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Interpersonal synchrony enhanced through 20 Hz phase-coupled dual brain stimulation

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Abstract

Synchronous movement is a key component of social behavior in several species including humans. Recent theories have suggested a link between interpersonal synchrony of brain oscillations and interpersonal movement synchrony. The present study investigated this link. Using transcranial alternating current stimulation (tACS) applied over the left motor cortex, we induced beta band (20 Hz) oscillations in pairs of individuals who both performed a finger-tapping task with the right hand. In-phase or anti-phase oscillations were delivered during a preparatory period prior to movement and while the tapping task was performed. In-phase 20 Hz stimulation enhanced interpersonal movement synchrony, compared with anti-phase or sham stimulation, particularly for the initial taps following the preparatory period. This was confirmed in an analysis comparing real *vs* pseudo pair surrogate data. No enhancement was observed for stimulation frequencies of 2 Hz (matching the target movement frequency) or 10 Hz (alpha band). Thus, phase-coupling of beta band neural oscillations across two individuals' (resting) motor cortices supports the interpersonal alignment of sensorimotor processes that regulate rhythmic action initiation, thereby facilitating the establishment of synchronous movement. Phase-locked dual brain stimulation provides a promising method to study causal effects of interpersonal brain synchrony on social, sensorimotor and cognitive processes.

Key words: interpersonal synchronization; brain-to-brain coupling; social interaction; beta oscillations; phase

Introduction

Synchronous behavior is a means of communication and social activity central to many species (Greenfield, 1994; Merker *et al.*, 2009). In humans, it underlies joint action (Sebanz *et al.*, 2006), widespread cultural practices (Néda *et al.*, 2000)—notably music (D'Ausilio *et al.*, 2015)—and promotes group cohesion (Hove and Risen, 2009).

Recent evidence suggests that interpersonal synchrony is associated with inter-brain synchrony. This phenomenon, here implying phase-coupled neural signals across multiple brains, has been observed in dual-EEG studies employing diverse tasks requiring joint rhythmic behaviour (Lindenberger *et al.*, 2009; Sänger *et al.*, 2012) and joint imitation (Dumas *et al.*, 2010; Yun *et al.*, 2012). Such findings have been interpreted as evidence that studying synchronous activity across individual brains will lead to a better understanding of joint action and social cognition (Hasson *et al.*, 2012). According to this view, the neural processes underlying human interactions could—and should—be studied in terms of coupled neural processes across multiple individuals' brains (Babiloni and Astolfi, 2014; Hari *et al.*, 2015; Hasson and Frith, 2016).

The co-occurrence of interpersonal synchrony and inter-brain synchrony raises a critical question regarding causality. Is inter-brain synchrony *per se* a condition that favors interpersonal synchronization, or is inter-brain synchrony an epiphenomenon resulting from intrinsic similarities reflected in the

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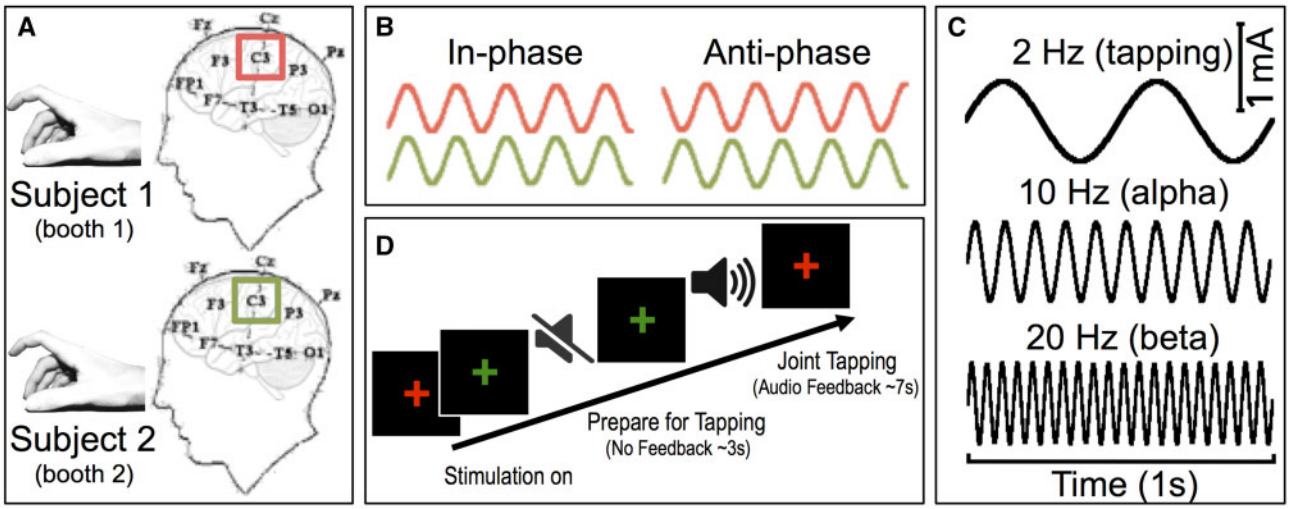

Fig. 1. (A) Pairs of participants performed a joint tapping task with their right index fingers from separate booths (no visual contact) while being simultaneously administered with transcranial alternating current stimulation (tACS) over their left primary motor cortices. (B) The relative stimulation phase between brains was manipulated to be either in phase (0° relative phase) or anti phase (180° relative phase), across three stimulation frequencies: 2 Hz (matching the instructed tapping tempo), 10 Hz (alpha band) or 20 Hz (beta band) (see (C), a sham stimulation condition is used as a baseline, not shown). (D) In a joint finger tapping task, the participants started tapping following a preparatory period during which they were inactive and could not exchange information but were administered tACS (audio feedback was provided only after this period).

