most attention and mentalizing to understand and predict. In contrast, for participants who show relatively little difference in the perceived synchrony of the synchronous and the asynchronous partners (and who show little difference in the activation of the vmPFC region; see Figure 3), it is the (synchronous) partner whose temporal behavior is reflective of the participant's behavior but is not rated as being synchronous who may evoke greater attention and mentalizing to understand and predict. Consistent with this reasoning, the correlational analyses between the BOLD differential synchrony scores (dBOLD: synchrony minus asynchrony) and reported feelings of perceived synchrony revealed negative correlations for the right lateral prefrontal

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cortex (BA 46), the right lingual gyrus (BA18/19), and the right middle occipital gyrus (BA 19; see Figure 4). The former is involved in control-related processes (Hare et al., 2009), the lingual gyrus has been involved in third-person perspective-taking (Jackson et al., 2006), and the middle occipital gyrus has been involved in visual attention and discrimination (Tu et al., 2013). Exploratory analyses based on median splits further indicated the lowest levels of activation when the participants whose ratings of perceived synchrony most distinguished between the conditions were performing with a synchronous partner and the highest levels of activation when these participants were performing with an asynchronous partner, whereas this pattern was reversed in participants who reported relatively little difference in perceived synchrony between their synchronous and asynchronous partners. In short, for participants who perceive large differences between their synchronous and asynchronous partners and show evidence of relative vmPFC activation and self-other overlap with the synchronous partner, it is the asynchronous partner who activates brain regions involved in attention, visual discrimination, and cognitive control, whereas for participants who see relatively little difference between these partners in terms of perceived synchrony and show little difference in vmPFC activation and little self-other overlap with the synchronous partner, it is the synchronous partner who activates these regions more than the asynchronous partner.

For the participants who show relatively large differences in perceived synchrony across conditions (and relatively large differences in vmPFC activity), the assimilation of the synchronous (in contrast to the asynchronous) partner to the self should result in the application of an abstract trait representation of the self to the synchronous partner, thereby diminishing the need for continued attention and mentalizing. For the participants who show relatively little difference in perceived synchrony across conditions (and relatively small differences in vmPFC

activity), both the synchronous and the asynchronous partner may be regarded as dissimilar others; as such, the temporal aspects of the asynchronous partner's behavior would be congruent with the abstract trait inference that this partner is dissimilar (e.g., outgroup homogeneity) and may therefore elicit little additional attention or mentalizing, whereas the temporal aspects of the synchronous partner's behavior would be more reminiscent of the self and therefore may require additional processing. Although speculative, the correlational analyses revealed a positive correlation in the right cerebellar tonsil, a region involved in trait abstraction particularly based on others' nonverbal behavior (van Overwalle et al., 2014). The median split analyses of activation in the cerebellar tonsil region were entirely consistent with high-level abstractions being formed (and attention, cognitive control, and mentalizing being truncated) for synchronous partners in the former group of participants and for asynchronous partners in the latter group of participants.

Finally, whole brain correlational analyses based on differences in reported feelings of affiliation for synchronous versus asynchronous partners, two regions emerged: the right lingual gyrus (BA 19) and in the inferior parietal/supramarginal gyrus (BA 40; see Figure 5). As noted above, the right lingual gyrus is involved in third person perspective taking, and the inferior parietal/supramarginal gyrus is involved in sensorimotor mirroring. These results suggest that for participants who perceive the synchronous partner as relatively more likable than the asynchronous partner, regions associated with third-person perspective-taking and mirroring are more active when the partner's behavior is asynchronous than synchronous. In contrast, for participants who perceive the synchronous and asynchronous partners as being more equivalent in likability, these regions are more active when the partner's behavior is synchronous rather than asynchronous.

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Limitations of the current study include the exploratory nature of the correlational analyses and the relatively small sample size of the fMRI study in contrast to the behavioral studies. Among the strengths of the current paradigm is the experimental control that it affords. For instance, rather than relying on natural variations in synchrony between two participants, the current paradigm permits the temporal parameters used to experimentally manipulate interpersonal synchrony to be standardized and precisely controlled using computer programs. Second, the task does not require face-to-face interactions, so characteristics of the ostensible partner (e.g., age, gender, attractiveness, group identity) that may prove to be moderator variables can be experimentally controlled. Third, participants can be an actor (e.g., trials on which participants bext with a partner) or an observer (e.g., trials on which they watch two partners bext), making it possible to examine the observational effects of interpersonal synchrony. Finally, the task involves minimal movement (finger tapping) so that the bexting paradigm can be used in neuroimaging studies.

