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Oxytocin enhances inter-brain synchrony during social coordination in male adults

Yan Mu,[1] Chunyan Guo,[2] and Shihui Han[1]

[1]School of Psychological and Cognitive Sciences, PKU-IDG/McGovern Institute for Brain Research, Beijing Key Laboratory of Behavior and Mental Health, Peking University, Beijing, China and [2]Beijing Key Laboratory of Learning and Cognition, Department of Psychology, Capital Normal University, Beijing, China

Correspondence should be addressed to Shihui Han, School of Psychological and Cognitive Sciences, Peking University, Beijing, China. E-mail: shan@pku.edu.cn

Abstract

Recent brain imaging research has revealed oxytocin (OT) effects on an individual's brain activity during social interaction but tells little about whether and how OT modulates the coherence of inter-brain activity related to two individuals' coordination behavior. We developed a new real-time coordination game that required two individuals of a dyad to synchronize with a partner (coordination task) or with a computer (control task) by counting in mind rhythmically. Electroencephalography (EEG) was recorded simultaneously from a dyad to examine OT effects on inter-brain synchrony of neural activity during interpersonal coordination. Experiment 1 found that dyads showed smaller interpersonal time lags of counting and greater inter-brain synchrony of alpha-band neural oscillations during the coordination (vs control) task and these effects were reliably observed in female but not male dyads. Moreover, the increased alpha-band inter-brain synchrony predicted better interpersonal behavioral synchrony across all participants. Experiment 2, using a double blind, placebo-controlled between-subjects design, revealed that intranasal OT vs placebo administration in male dyads improved interpersonal behavioral synchrony in both the coordination and control tasks but specifically enhanced alpha-band inter-brain neural oscillations during the coordination task. Our findings provide first evidence that OT enhances inter-brain synchrony in male adults to facilitate social coordination.

Key words: EEG; inter-brain synchrony; neural oscillation; oxytocin; social coordination

Introduction

The neuropeptide oxytocin (OT) plays a key role in human social interactions by modulating the underlying cognitive and neural processes (Bartz *et al.*, 2011; Meyer-Lindenberg *et al.*, 2011; Hurlemann and Scheele, 2015; Ma *et al.*, 2016). Behavioral research has shown that intranasal administration of OT compared to placebo increases social trust (Kosfeld *et al.*, 2005), enhances interpersonal coordination (Arueti *et al.*, 2013) and motivates ingroup favoritism during cooperation (De Dreu *et al.*, 2010a, 2011; De Dreu and Kret, 2015; Ma *et al.*, 2015). Brain imaging research has further revealed that intranasal administration of OT versus placebo influences social cognition and behavior by modulating the neural activity related to trusting behavior (Baumgartner *et al.*, 2008), reciprocated cooperation (Rilling *et al.*,

2012), and the processing of stimuli that probe social synchrony (Levy *et al.*, 2016). However, to our knowledge, previous brain imaging studies have focused on OT effects on an individual's brain activity related to social cognition and behavior. Social interactions require at least two brains to communicate mutually. This is particularly important for interpersonal coordination that precedes communication by means of language both evolutionarily and ontogenetically (Semin, 2007) and lays a key foundation for prosociality and cooperation (Noë, 2006; Wiltermuth and Heath, 2009; Reddish *et al.*, 2013).

Recent brain imaging research has taken advantage of hyperscanning technique that allows recording brain activity from two individuals simultaneously (Montague, 2002) to examine the functional role of inter-brain activity in social

interactions (Dumas *et al.*, 2011; Konvalinka and Roepstorff, 2012; Babiloni and Astolfi, 2014). For example, using functional magnetic resonance imaging (fMRI), researchers have localized inter-brain co-activations in the anterior and middle cingulate cortices during an economic exchange task (King-Casas *et al.*, 2005) and found enhanced inter –brain synchronization of the inferior frontal activity associated with shared attention during face-to-face communication (Koike *et al.*, 2016). Functional near infrared spectroscopy (fNIRS) and magnetoencephalographic (MEG) studies have also revealed enhanced inter-brain coherence associated with behavioral coordination during social cooperation (Cui *et al.*, 2012), leader-follower communication (Jiang *et al.*, 2015) and joint hand-action tasks (Zhdanov *et al.*, 2015). Electroencephalography (EEG) has also been used to examine dynamic inter-brain oscillatory activities with high time resolution (i.e. millisecond) (Dumas *et al.*, 2010; Astolfi *et al.*, 2012; Yun *et al.*, 2012). Particularly related to the current work, it has been shown that inter-brain synchrony in the alpha band (8–12 Hz) activity emerged and correlated with behavioral interactional synchrony (Dumas *et al.*, 2010). The alpha band inter-brain synchrony also occurred when two pilots coordinated with each other during simulating takeoff and landing (Astolfi *et al.*, 2012), suggesting that the alpha band inter-brain synchrony can be used as a neural marker of interpersonal coordination.

While the previous hyperscanning research has shown increasing evidence for a key role of inter-brain synchrony in social coordination, the molecular mechanism involved in inter-brain synchrony remains unknown. Given the previous findings of OT effects on brain activity involved in interacting behavior and the functional significance of inter-brain synchrony in social interactions, we hypothesized that OT is engaged in synchronization of neural activities of two brains during social coordination. Because the previous studies that examined inter-brain (Dumas *et al.*, 2010; Astolfi *et al.*, 2012) and intra-brain (Tognoli *et al.*, 2007) activity have shown consistent evidence for the involvement of alpha-band activity in social coordination, we further predicted that OT would enhance the inter-brain phase synchrony of alpha-band neural oscillations during coordination behavior.

Our hypothesis was tested using a novel combination of hyperscanning-EEG setup, OT (*vs* placebo) treatment and a new real-time coordination game (Figure 1). The real-time coordination game was designed for testing social coordination in which two participants (or a dyad) were instructed to count in mind with a 1-s rhythm for 6–10 s and to synchronize with each other in order to make a button press at the same time after counting (Figure 1A).The coordination task was compared with a control task, which required counting to coordinate with a computer clock, to control influences of cognitive/affective processes related to counting, social feedback and motor responses. Feedback regarding a dyad's synchronizing performance was given after counting on each trial so as to motivate participants for coordination with a partner and to help them to differentiate between coordination with a partner and synchronization with a computer. The behavioral performance and EEG activity were recorded simultaneously from a dyad via using a dual-EEG system (Figure 1B). This dual-EEG setup is suited for assessing interpersonal behavioral performance and inter-brain EEG activity and for testing the association between interpersonal behavioral synchrony (by calculating response time lags) and inter-brain synchrony (by calculating phase synchrony of continuous alpha-band activity) in a dyad. The inter-brain synchrony was estimated when a dyad viewed a fixation

without any action and thus was not contaminated by synchronous perceptual processing and motor responses.