EEGs of two (motorically and perceptually) synchronized people (Lindenberger *et al.*, 2009; Burgess, 2013)?

Here we tested whether synchronizing the phase of oscillations of two individuals' motor cortices is sufficient to enhance interpersonal (behavioral) synchronization. We employed transcranial alternating current stimulation (tACS) (Herrmann *et al.*, 2016), a non-invasive brain stimulation method that can entrain neural oscillations (Helfrich *et al.*, 2014) in a frequency-specific (Feurra *et al.*, 2011) and phase-specific (Polanía *et al.*, 2012) manner. In a dual-tACS protocol, pairs of participants were simultaneously stimulated, while the relative-phase between the oscillations induced was manipulated to be perfectly in-phase (0° relative phase) or in anti-phase (180° relative phase) (Figure 1a, b).

We hypothesized that synchronizing the phase of beta oscillations (20 Hz) of two individuals' motor cortices (cf. Feurra *et al.*, 2011, 2013) would lead to an increase in behavioral synchrony in a joint finger-tapping task requiring two participants to perform a series of rhythmic taps as synchronously as possible after a variable preparation period (~3 s). This hypothesis was based on (1) the well-established association between motor processes and neural oscillations in the beta frequency range (13–30 Hz) (Kilner *et al.*, 1999; Pogosyan *et al.*, 2009; Brinkman *et al.*, 2014), and (2) the notion that the phase of cortical oscillations reflects the timing of neural activity (Sauseng and Klimesch, 2008; Ng *et al.*, 2013).

Because beta oscillations become suppressed during (and immediately prior to) action execution (Pfurtscheller, 1981), stimulation began during the preparation period to align the phase of this neural rhythm in the resting motor system, and then continued until both participants had performed a short series of taps (Figure 1D). Behavioral synchrony was compared across in-phase and anti-phase stimulation conditions (and a sham stimulation condition included to assess baseline accuracy), as well as across early *vs* late taps following the preparatory period. Synchronizing early taps following the preparation period required establishing interpersonal movement synchrony (Fraisse and Repp, 2012) after an interval that introduced considerable temporal uncertainty. Later taps required maintaining interpersonal movement synchrony while auditory feedback about the partner's actions had been and continued to be available (note the gradual improvement of interpersonal synchrony from early to late taps in Figure 2, all panels).

Establishing and maintaining coordination are two complementary, yet different, aspects of motor coordination, and are likely to rely on distinct mechanisms. Although most research has focused on the maintenance of synchrony (Keller *et al.*, 2014), establishing synchrony is crucial in real instances of interpersonal coordination to the extent that it is a necessary precursor of maintenance (Fraisse and Repp, 2012). Indeed, in everyday life, coordination needs to be established anew for each episode in a succession of actions. The current paradigm permitted us to examine the effects of our manipulation upon establishing and maintaining coordination separately.

Finally, in order to establish the frequency specificity of the dual-brain stimulation employed, we included 10 Hz (alpha oscillations) and 2 Hz in-phase and anti-phase stimulation conditions. Stimulation at 10 Hz was included because previous studies have reported changes in intra-brain alpha power (i.e. more suppression) associated with enhanced interpersonal synchronization (Tognoli *et al.*, 2007; Naeem *et al.*, 2012; Konvalinka *et al.*, 2014; Novembre *et al.*, 2016). The 2 Hz condition was included to exclude the possibility that brain stimulation directly facilitated movements in a 1:1 period-to-movement ratio (the instructed tapping frequency was 2 Hz, Figure 1C).

Material and methods

Participants

Sixty individuals (24.76 ± 9.2 years old, 14 males) formed 30 pairs. All participants were right handed, had normal hearing and no history of brain injury or epileptic seizure. All procedures were approved by the local ethics committee.