References

Amodio DM, Frith CD (2006). Meeting of minds: The medial frontal cortex and social cognition*.* Nature Reviews Neuroscience 7: 268-277.

Bernieri FJ (1988). Coordinated movement and rapport in teacher-student interactions. Journal of Nonverbal Behavior 12(2): 120-138.

Bernieri FJ, Davis JM, Rosenthal R, Raymond Knee C (1994). Interactional synchrony and rapport: Measuring synchrony in displays devoid of sound and facial affect. Personality and Social Psychology Bulletin 20(3): 303-311. doi: 10.1177/0146167294203008.

Bijsterbosch JD, Lee KH, Hunter MD, Tsoi DT, Lankappa S, Wilkinson ID, Barker AT,

Woodruff PW (2011). The role of the cerebellum in sub-and supraliminal error correction during sensorimotor synchronization: evidence from fMRI and TMS. Journal of Cognitive Neuroscience, 23(5): 1100-1112.

Blakemore SJ, Fonlupt P, Pachot-Clouard M, Darmon C, Boyer P, Meltzoff AN, Segebarth C, Decety J (2001). How the brain perceives causality: an event-related fMRI study. Neuroreport 12(17): 3741-3746.

Brown EC, Brüne M (2012). Evolution of social predictive brains? Frontiers in psychology 3: 1- 2.

Cacioppo JT, Cacioppo S (2012). Decoding the invisible forces of social connections. Frontiers in Integrative Neuroscience, 6: 51.

- Cappella JN (1997). Behavioral and judged coordination in adult informal social interactions: Vocal and kinesic indicators. Journal of Personality and Social Psychology 72(1): 119.
- Chartrand TL, Bargh JA (1999). The chameleon effect: The perception-behavior link and social interaction. Journal of Personality and Social Psychology, 76(6): 893.
- Delaherche E, Chetouani M, Mahdaoui A, Saint-Georges C, Viaux S, Cohen D (2012). Interpersonal Synchrony : A Survey Of Evaluation Methods Across Disciplines. IEEE Transactions on Affective Computing. 3(3): 349 - 365.

Desmurget M, Reilly KT Richard N, Szathmari A, Mottolese C, Sirigu A (2009). Movement intention after parietal cortex stimulation in humans. Science 324(5928): 811-813.

Ehrenreich B (2006). *Dancing in the streets: A history of collective joy*. New York, NY: Metropolitan.

Engström DA, Kelso JAS, Holroyd T (1996). Reaction–anticipation transitions in human perception–action patterns. Human Movement Science 15: 809–832.

Epley N, Converse BA, Delbosc A, Monteleone GG, Cacioppo JT (2009). Believers' estimates of God's beliefs are more egocentric than estimates of other people's beliefs. Proceedings of the National Academy of Sciences, 106(51): 21533-21538.

Fairhurst MT, Janata P, Keller PE (2013). Being and Feeling in Sync with an Adaptive Virtual Partner: Brain Mechanisms Underlying Dynamic Cooperativity. Cerebral Cortex 23(11): 2592-2600. doi: 10.1093/cercor/bhs243

- Fox MD, Snyder AZ, Vincent JL, Corbetta M, Van Essen DC, Raichle ME (2005). The human brain is intrinsically organized into dynamic, anticorrelated functional networks. Proc Natl Acad Sci U S A 102: 9673-9678.
- Grafton ST (2009). Embodied cognition and the simulation of action to understand others. Annals of the New York Academy of Sciences 1156(1): 97-117.
- Grafton ST, Arbib MA, Fadiga L, Rizzolatti, G (1996). Localization of grasp representations in humans by positron emission tomography. Experimental Brain Research 112(1): 103-111.
- Grossberg S (2013). Adaptive resonance theory: How a brain learns to consciously attend, learn, and recognize a changing world. Neural Network 37: 1-47.
- Guionnet S, Nadel J, Bertasi E, Sperduti M, Delaveau P, Fossati P (2011). Reciprocal imitation: Toward a neural basis of social interaction. Cerebral Cortex 22(40): 971-978.