Experiment 1 aimed to identify the functional role of alpha band inter-brain synchrony in social coordination using the real-time coordination game. In addition, because it has been assumed that women develop a particular style of interacting with other women and are more cooperative with same-sex individuals compared to men (Maccoby and Jacklin, 1987; Maccoby, 1990), Experiment 1 further compared interpersonal behavioral synchrony and inter-brain synchrony in male and female dyads. A recent social adaptation model of OT function posits that the multifaceted role of OT in socio-affective processes is to improve the capability for social adaptation and the OT function is more significant in less socially adapted individuals (Ma *et al.*, 2016). If inter-brain synchrony plays a role in social adaptation, we would then expect greater OT effects on inter-brain synchrony in the subject group who show less interpersonal behavioral synchrony. Because Experiment 1 found that female relative to male dyads showed better interpersonal behavioral synchrony and greater alpha band inter-brain synchrony, Experiment 2 further investigated OT effects on inter-brain synchrony during the coordination tasks in male participants using a double blind, placebo-controlled between-subjects design. Of particular interest was whether interpersonal synchronous performance and inter-brain synchrony in male subjects could be improved by intranasal administration of OT compared to placebo. Findings of improved interpersonal coordination and inter-brain synchrony in male subjects due to OT (*vs* placebo) treatment would provide insight into the neurobiological mechanism of synchronized brain activity during social coordination.

Materials and methods

Participants

Experiment 1 recruited 68 healthy Chinese adults, including 17 male dyads (mean age $\pm$ SD = 22 $\pm$ 2 years) and 17 female dyads (mean age $\pm$ SD = 22 $\pm$ 2 years). There was no age difference between male and female groups ($t(66)$ = 1.13, P = 0.26). Experiment 2 recruited 60 male Chinese adults with 15 dyads randomly assigned to OT treatment and 15 dyads to placebo treatment (mean age $\pm$ SD = 22 $\pm$ 2 *vs* 23 $\pm$ 3 years). There was no age difference between OT and placebo groups ($t(58)$ = −0.85, P = 0.40). All participants were recruited by online advertisement and were randomly paired so that two participants of a dyad had not known each before their participation and had no discussion of strategy for the coordination game. All participants were right-handed, had normal or corrected-to-normal vision, reported no abnormal neurological history and were paid for their participation. Informed consent was obtained prior to the study. This study was approved by a local ethics committee.

Stimuli and procedure

EEG was recorded simultaneously from a dyad during the coordination and control tasks in Experiment 1. Two individuals of each dyad were seated in a sound-shielded room and separated by two monitors. All participants wore headphones to block sounds of their button press. This setup blocked both visual and auditory signals that might deliver messages between two individuals of a dyad. Stimuli were simultaneously presented to two participants of each dyad on two identical monitors and
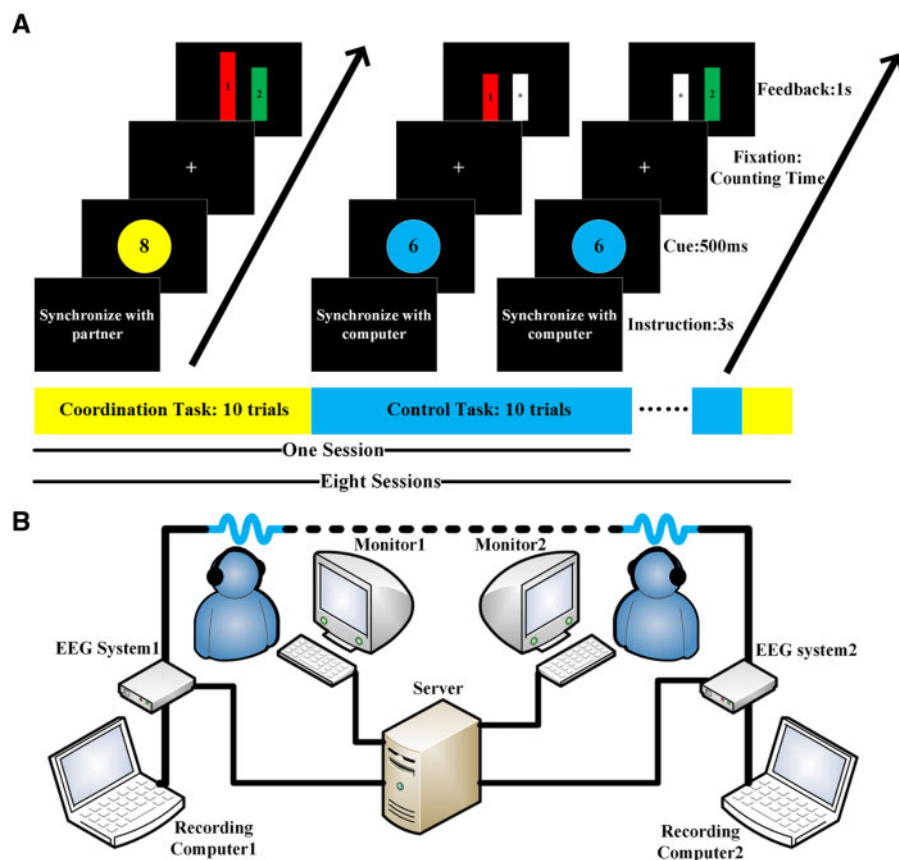
Fig. 1. Illustration of the design and EEG recording setup. (A) During EEG recording, each block of 10 trials started with a 3-s task instruction. On each trial a number was presented for 500 ms to indicate the time in second for counting in mind. Participants began to count in mind while looking at the fixation until they finished counting and pressed a button. Feedback bars were then presented for 1 s. During the coordination task, participants were asked to coordinate with their partners so as to respond simultaneously. During the control task, participants were asked to coordinate with the clock of a computer so as to count as accurately as possible. A red/green bar with numbers on a feedback screen indicated the performance of each participant in the coordination task and a white bar indicated the time recorded by a computer in the baseline task. The length of each bar represented the relative duration of participants' counting. (B) The setup for EEG recording. EEG was recorded from a dyad simultaneously and continuously using two 32-channel EEG systems. Stimuli were simultaneously presented to two individuals of a dyad on two monitors connected to the same server.