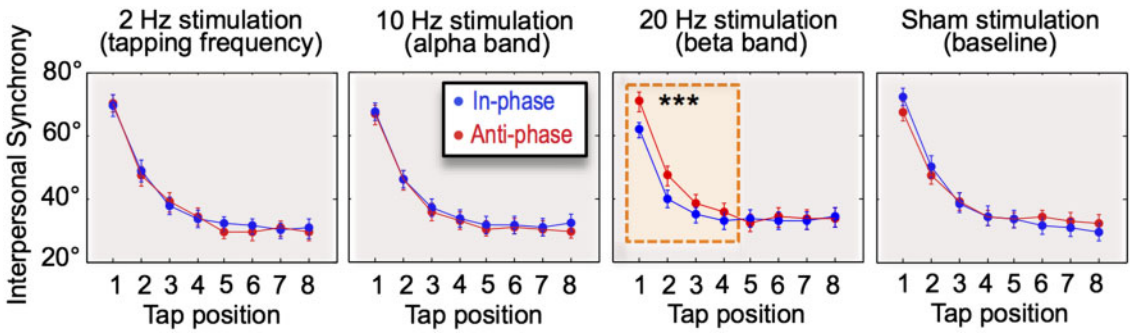

Fig. 2. Interpersonal synchrony (0° relative phase indicates perfect synchrony) for consecutive tap positions following the preparatory period in the FREQUENCY (2 Hz, 10 Hz, 20 Hz, Sham) and RELATIVE-PHASE (in-phase, anti-phase) conditions. Note the gradual improvement of interpersonal synchrony from early to late taps in all panels. 20 Hz in-phase stimulation enhances the synchronicity of movements for initial taps relative to 20 Hz anti-phase stimulation (*** $P<0.001$). Bars represent 1 standard error of the mean.

Procedure

The two participants forming a pair were placed into two separate soundproof booths (no visual contact) each equipped with a drum pad (Roland Handsonic 10), electrically shielded Insert Earphones (Etymotic Research ER•2), a computer monitor (BENQ e2200hd) and a direct current stimulator (DC Stimulator Plus, NeuroConn). All equipment (including connection cables) was identical across booths.

The experiment consisted of 18 blocks, presented in randomized order, each composed of 7 trials (see below). There were two blocks for each RELATIVE-PHASE (in-phase and anti-phase) and FREQUENCY (2 Hz, 10 Hz and 20 Hz) condition. Six additional blocks were used for sham stimulation, which served to estimate baseline task performance at joint tapping. A trial began with a red fixation cross presented on both computer monitors for 500 ms, after which the cross turned green and remained so for 9.5 s (i.e. trial duration was 10 s). Participants were instructed to wait approximately three seconds before starting tapping together, and to synchronize as accurately as possible for the remaining 6.5 s (i.e. until the fixation cross turned red again). They were asked to produce up to 12 taps at a 120 bpm (beats per minute) tempo (corresponding to 2 Hz) using their right index finger. This tempo corresponds to the human average preferred beat tempo (van Noorden and Moelants, 1999; Moelants, 2002).

To ensure participants would not start the synchronization task earlier than instructed, no audio feedback was provided if they tapped during the 2750 ms following the green fixation cross (an interval shorter than 3 s was chosen to accommodate variable time estimation). In order to avoid inducing stimulus-based synchronization in the pair, the fixation cross turned green at slightly different times for the two participants (random offset of either 25, 50, 75 or 100 ms). Furthermore, trials were separated by an inter-trial interval (associated with a red fixation cross) with variable duration of either 250, 500 or 750 ms. Thus, an entire block lasted 73.5 s on average (i.e. seven trials, each lasting 10 s, plus 0.5 s average inter-trial interval).

Participants were visually monitored (via cameras) by the experimenters, who were situated in a control room and changed the stimulator parameters between blocks (the stimulators' displays were covered to prevent the participants from seeing the settings). To familiarize the participants with the experimental task, they performed two practice blocks before beginning the actual experiment. They also practiced an unrelated task that served to avoid carry-over effects between experimental blocks (see below).

Sinusoidal stimulation was delivered at an intensity of 1000 μA (peak-to-peak) for the duration of the whole block, starting with the onset of the red fixation cross in the first trial of each block, and continuing for the whole block duration. For the sham blocks, the stimulation only occurred for the initial 2 s to match any potential skin sensations experienced by participants at the onset of true stimulation in the in-phase and anti-phase blocks. The stimulation had no DC offset, and it linearly increased (fade in) and decreased (fade out) within a time frame corresponding to one cycle of the frequency employed. The initial stimulation in sham blocks was either in-phase or anti-phase (3 blocks each) and had a frequency of 2 Hz, 10 Hz or 20 Hz frequency (counterbalanced across participants).

The stimulation was delivered through two rubber electrodes (5×7 cm) encased in saline soaked sponges (Reclens, with sodium chloride concentration of 7.67 g/L and 2.0 g/L of disodium hydrogen phosphate). The target electrode (attached to the anode port of the stimulator) was centered over C3 (with the longer side of the sponge oriented towards the left ear), approximating the location of the left primary motor cortex, while the reference electrode (attached to the cathode port of the stimulator) was placed over Pz, according to the International 10–20 EEG system (Jasper, 1958). Electrode montage followed previous studies reporting frequency specific effects of tACS on cortico-motor excitability (i.e. amplitude of motor evoked potentials, (Feurra *et al.*, 2011, 2013)). The sponges were secured over the scalp using three rubber straps (NeuroConn), one affixed around the circumference of the participant's head, and two running between the ears over the central and parietal scalp. Additionally, a plastic cap, obtained from a size adjustable construction helmet and supplemented with eight elastic straps, was used to ensure optimal pressure of the electrodes on the scalp and to secure their position. Impedances were kept below 10 kΩ throughout the experiment. At the end of the experiment, all participants were asked whether they had perceived phosphenes (which were described as 'flashes of light'). Nine out of the sixty participants reported having seen phosphenes. None of these individuals were paired together.