Haidt J. (2012). The righteous mind: Why good people are divided by politics and religion. New York, NY: Random House, Inc.

Haidt J, Seder P, Kesebir S (2008). Hive psychology, happiness, and public policy. Journal of Legal Studies, 37, S133–S156.

Hatfield E, Cacioppo JT, Rapson RL (1994). Emotional contagion. Current Directions in

Psychological Science, 2, 96-99.

- Hare TA, Camerer CF, Rangel A (2009). Self-control in decision-making involves modulation of the vmPFC valuation system. Science 324(5927): 646-648.
- Harrington DL, Boyd LA, Mayer AR, Sheltraw DM, Lee RR (2002). Formulating representations of time: an event-related fMRI study. In Neural Information Processing, 2002. ICONIP'02. Proceedings of the 9th International Conference on (Vol. 1, pp. 423- 427). IEEE.

Hove MJ, Risen JL (2009). It's all in the timing: Interpersonal synchrony increases affiliation. Social Cognition 27(6): 949-960.

IJzerman H, Semin GR (2010). Temperature perceptions as a ground for

social proximity. Journal of Experimental Social Psychology 46: 867-873.

- Jackson PL, Meltzoff AN, Decety J (2006). Neural circuits involved in imitation and perspective-taking. NeuroImage 31(1): 429-439.
- Jones SM, Wirtz JG (2007). "Sad monkey see, monkey do": Nonverbal matching in emotional support encounters. Communication Studies, 58, 71–86.
- Kelso JA (1984). Phase transitions and critical behavior in human bimanual coordination. American Journal of Physiology-Regulatory, Integrative and Comparative Physiology 246(6): R1000-R1004.

Kelso JAS, De Guzman GC, Reveley C, Tognoli, E (2009). Virtual partner interaction (VPI): exploring novel behaviors via coordination dynamics. PloS One 4(6): e5749.

Keysers C, Gazzola V (2007). Integrating simulation and theory of mind: from self to social cognition. Trends in Cognitive Sciences 11(5): 194-196.

Konvalinka I, Vuust P, Roepstorff A, Frith CD (2010). Follow you, follow me: continuous

mutual prediction and adaptation in joint tapping. The Quarterly Journal of Experimental Psychology 63(11): 2220-2230.

- Krause V, Pollok B, Schnitzler A (2010). Perception in action: The impact of sensory information on sensorimotor synchronization in musicians and non-musicians. Acta Psychologica 133(1): 28-37.
- Lakin JL, Chartrand TL (2003). Using nonconscious behavioral mimicry to create affiliation and rapport. Psychological Science 14(4): 334-339.

Lewis PA, Wing AM, Pope PA, Praamstra P, Miall RC (2004). Brain activity correlates differentially with increasing temporal complexity of rhythms during initialisation, synchronisation, and continuation phases of paced finger tapping. Neuropsychologia 42(10): 1301-1312.

- Lumsden J, Miles LK, Macrae CN (2012). Perceptions of synchrony: Different strokes for different folks? Perception 41: 1529-1531.
- Maddux WW, Mullen E, Galinsky AD (2008). Chameleons bake bigger pies and take bigger pieces: Strategic behavioral mimicry facilitates negotiation outcomes. Journal of Experimental Social Psychology, 44(2): 461-468.
- Macrae CN, Duffy OK, Miles LK, Lawrence J (2008). A case of hand waving: Action synchrony and person perception. Cognition 109(1): 152-156.

Marsh KL, Richardson MJ, Schmidt RC (2009). Social connection through joint action and interpersonal coordination. Topics in Cognitive Science 1(2): 320-339.

Marzoli D, Palumbo R, Di Domenico A, Penolazzi B, Garganese P, Tommasi L (2011). The relation between self-reported empathy and motor identification with imagined agents. PloS One, 6(1): e14595.