their responses were recorded using two identical keyboards. Both the monitors and keyboards were connected to the same server computer. This setup enabled to compare interpersonal behavioral synchrony and inter-brain EEG activity (Figure 1B). On each trial a dyad were presented with an integer (from 6 to 10) for 500 ms that indicated time in seconds. Participants were asked to start counting in minds once the integer was replaced by a fixation. Participants were asked to synchronize with his/her partner (the coordination task) or with a computer (the control task) during counting in order to press a button simultaneously using the left/right index finger with a partner or with a computer when finishing counting (Figure 1). The coordination and control tasks were indicated by the color (yellow or blue) of a disk on which an integer was displayed. On each trial, after a delay of 1500–2500 ms following participants' responses, feedback on their performances was displayed on each monitor simultaneously. A red and a green bar with numbers assigned to each participant were presented for 1000 ms to indicate their performances in the coordination task. A white bar with '*' indicated the time recorded by a computer in the control task. The length of each bar represented the relative duration of a participant's counting and such intuitionistic information helped participants to adjust their counting speed. The assignments of different colors to instructions and feedback bars were counterbalanced across participants. All the stimuli were created and displayed using the Matlab PsychoToolbox (Brainard, 1997; Pelli, 1997). To promote participants' motivation for synchronization, they were given a credit for each successful synchronous response (i.e. an interval less than 300 ms between the responses of a dyad or between the responses of a participant and a computer) and their payments for participation were calculated based on the credits they obtained. Prior to the EEG recording, participants were given 20 trials for practice. There were eight sessions of EEG recording. Each session consisted of two blocks of 10 trials. The order of the coordination and control tasks was counterbalanced over sessions so that half sessions started with the coordination task and half with the control task.

A double-blind, placebo-controlled between-subjects design was used in Experiment 2. The stimuli and procedures in Experiment 2 were the same as those in Experiment 1 except that 15 dyads were randomly treated with OT and 15 dyads with placebo 40 min before EEG recording. Each participant was administered with 24 IU OT or placebo (containing all of the active ingredients except for the neuropeptide) with intranasal sprays (three times of four IU into each nostril), similar to the previous work (Shamay-Tsoory *et al.*, 2009; Hurlemann *et al.*, 2010; Ma *et al.*, 2015). Before OT or placebo treatment, participants

completed the Self-Construal Scale(Singelis, 1994) and Interpersonal Reactivity Index (Davis, 1983) to assess their cultural orientations (i.e., independent/interdependent self-construals) and empathy ability.

Analysis of behavioral performance

To quantify synchronous behavior of each dyad, we calculated several indices of participants' performances during the coordination and control tasks in Experiments 1 and 2. First, the overall mean interpersonal synchrony performance of each dyad was quantified by calculating the *interpersonal time lag*:

$$\delta_{\text{inter\_i}} = |(\text{RT}_{i,\text{sub\_1}} - \text{RT}_{i,\text{sub\_2}})|/(\text{RT}_{i,\text{sub\_1}} + \text{RT}_{i,\text{sub\_2}})$$

where $\text{RT}_{i,\text{sub\_1}}$ and $\text{RT}_{i,\text{sub\_2}}$ are reaction times of two individuals of a dyad on the ith trial. A smaller $\delta_{\text{inter\_i}}$ reflects better synchrony of a dyad's responses during counting in mind.

Then, to further assess the probability distributions of highly synchronous behavior of each dyad, we applied a normal kernel function to compute probability density estimate of time lags between a dyad's behavioral responses using n ($n = 100$) equally spaced points, $x_1, \ldots, x_n$ that cover the whole range of the data (x). The kernel density estimator at the point x is defined as:

$$f(x) = \frac{1}{n}\sum_{i=1}^{n} K_{\text{h}}(x - x_i)$$

Where x_i is an independent and identically distributed sample drawn from a distribution with an estimated probability density f. K_{h} is the kernel function and h (> 0) is a smoothing parameter of the bandwidth. The probability densities were estimated in MATLAB using these parameters (Gaussian kernel, bandwidth $= 1.15$). The probability density in each two-spaced points was compared between the coordination and control tasks in Experiment 1 and between OT and placebo groups in Experiment 2. Higher probability density of trials with smaller time lags between a dyad's behavioral responses manifests better synchronous behavior.

The behavioral measures of interpersonal coordination were subjected to repeated measures analyses of variance (ANOVAs) with Task (Coordination *vs* Control Tasks) as a within-subjects independent variable in Experiment1 and with Task (Coordination *vs* Control Tasks) as a within-subjects independent variable and Treatment (OT *vs* Placebo) as a between-subjects variable in Experiment 2. Post hoc independent sample t tests on behavioral measures were conducted to test sex differences on behavioral performance of each task in Experiment 1.

Dual-EEG data acquisition and analysis

EEG was recorded from a dyad simultaneously and continuously during the coordination and control tasks using two 32-channel Neuroscan systems that received synchronizing triggers from a parallel port of a server computer (Figure 1B). EEG was recorded from 30 electrodes arranged according to the international 10/20 system and referenced to the electrode at the right mastoid. The electrode impedance was kept less than 5 kohms. Eye blinks and vertical eye movements were monitored using two electrodes located above and below the left eye. The horizontal electro-oculogram was recorded from two electrodes placed 1.5 cm lateral to the left and right external canthi. EEG was amplified (band pass 0.01–100 Hz), digitized at a

sampling rate of 250 Hz and stored for off-line analysis. During the off-line analysis, EEG was treated with band-pass filtering (0.1–45 Hz) and re-referenced to the algebraic average of the electrodes at the left and right mastoids. Regression-based approach was used for artifact rejection. The ocular channel was used to estimate the parameters of ocular artifacts which were removed from continuous EEG signal for each participant.

EEG during each trial was segmented from -200 to 6000 ms after the onset of number presentation. The 6000 ms was set as the cut off for segmentation because the range of counting time (6–10 s) is equal or longer than 6 s. After segmentation, the inter-brain phase synchrony index (phase-locking value, PLV) were quantified based on a wavelet decomposition of the signal between 8 and 13 Hz in 1 Hz steps, similar to previous studies (Linkenkaer-Hansen *et al.*, 2001; Mu *et al.*, 2008; Mu and Han, 2010; 2013). The signal was then convoluted by the complex Morlet wavelet w (t, f0) (Kronland-Martinet *et al.*, 1987) with a Gaussian shape in time (SD σt) and frequency (SD σf) domains around its central frequency f0 in the following way:

$$w(\text{t}, f_0) = A e^{(-t^2/2\sigma_t^2)} \cdot e^{2i\pi f_0 t}$$

with $\sigma_{\text{f}} = 1/2\pi\sigma_{\text{t}}$. Wavelets were normalized so that their total energy was 1. The normalization factor A was equal to: $(\sigma_{\text{t}}\sqrt{\pi})^{-1/2}$. Convolution of the signal by a family of wavelets provided a time frequency (TF) representation of the signal. A wavelet family is characterized by the number of cycles of wavelets (NCW). Here, to acquire better temporal and frequency resolution, we used slowly ascending NCWs which provide better temporal resolution at low frequencies and better frequency resolution at high frequencies, similar to the previous studies(Delorme and Makeig, 2004). From the resulting TF presentation of signal, we respectively obtained the estimates of instantaneous power and phase. For statistical analyses, the power was first normalized by conversion to a decibel scale, which allowed a direct comparison of effects across frequency bands(Pfurtscheller and Aranibar, 1979) and then divided into six consecutive 1000-ms time intervals. The ANOVAs of alpha spectral power were conducted on each electrode to test Task effect (Coordination *vs* Counting Tasks) in Experiment1 and to test the effects of Task and Treatment (OT *vs* Placebo) and Task x Treatment interactions in Experiment 2.

Similar to the previous studies (Lachaux *et al.*, 1999; Gross *et al.*, 2004; Lutz *et al.*, 2004; Doesburg *et al.*, 2008), we used the same Morlet wavelet transform to estimate the inter-brain phase synchrony in the alpha band. The phase-locking value (PLV) defined as the absolute value of the sum of the phase differences of two electrodes (j, k) at time *t* and frequency *f* across N epochs was calculated as:

$$\text{PLV}_{j,k,t} = N^{-1}|\sum_N e^{i[\Phi_j(f,t) - \Phi_k(f,t)]}|$$

PLV is a value between 0 and 1, where 0 indicates randomly dispersed phases among all trials and 1 indicates fully phase locked oscillations between electrodes *j* and *k* in a specific time window. Inter-brain phase synchrony was estimated by examining two electrodes from two individuals of a dyad. We selected 12 representative electrodes from each individual over the frontal (F3, F4, Fz), central (C3, C4, Cz), parietal (P3, P4, Pz), and occipital (O1, O2, Oz) regions for the inter-brain phase synchrony analysis, resulting in 144 (12 × 12) electrode pairs.

The modulations of inter-brain PLV were assessed using ANOVAs with Task as a within-subjects independent variable in

Experiment1 and with Task as a within-subjects independent variable and Treatment (OT *vs* Placebo) as a between-subjects variable in Experiment 2. The Greenhouse and Geisser correction was applied to ANOVAs with more than one degree of freedom, and a significance level of alpha = 0.05 was used for all comparisons (Greenhouse and Geisser, 1959). In addition, to avoid multiple comparison problems, all the EEG results reported in our paper were corrected using cluster-based correction. Clusters were defined by any three adjacent data points (each point covered 100 ms) and any three adjacent electrodes pairs. We only reported results from electrode pairs in the clusters that exceeded the cluster-level threshold (P < 0.05). Pearson correlation coefficients were computed to evaluate the relationship between behavior performance and inter-brain neural activity.

Results

Inter-brain synchrony associated with interpersonal coordination

To identify inter-brain neural oscillations related to interpersonal coordination, we first analyzed the mean interpersonal time lag between two individuals of each dyad in Experiment 1 in the coordination and control tasks, respectively. We predicted that the motivation to coordinate with a partner can increase interpersonal behavioral synchrony in a dyad during the coordination than control tasks. Indeed, the analysis of participants' behavioral performance across female and male dyads revealed a smaller mean interpersonal time lag (3.21 *vs* 3.52%, F(1,33) = 9.12, P < 0.005, Figure 2A) in the coordination than control tasks. We further examined whether the smaller mean interpersonal time lag was due to the variation of distribution of trials with smaller interpersonal time lags in the two tasks by calculating the probability density of interpersonal time lags. This analysis confirmed a higher proportion of small interpersonal time lags (<4%) (15.3 *vs* 14.3%, (F(1,33) = 7.37, P < 0.01, Figure 2B) in the coordination than control tasks. These results indicated that the motivation to coordinate with a partner (compared to a computer) promoted synchronized counting in mind and gave rise to better interpersonal behavioral synchrony.

Inter-brain synchrony during the coordination and control tasks was assessed by calculating the inter-brain *phase-locking-value* (PLV) that reflects the phase synchrony of inter-brain activities from two individuals of a dyad. The inter-brain PLV analysis focused on alpha band activity because the previous work reported increased alpha band inter-brain synchrony during interpersonal coordination (Astolfi *et al.*, 2012). The ANOVAs of PLVs revealed significantly greater PLVs of alpha-band activity between the central electrodes of one participant and the posterior electrodes of his/her partner at 4000–5000 ms during the coordination than control tasks (F(1,33) = 4.17–7.41, ps < 0.05, Figure 2C and D, Supplementary Table S1).

To further verify that the increased inter-brain synchrony was specific to two participants who constituted a dyad for coordination, we conducted a bootstrap analysis to examine whether the increased interpersonal behavioral and inter-brain synchrony in the coordination (*vs* counting) task occurred in any two individuals who did not constitute a dyad for coordination but performed similar counting tasks. Two participants from different dyads were randomly selected to create a new dyad sample and their interpersonal behavioral synchrony and inter-brain synchrony were calculated. We found that the

interpersonal behavioral synchrony and inter-brain synchrony of alpha-band activity occurred in two individuals of a dyad who tried to coordinate with each other but not in two individuals of a randomly created dyad (see Supplementary Figure S1). The results indicate that the coordination task itself was unable to induce increased inter-brain synchrony between two individuals from different dyads.

Next we examined whether the degree of inter-brain synchrony was able to predict synchronous behavioral performances across dyads. We conducted a correlation analysis of the mean differential interpersonal time lags (coordination *vs* control tasks) and the mean differential alpha band PLVs (coordination *vs* control tasks) between the central/posterior electrodes of one participant and the posterior electrodes of his/her partner at 4000–5000 ms. This analysis, after excluding one dyad as an outlier whose behavioral performances exceeded two standard deviations from the mean, confirmed that the mean PLV was negatively correlated with the differential interpersonal time lag (r(33) = −0.59, P < 0.001, Figure 2E) and positively correlated with probability density across all dyads (r(33) = 0.47, P < 0.01, Figure 2F). These results indicate that the increased alpha-band inter-brain synchrony predicted more highly synchronous behavioral performances during the coordination (*vs* control) task and thus provides a potential neural marker of social coordination.