To control for carryover effects, participants performed additional tasks between experimental blocks. The duration of these 'intermediate blocks' was precisely twice as long as the duration of an experimental block (147 s). The tasks consisted in listening and tapping (20 s), only listening (24 s) and then again listening and tapping (20 s) with a metronome beating at 2 Hz. Hence, besides controlling for carryover effects, these tasks were also meant to train participants to tap as accurately as

possible at the target tempo. These tasks were also preceded and followed by two pauses (41.5 s), during which the participants were instructed to relax.

Presentation software (Neurobehavioral systems Inc.) was used to control the stimuli, trigger the stimulators, and record the timing of the taps. Presentation was running on a Dell OptiPlex 960 computer, with dual 3.0 GHz Xenon processors, which was situated in the control room. Each of the two drum pads produced a distinct sound ('Tabla' sounds from the pads' 'India' library), which was chosen for clear onset and rapid decay. The tuning of the sound was different across the two participants (one set at zero, the other at +1200) to assist discriminability. The audio plug and MIDI ports of each drum pad were used to output the timing of auditory events and taps. The audio outputs were mixed and passed through a feedback control device (custom built), through which Presentation could control audio feedback (see above). Custom-built devices were used to convert the MIDI signals into serial codes, for compatibility with Presentation. Presentation triggered the stimulators via a single code sent through parallel port and transmitted into BNC plug (for compatibility with the NeuroConn stimulators).

Data analysis

Interpersonal synchrony was calculated using a circular measure (i.e. 0°–360°) (Kelso, 1984; Tognoli *et al.*, 2007; Oullier *et al.*, 2008), which obviated the issue of assigning complementary taps arbitrarily (Kirschner and Tomasello, 2009; Pecenka and Keller, 2011). Importantly, this measure is robust to inter-trial and inter-participant tempo variability, which was expected due to the demands of present task leading to considerable temporal uncertainty. Because computing such bivariate measures involves assigning one participant's taps as 'reference' to the other's (Pecenka and Keller, 2011), we randomly selected one participant to be the reference in half of the trials (odd trial numbers) and the other participant for the other half (even trial numbers). This ensured that the datapoints collected for each individual participant were independent across members of a pair, and were analyzed independently (see below). The circular measure was calculated as follows:

$$\alpha = \left[\frac{T1_{p2} - T1_{p1}}{T2_{p1} - T1_{p1}}\right] * 360$$

where $T1_{p1}$ and $T2_{p1}$ stand for the time points at which two consecutive taps are produced by the 'reference' participant (their difference representing the inter-tap interval or current period), while $T1_{p2}$ is a tap produced by the other participant between these two taps produced by the reference participant. The resultant angular measure is termed α.

The circular values were converted into a linear measure ranging between 0° and 180°, with 0° indicating perfect synchronization (i.e. coincident taps) and 180° indicating perfect anti-phase coordination (i.e. a tap produced by one participant occurs at the midpoint between two consecutive taps of the reference participant). This conversion permitted us (1) to extract a synchronization accuracy measure that was not affected by whose taps were momentarily leading or lagging (analogous to analyzing 'absolute asynchronies' cf. Repp, 2005) and (2) to analyze our data using an analysis of variance (see below) that matched our factorial design. This linear conversion was achieved by transforming angular measures in the 180°–360° range using the formula below (where α is an angular measure):

$$\alpha_{linear} = 180 - (\alpha - 180)$$

Trials in which it was possible to obtain at least eight synchronization data points (i.e. when the two participants produced a sufficiently high number of taps) were analyzed (98.4% of the trials). Furthermore, trials associated with extreme synchronization values (i.e. when the average of the eight synchrony values was higher or lower than 2 s.d. from the participant's mean synchrony) were discarded (4.99% of the trials).

Before submitting these data to statistical tests, the data were log-transformed to correct for a positive skew (due to converting the circular values into a linear measure, see above). Next, mean synchronization values were computed for each participant and condition, separately for early (averaged taps 1–4) and late (averaged taps 5–8) taps. The synchronization values obtained from the sham conditions (baseline) were subtracted from the means of each stimulation condition (in-phase and anti-phase stimulations, respectively) (compare Figure 2 with Figure 3). Finally, the baseline-corrected mean synchronization values were entered into a 2×3×2-repeated measures ANOVA with factors: TIME (early, late), FREQUENCY (2 Hz, 10 Hz, 20 Hz) and RELATIVE-PHASE (in-phase, anti-phase). Significant interactions were followed up by paired samples *T*-tests (comparing in-phase vs. anti-phase within specific stimulation frequencies and times) and one-sample *T*-tests (comparing either in-phase or anti-phase *vs* zero, indexing baseline synchronization).

A control analysis was run to confirm that significant effects—which were observed selectively for 20 Hz stimulation (see below)—were attributable to the interaction between participants, as opposed to individual modulations of behavior incidentally affecting interpersonal synchrony. For this analysis, the timing of the taps produced by each member of a pair was analyzed in relation to taps produced by participants occupying the other booth from all pairs apart from the actual partner's taps. Note that the timing of all participants' taps was computed relative to the trial onset (red fixation cross presentation), and that the instantaneous phase of 20 Hz stimulation at trial onset was constant across all trials and pairs (i.e. the summed trial and inter-trial duration was always multiple of 50 ms, the period of 20 Hz). 'Surrogate' data were thus generated from 'pseudo' pairs, yielding synchronization values that were analyzed analogously to the genuine data (see above), and compared to the genuine data in a 2×2 ANOVA with factors RELATIVE-PHASE and PAIR-AUTHENTICITY (genuine data, surrogate data).