- McNeill WH (1995). Keeping together in time: Dance and drill in human history. Cambridge, MA: Harvard University Press.
- Miles LK, Nind LK, Macrae CN (2009). The rhythm of rapport: Interpersonal synchrony and social perception. Journal of Experimental Social Psychology 45(3): 585-589.
- Miles LK, Nind LK, Henderson Z, Macrae CN (2010). Moving memories: Behavioral synchrony and memory for self and others. Journal of Experimental Social Psychology 46(2): 457- 460.
- Miles LK, Lumsden J, Richardson MJ, Macrae CN (2011). Do birds of a feather move together? Group membership and behavioral synchrony. Experimental Brain Research 211: 1-9.
- Mitchell JP, Banaji MR, Macrae CN (2005). The link between social cognition and self-referential thought in the medial prefrontal cortex. Journal of Cognitive Neuroscience 17:1306–1315.
- Molenberghs P, Cunnington R, Mattingley JB (2009). Is the mirror neuron system involved in imitation? A short review and meta-analysis. Neuroscience & Biobehavioral Reviews 33(7): 975-980.
- Müller BC, Maaskant AJ, van Baaren RB, Dijksterhuis AP (2012). Prosocial consequences of imitation. Psychol Rep. 110(3): 891-898.

Nichols T (2012) Multiple testing corrections, nonparametric methods, and random field theory. NeuroImage 62(2): 811-5.

Ortigue S, Thompson JC, Parasuraman R, Grafton, ST (2009). Spatio-temporal dynamics of human intention understanding in temporo-parietal cortex: a combined EEG/fMRI repetition suppression paradigm. PloS One 4(9): e6962.

Ortigue S, Sinigaglia C, Rizzolatti G, Grafton ST (2010). Understanding actions of others: the

electrodynamics of the left and right hemispheres. A high-density EEG neuroimaging study. PLOS ONE 5: e12160.

- Oullier O, De Guzman GC, Jantzen KJ, Lagarde J, Kelso JAS (2008). Social coordination dynamics: Measuring human bonding. Social Neuroscience 3(2): 178-192.
- Paladino MP, Mazzurega M, Pavani F, Schubert TW (2010). Synchronous multisensory stimulation blurs self-other boundaries. Psychological Science 21(9): 1202-1207.
- Raichle ME, MacLeod AM, Snyder AZ, Powers WJ, Gusnard DA, Shulman GL (2001). A default mode of brain function. Proc Natl Acad Sci U S A 98(2): 676-682. doi: 10.1073/pnas.98.2.676.
- Raichle ME, Snyder AZ (2007). A default mode of brain function: A brief history of an evolving idea. NeuroImage 37: 1083-1090.
- Rao AS, Georgeff MP (1997). Modeling rational agents within a BDI-architecture. Readings in Agents 317-328.

Repp BH (2005). Sensorimotor synchronization: A review of the tapping literature.

Psychonomic Bulletin & Review 12(6): 969-992.

Repp BH, Su YH (2013). Sensorimotor synchronization: A review of recent research (2006- 1012). Psychonomic Bulletin & Review 20(3):403-452. doi: 10.3758/s13423-012-0371- $\mathcal{D}_{\mathcal{L}}$

Richardson MJ, Marsh KL, Schmidt RC (2005). Effects of visual and verbal interaction on unintentional interpersonal coordination. Journal of Experimental Psychology: Human Perception and Performance 31(1): 62.

Rizzolatti G, Craighero L (2004). The mirror-neuron system. Annual Review of Neuroscience 27: 169-192.

- Rizzolatti G, Sinigaglia C (2007). Mirror neurons and motor intentionality. Functional Neurology 22(4): 205-210.
- Salman MS (2002). Topical Review: The Cerebellum: It's About Time! But Timing Is Not Everything-New Insights Into the Role of the Cerebellum in Timing Motor and Cognitive Tasks. Journal of Child Neurology 17(1): 1-9.
- Schmidt RC, Carello C, Turvey MT (1990). Phase transitions and critical fluctuations in the visual coordination of rhythmic movements between people. Journal of Experimental Psychology: Human Perception and Performance 16(2): 227.
- Schmidt RC, O'Brien B (1997). Evaluating the dynamics of unintended interpersonal coordination. Ecological Psychology, 9: 189–206.
- Semin GR (2007). Grounding communication: Synchrony. In A. W. Kruglanski & E. T. Higgins (Eds.), Social psychology: Handbook of basic principles (2nd ed., pp. 630–649). New York: Guilford.
- Semin GR, Cacioppo JT (2008). Grounding social cognition: Synchronization, coordination, and co-regulation. In G.R. Semin & E.R. Smith (Eds.), Embodied grounding: Social, cognitive, affective, and neuroscientific approaches (pp. 119-147). New York, NY: Cambridge University Press.
- Semin GR, Cacioppo JT (2009). "From embodied representation to co-regulation," in Mirror Neuron Systems: Role of Mirroring Processes in Social Cognition, ed J. A. Pineda (Totowa, NJ: The Humana Press), 107–120.
- Semin GR, Smith E (2002). Interfaces of social psychology with situated and embodied cognition. Cogn. Syst. Res. 3: 385–396.