Gender differences in interpersonal coordination and inter-brain synchrony

To examine gender differences in interpersonal coordination, we conducted independent sample t-tests to compare the behavioral measures between female and male dyads in Experiment 1. The results of the mean interpersonal time lag of the coordination task was significantly smaller in female than male dyads (2.97 *vs* 3.45%, t(32) = −2.05, P < 0.05). In line with this, the probability density of small interpersonal time lags (<4%) was greater in female than male dyads (16.30 *vs* 14.22%, t(32) = 2.41, P < 0.05, Figure 3A). However, there was no significant difference in these behavioral indexes of interpersonal coordination in the control task between female and male dyads (mean interpersonal time lag: 3.30 *vs* 3.74%, t(32) = −1.46, P = 0.15; probability density of small interpersonal time lags: 14.99 *vs* 13.51%, t(32) = 1.59, P = 0.12, Figure 3B). These results suggested better interpersonal coordination in female than male dyads.

Interestingly, the analysis of EEG data further revealed significant gender differences in alpha band inter-brain synchrony between male and female dyads. Specially, female compared to male dyads exhibited stronger task effects on the inter-brain synchrony of alpha band activity between the posterior electrodes from two individuals of a dyad at 4000–5000 ms (F(1,32) = 5.49 to 9.04, ps < 0.05, Figure 4A. Post hoc analyses further confirmed that female relative to male dyads exhibited stronger inter-brain synchrony of alpha band activity during the coordination task (t(32) = 2.17 to 3.11, ps < 0.05) but weaker alpha band inter-brain synchrony in the control task (t(32) = −2.11 to −3.17, ps < 0.05). Figure 4B illustrates the electrodes that showed increased interbrain alpha band synchrony in female than male dyads during the coordination task.

Improved interpersonal coordination by OT

Because Experiment 1 showed evidence that male compared to female dyads showed less interpersonal coordination and
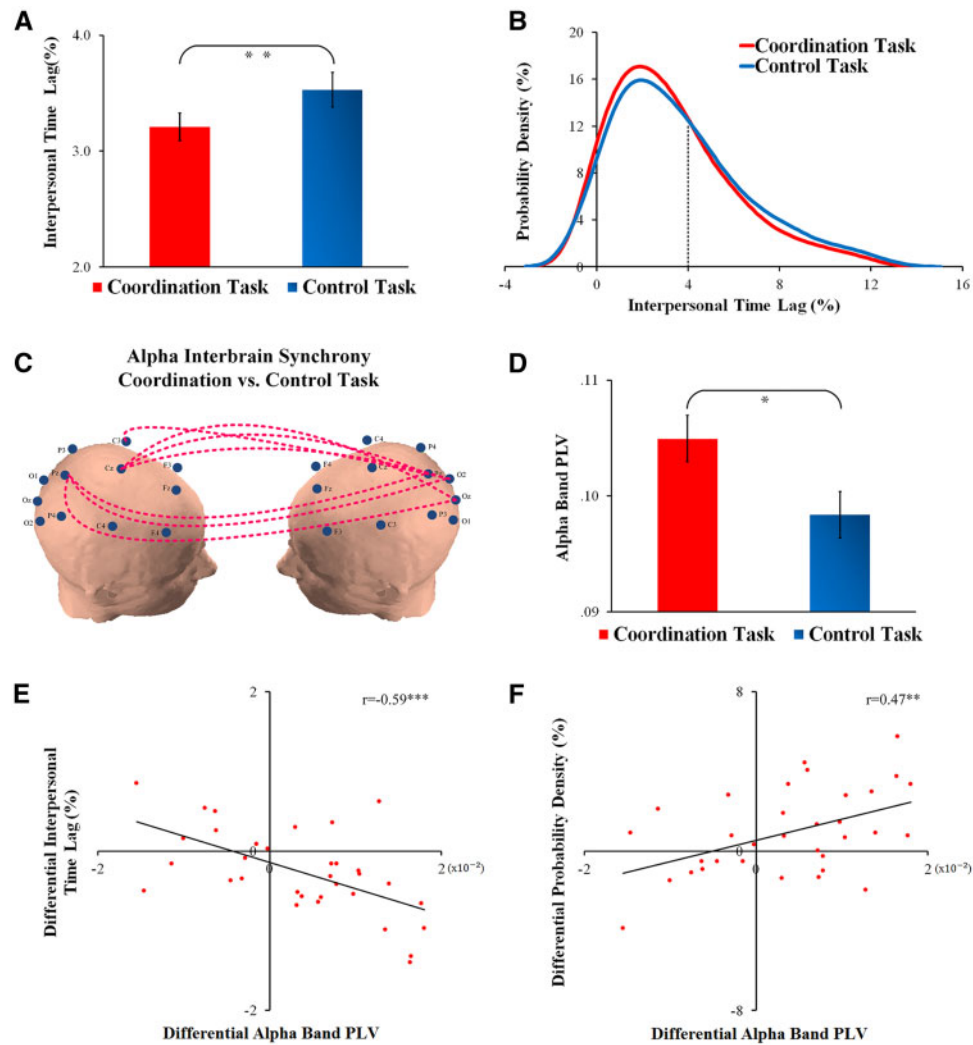
Fig. 2. Behavioral and EEG results of Experiment 1. (A) The mean interpersonal time lags during the coordination and control tasks. (B) The probability density estimation of interpersonal time lags during the coordination and control task. (C) The electrode pairs that showed enhanced alpha-band inter-brain PLVs in the coordination *vs* control tasks. These were evident mainly between the central/posterior electrodes of one participant and the posterior electrodes of his/her partner at 4000–5000 ms. (D) The mean inter-brain PLV between the central/posterior electrodes of one participant and the posterior electrodes of his/her partner at 4000–5000 ms during the coordination than control tasks. (E) The negative correlation between differential interpersonal time lag and differential alpha-band inter-brain PLV in the coordination and control tasks. (F) The positive correlation between differential probability density and differential alpha-band inter-brain PLV in the coordination and control tasks. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

weaker inter-brain synchrony during the coordination task, Experiment 2 recruited only male dyads to examine potential OT effects on interpersonal coordination and inter-brain synchrony. In Experiment 2, each male dyad were randomly assigned to one of the two treatment conditions (OT or placebo) and were then instructed to perform the coordination and control tasks that were identical to those in Experiment 1. EEG signals were recorded simultaneously from two participants of a dyad. We first tested whether OT *vs* placebo treatment facilitated interpersonal synchrony by calculating interpersonal time lags in the coordination and control tasks, respectively. 2 (Task: coordination *vs* control tasks) x 2 (Treatment: OT *vs* placebo) ANOVAs of behavioral performance showed significant main effect of Task on the mean interpersonal time lag (coordination *vs* control tasks: 3.12 *vs* 3.41%, $F(1, 28) = 11.32$, $P < 0.005$) and the probability density of smaller time lags (coordination *vs* control tasks: 15.0 *vs* 14.2%, $F(1, 28) = 6.57$, $P < 0.05$). These results replicated the findings of Experiment 1 and suggested better