An additional analysis was performed on the mean inter-tap intervals, which are represented by the denominator of the first formula above, as well as on the interval between the first tap and the green fixation cross (appearing on the screens at slightly different times) from each trial. These analyses controlled for potential differences in tapping tempo and the onset of tapping across experimental conditions.

Results

The baseline-corrected synchronization values (expressed in degrees) for the FREQUENCY and RELATIVE-PHASE conditions and tap positions are presented in Figure 3 (raw synchronization values, prior to baseline correction, are presented in Figure 2). The ANOVA on the (log-transformed) baseline-corrected data yielded a statistically significant three-way interaction between TIME, FREQUENCY and RELATIVE-PHASE

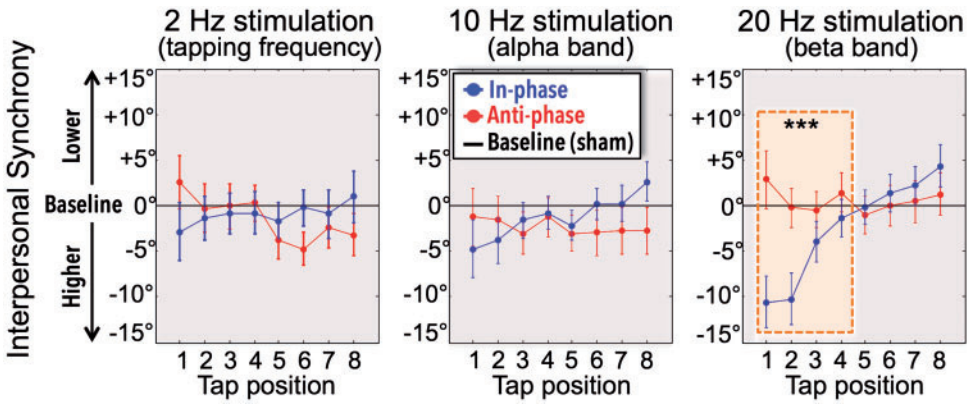

Fig. 3. Baseline-corrected interpersonal synchrony (in degrees) in the FREQUENCY (2 Hz, 10 Hz, 20 Hz) and RELATIVE-PHASE (in-phase, anti-phase) conditions. The zero line (baseline) indicates synchronization during sham stimulation, values below zero indicate enhanced synchronization relative to baseline, values above zero indicate the opposite. 20 Hz in-phase dual brain stimulation enhances the synchronicity of movements for initial taps relative to 20 Hz anti-phase stimulation (*** $P<0.001$) and sham stimulation. Bars represent 1 standard error of the mean.

($F_{(2,118)}=5.33$, $P=0.006$) and a two-way interaction between TIME and FREQUENCY ($F_{(2,118)}=3.34$, $P=0.039$).

Breaking the ANOVA for the factor TIME revealed an interaction between FREQUENCY and RELATIVE-PHASE for early taps ($F_{(2,118)}=4.86$, $P=0.009$), but not for late taps (all $F<1.06$, all $Ps>0.3$). We, therefore, tested the effect of RELATIVE-PHASE in the early TIME window, by comparing in-phase *vs* anti-phase synchronization values for each FREQUENCY. There were no effects of RELATIVE-PHASE for 2 Hz ($t_{(59)}=-1.175$, $P=0.24$) or 10 Hz stimulation ($t_{(59)}=0.50$, $P=0.61$). However—for the 20 Hz stimulation FREQUENCY—in-phase stimulation was associated with higher interpersonal synchronization than anti-phase stimulation ($t_{(59)}=-3.521$, $P<0.001$). This was due to in-phase stimulation leading to higher interpersonal synchronization compared with baseline ($t_{(59)}=-3.14$, $P=0.003$), while anti-phase stimulation did not significantly affect synchronization relative to baseline ($t_{(59)}=1.09$, $P=0.277$).

This pattern of results—which was specific for 20 Hz stimulation—was not observed in the surrogate data (i.e. synchronization values from pseudo pairs, see above and Figure 4A). The 2×2 repeated measure ANOVA with factors RELATIVE-PHASE and PAIR-AUTHENTICITY (genuine data, surrogate data) yielded a significant two-way interaction ($F_{(1,59)}=14.609$, $P<0.001$), indicating that the difference in interpersonal synchronization between 20 Hz in-phase and anti-phase conditions was significant only in real pairs' data ($t_{(59)}=-3.521$, $P<0.001$), but not in pseudo pairs' data ($t_{(59)}=0.661$, $P=0.511$) (see Figure 4). Likewise, 20 Hz in-phase stimulation significantly enhanced interpersonal synchronization with respect to baseline only in genuine data ($t_{(59)}=-3.14$, $P=0.003$), but not in surrogate data ($t_{(59)}=0.477$, $P=0.635$) (see Figure 4C). This result indicated that the enhancement of interpersonal synchrony due to 20 Hz dual-brain stimulation could not be solely explained by means of individual modulations of motor processes incidentally affecting interpersonal synchrony. Rather, dual brain stimulation facilitated interpersonal coordination only in those pairs of participants (real pairs) who actually performed the tapping task together.