Shimada S, Hiraki K, Oda I (2005). The parietal role in the sense of self-ownership with

temporal discrepancy between visual and proprioceptive feedbacks. NeuroImage 24(4): 1225-1232.

- Sonnby-Borgström M (2002). Automatic mimicry reactions as related to differences in emotional empathy. Scandinavian Journal of Psychology, 43(5): 433-443.
- Stel M, van Baaren RB, Blascovich J, van Dijk E, McCAll C, Pollmann MM, van Leeuwen ML, Mastop J, Vonk R. (2010). Effects of a priori liking on the elicitation of mimicry. Exp Psychol. 57(6): 412-418.
- Strick PL, Hoover JE, Mushiake H (1993). Evidence for "output channels" in the basal ganglia and cerebellum. Role of the cerebellum and basal ganglia in voluntary movement 171.
- Talairach J, Tournoux P (1988). Co-planar stereotaxic atlas of the human brain (Vol. 147). New York: Thieme.
- Tickle-Degnen L, Rosenthal R (1990). The nature of rapport and its nonverbal correlates. Psychological Inquiry, 1: 285**–**293.
- Tognoli E, Magne C, de Guzman GC, Tuller B, Kelso JAS (2007). Brain rhythms underlying intentional social coordination. Society for Neuroscience Itinerary Planner Program 304.24, San Diego, USA, November 3rd-7th.
- Tu S, Qiu J, Martens U, Zhang Q (2013). Category-selective attention modulates unconscious processes in the middle occipital gyrus. Conscious Cognition 22(2): 479-485.
- van Baaren RB, Holland RW, Kawakami K, van Knippenberg A (2004). Mimicry and prosocial behavior. Psychological Science 15(1): 71-74.
- van Baaren RB, Holland RW, Steenaert B, van Knippenberg A (2003). Mimicry for money: Behavioral consequences of imitation. Journal of Experimental Social Psychology, 39(4): 393-398.
- van Baaren R, Janssen L, Chartrand TL, Dijksterhuis A. (2009). Where is the love? The social aspects of mimicry. Philos Trans R Soc Lond B Biol Sci. 364(1528): 2381-2389.
- Vacharkulksemsuk T, Fredrickson BL (2012). Strangers in sync: achieving embodied rapport through shared movements. Journal of Experimental Social Psychology 48(1): 399-402.
- Valdesolo P, Ouyang J, DeSteno D (2010). The rhythm of joint action: Synchrony promotes cooperative ability. Journal of Experimental Social Psychology 46(4): 693-695.

Valdesolo P, DeSteno D (2011). Synchrony and the social tuning of compassion. Emotion,11(2): 262.

- van Baaren RB, Maddux WW, Chartrand TL, De Bouter C, van Knippenberg A (2003). It takes two to mimic: behavioral consequences of self-construals. Journal of Personality and Social Psychology 84: 1093–1102. [doi:10.1037/0022-3514.84.5.1093.](http://dx.doi.org/doi:10.1037/0022-3514.84.5.1093)
- van Overwalle F, Baetens K (2009). Understanding others' actions and goals by mirror and mentalizing systems: a meta-analysis. NeuroImage 48(3): 564-584. doi: 10.1016/j.neuroimage. 2009.06.009.
- van Overwalle F, Baetens K, Marien P, Vandekerckhove M (2014). Social cognition and the cerebellum: a meta-analysis of over 350 fMRI studies. NeuroImage 86: 554-572. doi: 10.1016/j.neuroimage.2013.09.033

Ward BD (2002). Deconvolution analysis of fMRI time series data. Milwaukee, WI: Biophysics Research Institute, Medical College of Wisconsin.

Wiltermuth SS, Heath C (2009). Synchrony and cooperation. Psychological Science 20(1): 1-5.

Yamanishi JI, Kawato M, Suzuki R (1980). Two coupled oscillators as a model for the coordinated finger tapping by both hands. Biological Cybernetics 37(4): 219-225.