interpersonal synchrony during the coordination relative to control tasks across treatment groups. Moreover, there was a significant effect of Treatment on the two behavioral indexes of coordination (mean interpersonal time lag: $F(1, 28) = 10.18$, $P < 0.005$; probability density of small interpersonal time lag: $F(1, 28) = 11.36$, $P < 0.002$, see Figure 5A and B), indicating that OT treatment improved interpersonal synchronous performances. However, OT effects on behavioral synchrony did not differ between two tasks (mean interpersonal time lag: $F(1, 28) = 0.96$, $P = 0.34$; probability density of small interpersonal time lag: $F(1, 28) = 0.01$, $P = 0.94$), suggesting that OT promotes behavioral synchronous performance regardless of type of partner (person *vs* computer). Because the previous research suggested that OT effects on both brain (Liu *et al.*, 2013) and behavioral (Pfundmair *et al.*, 2014) responses varied across individuals with different personal traits, we collected measures of self-construals and empathy traits from participants in Experiment 2 before EEG recording. These measures did not differ between placebo and OT
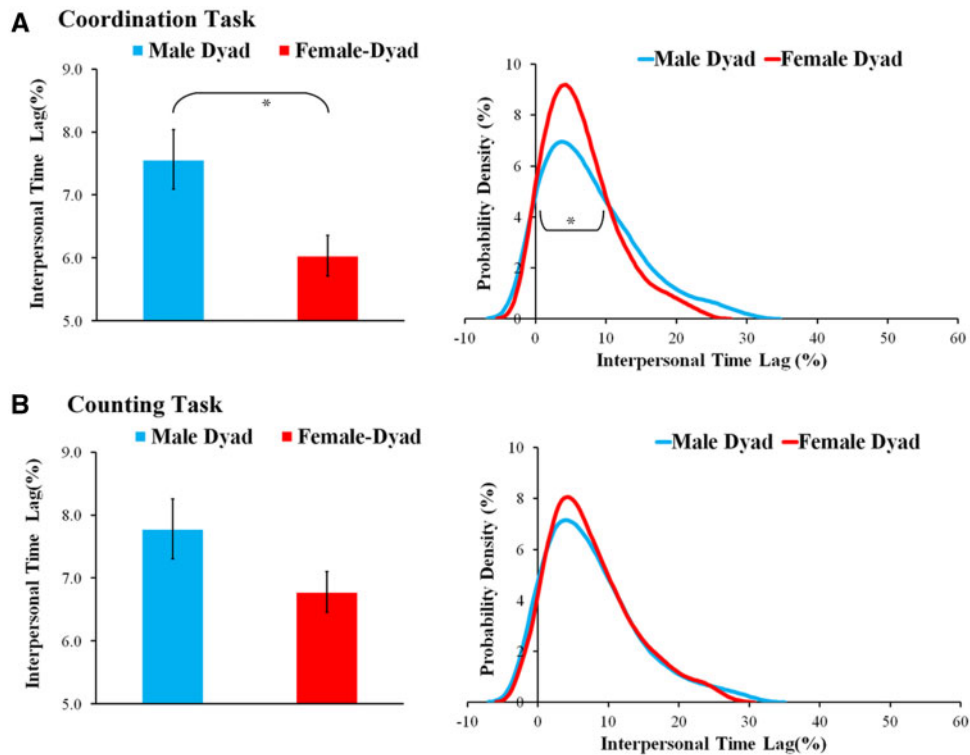
Fig. 3. Gender differences in behavioral performances in Experiment 1. (A) The mean value (left panel) of interpersonal time lags and the probability density estimation (right panel) of female and male dyads during the coordination task. (B) The mean value (left panel) of interpersonal time lags and the probability density estimation (right panel) of female and male dyads during the counting task.
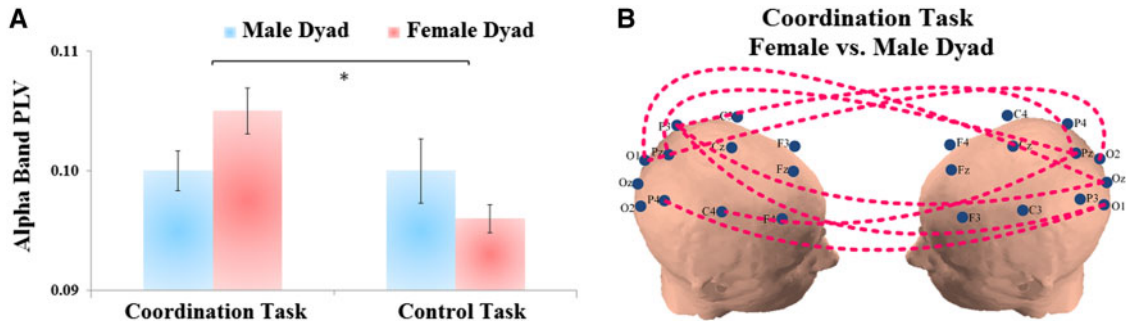

Fig. 4. Gender differences in interbrain activity in Experiment 1. (A) Gender differences in the alpha band inter-brain phase synchrony at 4000–5000 ms. The mean values of inter-brain PLV over the central/posterior electrodes in each condition are illustrated for female and male dyads, respectively. (B) The electrodes showing increased alpha band inter-brain synchrony in female than male dyads during the coordination task.

groups (ps > 0.05, see Supplementary Table S2), indicating that the group differences in interpersonal coordination in Experiment 2 cannot be attributed to group differences in personal traits. To examine dynamic change of behavioral synchrony and OT effects over time, we conducted a growth coefficient modeling (RCM) analysis to assess whether OT modulations on interpersonal time lag changed over time. The RCM results showed evidence for decreased interpersonal time lag over time, whereas the OT effect on interpersonal coordination failed to change over time (see supplementary Results and Table S3 for details).