Finally, in the analysis of mean inter-tap-intervals (see Table 1), indexing average tapping tempo, the ANOVA yielded no significant results (all $Fs<3.4$, all $Ps>0.07$), nor did the *T*-tests (all absolute $ts<1.00$, all $Ps>0.32$). Similarly, the interval between the green fixation cross and the first tap (see Table 2) did not differ across conditions (ANOVA: all $Fs<1.52$, all $Ps>0.22$, *T*-tests: all absolute $ts<1.82$, all $Ps>0.07$). These results indicate that the observed differences in interpersonal synchronization across experimental conditions were not accompanied by differences in tapping tempo or tapping onset.

Discussion

This study demonstrated that phase coupling of beta oscillations induced with tACS across two individuals' motor cortices enhanced interpersonal movement synchrony. The enhancement of synchrony for in-phase stimulation relative to anti-phase stimulation and sham stimulation occurred only at 20 Hz but not at 2 Hz or 10 Hz. Our proposed explanation for this result is that induction of 20 Hz inter-brain synchrony between two individuals' motor cortices aligned sensorimotor processing in the two individuals within a pair. This, in turn, affected the time of joint action initiation and facilitated achieving interpersonal movement synchrony.

The enhancement in interpersonal synchrony was observed specifically for early taps following a preparation period that made it difficult for the two individuals to initiate their movements at the same time. No such enhancement was observed for later taps for which interpersonal synchrony was high. A likely explanation for high interpersonal synchrony on later taps is that the presence of auditory feedback enabled participants to be tightly coupled so that the 20 Hz in-phase stimulation could not further enhance performance.

The specific synchrony enhancement for early taps might also be due to the fact that beta oscillations become suppressed just prior to, and during, motor execution (Pfurtscheller, 1981). Here the stimulation began about 3 s before task initiation, i.e. when participants were not yet moving and endogenous oscillations were (presumably) not yet suppressed. Thus, the 20 Hz in-phase stimulation may have been effective only during this initial stage, and thus have influenced only early taps. For later taps, subsequent motor processes may have overridden the effects of aligned stimulation. In this interpretation, stimulation would have impacted on the resting state of the motor system prior to task initiation, and enhanced synchrony of early but not later taps. A potential problem for such an account, however, is that endogenous beta oscillations would not be constantly suppressed at a tapping rate of two taps per second. Rather, a decrease (suppression) and increase (rebound) in amplitude would be expected for each individual tap (see e.g. Toma *et al.*, 2002).