Yun K, Watanabe K, Shimojo S (2012). Interpersonal body and neural synchronization as a

marker of implicit social interaction. Scientific Reports 2:959. doi: 10.1038/srep00959.

Figure Captions

Figure 1. Screenshot of the computer interface of the "*bexting*" task.

Figure 2. BOLD responses obtained for synchrony compared to asynchrony. A. Synchrony > asynchrony is shown in yellow on lateral views of the fiducial left side of the brain (A). Brain activities were mapped on the AFNI Colin brain using Caret 5.65 software (Van Essen, 2005). (B). Plots of percent (%) signal change were extracted for the three significant regions (IPL, left; parahippocampal region, center; and vmPFC, right) between synchrony (orange) and asynchrony (blue). All clusters were significant at $p < .01$ corrected to alpha < .05.

Figure 3. Correlations between neural activity and behavioral measures in the ventromedial prefrontal cortex (vmPFC). The BOLD effect for synchrony found in vmPFC (see Figure 2) significantly correlated with measures of perceived synchrony and feelings of affiliation. The ordinate indicates behavioral difference scores for synchronous - asynchronous trials; the abscissa indicates difference scores in BOLD activity (dBOLD). Participants reporting higher perception of synchrony and feelings of affiliation for synchronous items also showed greater corresponding vmPFC activity. Results were obtained with a voxelwise cluster threshold of *p* < .025, corrected for multiple comparisons to alpha < .05.

Figure 4. A. Results of voxelwise correlation analyses between the BOLD differential synchrony scores (dBOLD: synchrony minus asynchrony) and reported feelings of perceived

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synchrony projected onto a slice from the MNI atlas (left, $z = -42$) and mapped on the Caret AFNI Colin brain right hemisphere, lateral view (center) and medial view (right). B. Scatter plots for each respective cluster, from left to right: cerebellar tonsil, right middle occipital gyrus (BA 19), right lateral prefrontal cortex (BA 46), dorsomedial prefrontal cortex (BA 9), and right lingual gyrus (BA18/19). C. Median split plots indicating each cluster's BOLD activity in each condition for the subsamples above and below the behavioral median. Results were obtained with a voxelwise cluster threshold of $p < .025$, corrected for multiple comparisons to alpha $< .05$.

Figure 5. Results of correlation analyses between the BOLD differential synchrony scores (dBOLD between synchrony minus asynchrony) and reported feelings of affiliation. A. Correlation clusters mapped onto the Caret AFNI Colin brain right hemisphere, lateral view (left) and medial view (right). B. Scatter plots for each respective cluster from left to right: inferior parietal / supramarginal gyrus (BA40), lingual gyrus (BA 19). C. Median split plots indicating each cluster's BOLD activity in each condition for the subsamples above and below the behavioral median. Results were obtained with a voxelwise cluster threshold of *p* < .025, corrected for multiple comparisons to alpha < .05.

Figure 1

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Centre

Table 2. Feelings of social affiliation with an adaptive partner

Table 3. Feelings of perceived synchrony with an adaptive partner

Table 4. Feelings of social affiliation with an adaptive partner

Table 5. Variance range main effect results of the whole-brain factorial ANOVA. All clusters were significant at $p < .01$ corrected to alpha $< .05$. Regions are indexed with MNI coordinates; Brodmann areas are indicated for appropriately located clusters.

Table 6: Clusters resulting from the voxelwise analysis correlating BOLD signal during task period and behavioral ratings of perceived synchrony. Results were obtained with a voxelwise cluster threshold of $p < .025$, corrected for multiple comparisons to alpha $< .05$. Regions are indexed with MNI coordinates; Brodmann areas are indicated for appropriately located clusters.

Table 7. Clusters resulting from the voxelwise analysis correlating BOLD signal during task period and behavioral ratings of feelings of affiliation. Results were obtained with a voxelwise cluster threshold of $p < .025$, corrected for multiple comparisons to alpha $< .05$. Regions are indexed with MNI coordinates; Brodmann areas are indicated for appropriately located clusters.

Highlights:

- First fMRI study on social consequences of synchrony where the participant served as referent.
- Referents recruit brain areas involved in social and embodied cognition during synchrony.
- Referents expressed greater feelings of affiliation toward synchronous partners.