Improved inter-brain synchrony by OT

To examine OT effects on inter-brain synchrony during interpersonal coordination, we calculated the alpha-band PLVs in the OT and placebo groups, respectively. ANOVAs of the PLVs with Task (coordination vs control tasks) as a within-subjects variable and Treatment (OT vs placebo) as a between-subjects variable revealed greater PLVs of alpha-band activity at 4000-6000 ms between the posterior regions of the two brains of a dyad during the coordination than control tasks ($F_{(1,28)}$ = 4.19–9.15, ps < 0.05, Figure 5C, Supplementary Table S4), indicating increased alpha band inter-brain synchrony when coordinating with a partner compared to a computer. Moreover, relative to the control task, the coordination task showed stronger OT effects on the inter-brain synchrony of alpha-band activity at 1000–3000 ms between the central region of one participant and the posterior regions of his partner ($F_{(1,28)}$ = 5.39–9.88, ps < 0.05, Figure 5D, Supplementary Table S5). Post hoc analyses confirmed that OT vs placebo treatments increased inter-brain synchrony of alpha-band
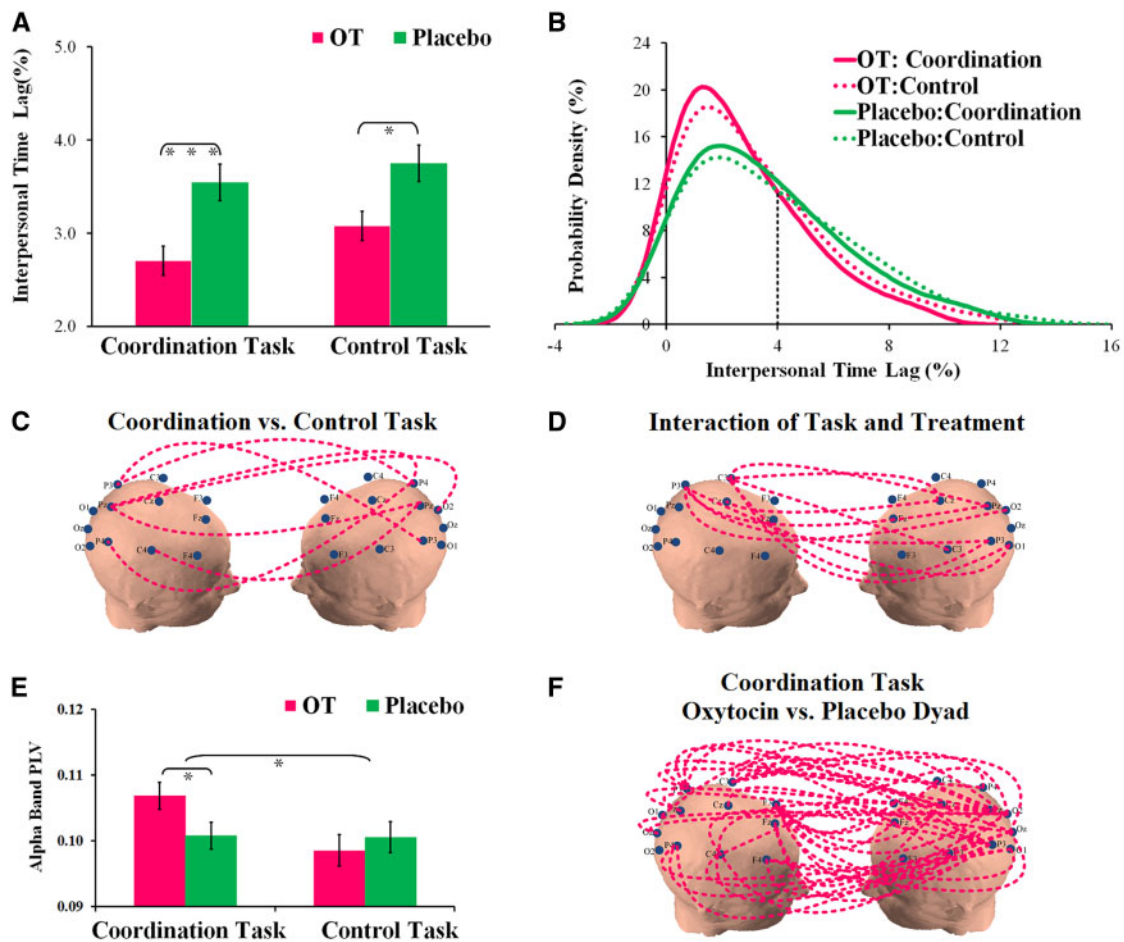
Fig. 5. Behavioral and EEG results of Experiment 2. (A) The mean interpersonal time lags of the OT and placebo groups during the coordination and control tasks. (B) The probability density estimation of interpersonal time lags of OT and placebo groups during the coordination task and control tasks. (C) The electrode pairs that showed enhanced alpha-band inter-brain PLVs at 4000–6000 ms in the coordination (*vs* control) task. These were evident mainly between the posterior regions of the two brains of a dyad. (D) The electrode pairs that showed significant Task (Coordination, Control) x Treatment (Placebo, OT) interaction at 1000–3000 ms. These were evident mainly between the central/posterior electrodes of one participant and the posterior electrodes of his/her partner. (E) The mean alpha-band inter-brain PLV between central and posterior electrodes at 1000–3000 ms of OT and placebo groups. There were significant OT effects during the coordination but not control tasks. F) The electrodes that showed increased alpha-band inter-brain PLVs by OT (*vs* placebo) treatment during the coordination task. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

oscillations at 1000–3000 ms during the coordination task (ps < 0.05) but not during the control task (ps > 0.05, Figure 5E and F, Supplementary Table S5).

Discussion

The current study investigated the functional role of inter-brain synchrony in social coordination based on simultaneous counting in mind in two individuals and the potential function of OT in inter-brain synchrony. Experiment 1 revealed increased interpersonal behavioral synchrony, as indexed by smaller interpersonal time lags of behavioral responses, when a participant coordinated with a partner than with a computer. This finding provided evidence that the motivation to coordinate with each other can improve a dyad's synchronous responses even when no visual or aural cues were available to guide their coordination. In addition, dyads showed enhanced inter-brain synchrony of alpha-band neural oscillations (indexed by larger inter-brain PLVs) when coordinating with a partner compared with a computer. Furthermore, the degree of alpha-band inter-brain synchrony positively predicted synchronous behavioral performances across dyads. The inter-brain synchrony of

alpha-band activity emerged within a time window (e.g., 4000–5000 ms) close to behavioral responses rather than immediately after participants started to count in mind. These EEG results were mainly due to the effect of intention of coordination because any processes related to perception, timing and motor responses were comparable in the coordination and control tasks. The inter-brain synchrony observed in our work occurred later than that observed during face-to-face imitation of hand movement (Dumas *et al.*, 2010). It seemed that some time was required for adjusting the phase of neural oscillations in order to reach inter-brain synchrony when participants were unable to see/hear each other but tried to coordinate with each other in mind. A neural circuit consisting of the supplementary motor area, basal ganglia and cerebellum is activated during interval timing (Buhusi and Meck, 2005). The parietal cortex and visual cortex are also engaged in event timing (Coull *et al.*, 2004; Zhou *et al.*, 2014). Consistent with these findings, the inter-brain synchrony of alpha-band neural oscillations in our work took place between the central/posterior electrodes in a dyad. Previous research has reported inter-brain synchrony of neural synchronization in a wide range of frequency bands depending on the tasks participants performed (Astolfi *et al.*, 2010; Dumas *et al.*,

2010). The task in our study required counting in mind with a low frequency (i.e., in a 1-s step) and this may be why the coordination task enhanced the inter-brain synchrony in the alpha-band activity.