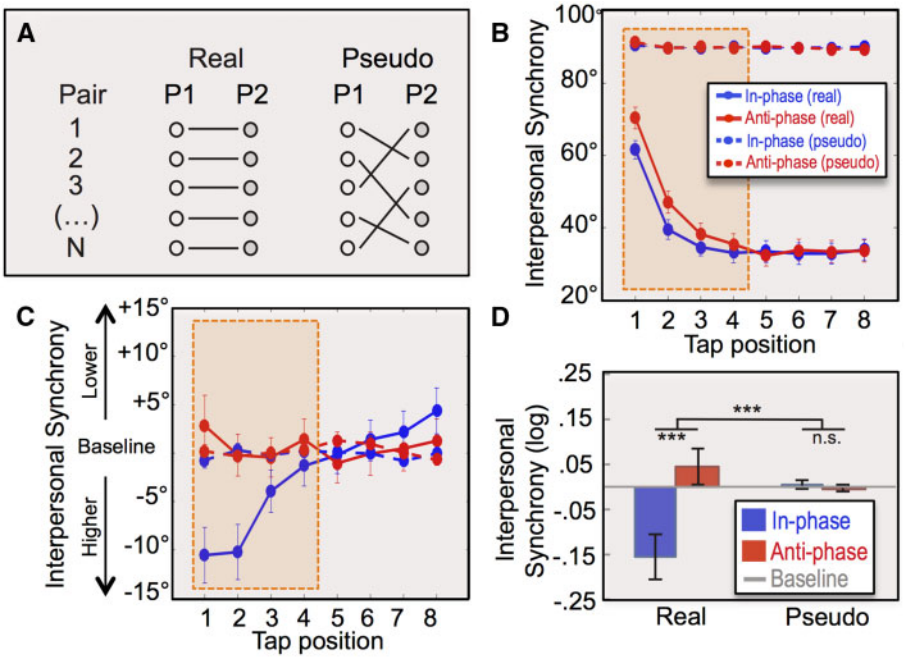

Fig. 4. (A) Schematic illustrating how genuine and surrogate data were obtained by computing synchronization between a participant and his or her actual partner (real pairs) or a participant and participants occupying the other booth in the remaining pairs (pseudo pairs; NB, not all pairings shown). (B) Interpersonal synchrony (0° relative phase indicates perfect synchrony) across consecutive tap positions following the preparatory period (for 20 Hz stimulation) in the RELATIVE-PHASE (in-phase, anti-phase) conditions, and across real pair (continuous line) and pseudo pair (dashed line) data. Note the gradual improvement of interpersonal synchrony from early to late taps in genuine data (real pair), as opposed to the low synchrony (~90°) observed in the pseudo pair data. (C) Same as (B), but baseline corrected by subtracting interpersonal synchrony values during the sham stimulation condition from synchrony values in each other condition. Zero indicates baseline (level of synchrony in the sham condition), values below zero indicate enhanced synchronization relative to baseline, and values above zero indicate a decrease in synchronization. Note how 20 Hz in-phase dual brain stimulation enhances early interpersonal synchronization with respect to baseline in real pairs, but not in pseudo pairs. (D) Log transformed baseline-corrected interpersonal synchrony values for early taps (1–4) during 20 Hz dual brain stimulation.

Table 1. Mean inter-tap intervals (in ms) ± 1 s.d. of the mean for early and late taps in the FREQUENCY (2 Hz, 10 Hz, 20 Hz) and RELATIVE-PHASE (in-phase, anti-phase) conditions

	2 Hz, in-phase	2 Hz, anti-phase	10 Hz, in-phase	10 Hz, anti-phase	20 Hz, in-phase	20 Hz, anti-phase	Sham, in-phase	Sham, anti-phase
Early taps	472 ± 28	468 ± 34	469 ± 33	466 ± 32	470 ± 31	466 ± 42	472 ± 34	468 ± 37
Late taps	462 ± 32	458 ± 34	457 ± 28	457 ± 30	463 ± 29	457 ± 40	464 ± 31	461 ± 36

Table 2. Average tapping onset times (in ms) ± 1 s.d. of the mean in the FREQUENCY (2 Hz, 10 Hz, 20 Hz) and RELATIVE-PHASE (in-phase, anti-phase) conditions

	2 Hz	10 Hz	20 Hz	Sham
In-phase	3066 ± 141	3092 ± 159	3076 ± 119	3069 ± 98
Anti-phase	3082 ± 144	3068 ± 137	3077 ± 148	3074 ± 128

Another potential explanation of our findings is that the modulation of beta oscillations selectively interfered with the neural mechanisms that govern internally driven rather than stimulus-driven rhythmic movements (cf. Fujioka *et al*,. 2012; Bartolo *et al*., 2014). Such a mechanism would affect interpersonal synchrony during initial taps where feedback is absent or not yet fully effective, and would not affect interpersonal synchrony during subsequent task execution (see Figure 2). This account is supported by findings showing that the (pre-stimulus) phase of neural oscillations impact on temporal predictions (Samaha *et al*., 2015) and perceptual processes (Busch *et al*., 2009; Baumgarten *et al*., 2015; Gundlach *et al*., 2016) and findings demonstrating that beta oscillations play a pivotal role in deriving *internalized* timing estimates (Arnal and Giraud, 2012; Fujioka *et al*., 2012) that drive motor processes such as rhythmic tapping (Bartolo *et al*., 2014). Finally, this account fits with the observation that inter-brain synchrony is particularly pronounced under high coordination demands, such as when two musicians establish synchronization in a duet (Lindenberger *et al*., 2009; Sänger *et al*., 2012).

No enhancement of interpersonal movement synchrony resulted from 2 Hz or 10 Hz in-phase stimulation. The specific effect of 20 Hz circumvents the limitation that brain stimulation studies often lack control over which specific brain areas are stimulated: This specificity supports the assumption that the stimulation affected precentral motor regions because these regions are known to be an important source of beta oscillations (Ritter *et al*., 2009). Indeed, previous studies using montages analogous to the present one found increased cortico-spinal excitability during 20 Hz tACS over the primary motor cortex (Feurra *et al*., 2011, 2013). The lack of effects at 2 Hz further suggests that synchronous inter-brain stimulation interfered with

the motor system at preparatory rather than execution level. Direct effects on motor output, such as triggering movements in a 1:1 ratio with the stimulation, would have predicted an effect of 2 Hz stimulation because this was the instructed movement tempo. It should be noted, however, that these predictions concerning the functional role played by 2 Hz and 20 Hz frequencies could be partially reconciled by a single signal featuring a 2 Hz envelope and a 20 Hz carrier frequency. Future studies could explore this issue directly by inducing more complex alternating current stimulations comprising multiple frequencies (Engel *et al.*, 2013).

The lack of effects at 10 Hz informs EEG research associating changes in intra-brain alpha power with interpersonal synchronization (Tognoli *et al.*, 2007; Naeem *et al.*, 2012; Konvalinka *et al.*, 2014; Novembre *et al.*, 2016). This research dates back to the seminal study by Tognoli *et al.* (2007), identifying neural oscillatory components (within the alpha band) that distinguished coordinated from independent interpersonal behavior. In relation to this literature, our result suggests that irrespective of whether such modulations are accompanied by changes in inter-brain synchrony (Dumas *et al.*, 2010, 2012), they are unlikely to be generated by the motor system in the two individuals. Indeed, (alpha) neuromarkers of interpersonal coordination have been typically observed over right parietal scalp regions (Tognoli *et al.*, 2007; Dumas *et al.*, 2010; Naeem *et al.*, 2012; Novembre *et al.*, 2016). Thus, it would be informative to use the dual-brain stimulation protocol introduced here to test the causal nature of these (and other) frequencies and regions in the context of tasks involving interpersonal coordination.

Regarding the neurophysiological mechanisms underlying the observed enhancement of interpersonal synchrony, we suggest that, by aligning the phase of 20 Hz beta oscillations, we effectively modulated the probability distribution of movement initiation times across two individuals. This manipulation increased the probability that the two individuals executed movements at the same time because high excitability phases of the oscillations were aligned across their two brains. Note that this is not a 'decision'-based account of our findings, according to which the phase or frequency of the stimulation interfered with (e.g. by advancing or delaying) the time at which the first tap was produced. Indeed, arguing against this, we showed that the tempo and onset of tapping were comparable across conditions. This indicates that the observed effect on interpersonal synchrony was not due to 20 Hz stimulation simply slowing down or speeding up tapping tempo similarly in paired participants, or causing them both to start tapping at relatively early or late time points.

Rather, we suggest that the instantaneous phase of beta oscillations may carry information about the time course of sensorimotor—i.e. motor and perceptual—processes at high temporal resolution. With regard to motor processes, phase changes might reflect different levels of motor excitability (Berger *et al.*, 2014; Keil *et al.*, 2014; Guerra *et al.*, 2016; Nakazono *et al.*, 2016; Raco *et al.*, 2016) and, therefore, a different likelihood of issuing a motor command at a given time point. Similarly, the changing phase of beta oscillations might modulate perceptual sensitivity (Busch *et al.*, 2009; Baumgarten *et al.*, 2015; Gundlach *et al.*, 2016), and thus facilitate the reactive response of one participant to the partner's first tap. Considering that our effects were selectively observed for stimulation at 20 Hz (beta band), this account would predict that the magnitude of the difference in interpersonal synchronization across in- and anti-phase conditions would be in the order of 25 ms (i.e. half the 50 ms period at 20 Hz), which is compatible with the magnitude of the observed effect. It can also be noted that this sensorimotor account is generally consistent with other research highlighting the potential role of the motor-related beta oscillations in perceptual tasks requiring temporal processing (Arnal and Giraud, 2012; Fujioka *et al.*, 2012; Arnal *et al.*, 2015).

It follows from our account that interpersonal phase alignment across two brains would increase the probability of tapping at the same time, and lead to higher interpersonal synchronization. Whether and how individuals reach a similar state of brain-to-brain phase coupling during real-life interactions is an issue that our study cannot address directly (but see EEG evidence from: Lindenberger *et al.*, 2009; Dumas *et al.*, 2010; Sänger *et al.*, 2012; Yun *et al.*, 2012). However, our study reports for the first time that this state is a sufficient condition for the enhancement of interpersonal coordination, and might possibly enhance other forms of interaction, including different varieties of verbal and non-verbal communication (see Jiang *et al.*, 2012; Silbert *et al.*, 2014; Schoot *et al.*, 2016). This empirical question, and its potential applications, deserves to be explored further.

The social nature of the observed tACS-related enhancement of interpersonal coordination was corroborated by a control analysis comparing genuine data from real pairs of participants with surrogate data from pseudo pairs. Although the phase of 20 Hz stimulation was equally aligned in both real and pseudo pairs (see Methods section), dual brain stimulation facilitated interpersonal coordination only in those pairs of participants (real pairs) who actually performed the tapping task together. More specifically, this analysis elucidated two important facts. First, interpersonal synchronization was better in real pairs than in pseudo pairs, and this was true for all tap positions including the first tap (see Figure 4). This demonstrated that participants belonging to the same pair relied on common history of performing coordinated actions together, i.e. receiving (auditory) feedback about their joint action outcomes throughout the experiment served to form a joint action plan. Thus, the real pairs benefitted from interpersonal interactive processes from task onset, and began the process of establishing synchrony already starting with the first tap. Second, comparing the effect of 20 Hz in-phase dual brain stimulation across real and pseudo pairs revealed that the enhancement of interpersonal synchronization was specific to real pairs. This indicated that these effects are not a by-product of individual motor processes within each member of a pair but occur in the context of performing coordinated actions with others and receiving feedback about joint outcomes of these actions. In other words, inter-brain synchrony was a sufficient condition to enhance interpersonal behavioral synchrony only in pairs of individuals who were actually collaborating to achieve synchrony.

In conclusion, the present results provide evidence that inducing inter-brain 20 Hz phase coupling (with 0° relative phase) causes enhancement of interpersonal movement synchronization in a joint action task. The results provide new support for neuroscience theories postulating that brain-to-brain coupling may be a valid marker of social cognition and group behavior (Hasson *et al.*, 2012). The technique of concurrent dual-brain stimulation employed here might provide an empirically sound method to determine causal effects of entrained brain oscillations in other domains such as perception, cognition (Hasson *et al.*, 2008; Nummenmaa *et al.*, 2014), and communication (Jiang *et al.*, 2012; Silbert *et al.*, 2014; Schoot *et al.*, 2016) in humans and other social species.

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