Most interestingly, our findings provided the first neuroscience evidence that OT is engaged in inter-brain synchrony during social coordination. Experiment 2 first showed that intranasal administration of OT *vs* placebo significantly reduced interpersonal time lags and increased the number of highly synchronous responses during the coordination task in male dyads. In addition, the effect of OT on interpersonal time lags was sustained over time. These results indicate that OT can improve behavioral synchrony even when dyads were unable to receive any visual or aural cues (e.g., body movement and verbal instruction) from each other and reinforces the previous findings of OT-related improvement of behavioral coordination (Astolfi *et al.*, 2010; Arueti *et al.*, 2013). Experiment 2 also showed that OT increased behavioral synchrony in the control task. Recent research has shown that OT can increase people's tendency to anthropomorphize a non-social agent (Scheele *et al.*, 2015). It is likely that participants under OT treatment may attribute social meaning to a computer so as to treat it like a person. Alternatively, OT may generally increase participants' motivation for good performance during their participation. Most interestingly, Experiment 2 showed evidence that OT compared to placebo treatment significantly enhanced inter-brain synchrony of alpha-band activity in the coordination task. Unlike the EEG results in Experiment 1, the increased alpha-band inter-brain synchrony in the coordination *vs* control tasks in Experiment 2 was evident at 1000–3000 ms after participants had started to count in mind. This result suggests that OT compared to placebo treatment modulated the brain activity associated with interpersonal coordination by shifting inter-brain synchrony to an earlier and wider time window. Although OT treatment reduced the interpersonal time lags during the control task, the related inter-brain synchrony was not affected by OT treatment. Thus the OT effect on inter-brain synchrony was specific to the coordination task during which two participants of a dyad intended to coordinate with each other by counting in mind.

Previous brain imaging studies have uncovered OT effects on neural responses related to trusting behavior (Baumgartner *et al.*, 2008), reciprocated cooperation (Rilling *et al.*, 2012) and social synchrony (Levy *et al.*, 2016). These studies focused on OT effects on intra-brain activity related to social behavior but did not clarify OT effects on inter-brain activity involved in social interactions. Our findings that OT enhanced alpha-band inter-brain neural activity that covaried with and predicted interpersonal behavioral synchrony suggest an OT-related neurobiological mechanism that helps to couple two agents' minds and may mediates the OT improvement effects on interpersonal motor coordination (Arueti *et al.*, 2013) and social cooperation (De Dreu *et al.*, 2010a). Behavioral synchrony has novel affective and social consequences regarding cooperation such that movement synchrony is associated with stronger feelings of rapport (Bernieri, 1988) and belonging to a social unit (Lakens, 2010). People who synchronize with others relative to controls showed a greater tendency to cooperate with others in group economic exercises (Wiltermuth and Heath, 2009) and more compassion and altruistic behavior (Valdesolo and Desteno, 2011). Our EEG findings suggest a new intermedial neural mechanism (e.g., inter-brain synchrony) by which OT influences interpersonal coordination and social cooperation.

Our results in Experiment 1 showed evidence for better behavioral synchrony in female than male dyads when synchronization with a partner (compared to a computer). In consistent with the better behavioral synchrony, female dyads also showed enhanced inter-brain synchrony of alpha-band neural oscillations relative to male dyads. The results are consistent with a sociocultural perspective that emphasizes the role of ontogenetic experiences and assumes that women surpass men during cooperation with same-sex individuals (Maccoby and Jacklin, 1987; Maccoby, 1990). It has been reported that OT, as a peptide hormone of which the plasma level is higher in female than male animals (Kramer *et al.*, 2004) and the serum level increases after social interaction in women but not in men (Miller *et al.*, 2009). Thus one may speculate that the higher plasma level of OT may contribute to the greater inter-brain oscillatory synchronization and facilitate interpersonal synchrony in females. Female advantages in behavioral and its neural synchrony mechanism provide further insight into molecular mechanisms of synchronized mind and brain activity.

Several theoretical frameworks have been proposed to account for OT effects on human cognition and behavior. The salience account argues that OT regulates the salience of social cues through its interaction with cognitive (e.g., attention) and neural (e.g., the dopaminergic) systems (Shamay-Tsoory and Abu-Akel, 2015). Other accounts emphasizes that OT enhances affiliative prosocial behaviors (Zak *et al.*, 2007), attenuates stress during social interaction (McCarthy *et al.*, 1996) and regulates cooperation and conflict among individuals in the context of intergroup relations (De Dreu *et al.*, 2010a; 2010b). The OT effects on the inter-brain synchrony observed in the current study occurred when no social cue was presented (i.e., participants only viewed a fixation cross) and participants did not engage any interacting behavior or intergroup interactions, and thus cannot be reconciled with these theoretical frameworks. However, our EEG findings can be understood within a recent social adaptation model of OT function that argues that the fundamental function of OT is to promote social adaptation by modulating mental processes and adjusting behaviors during social interactions (Ma *et al.*, 2016). Alpha-band oscillations have been suggested to be related to the understanding of others' mental states, emotion and behavior (Muthukumaraswamy and Johnson, 2004; Oberman *et al.*, 2005; Oberman *et al.*, 2008).Thus the enhanced alpha-band inter-brain synchrony by OT observed in the current study may reflect a consequence of motivation to understand other mental states so as to coordinate with others well, suggesting a fundamental neurobiological mechanism for social adaption.

The current work has several limitations which should be addressed in future research. For example, the current work tested OT effects on inter-brain synchrony during coordination only in male participants. Because previous studies have shown evidence for distinct OT effects on neural underpinnings of social cognitive/affective processes in male and female participants (Kirsch *et al.*, 2005; Domes *et al.*, 2010; Ditzen *et al.*, 2012), future research should integrate EEG recording and intranasal administration of OT to clarify whether OT increases or decreases inter-brain synchrony during coordination in female participants. Second, the small sample size in our work limited the statistical power of EEG data analysis. The alpha band PLV did not differ significantly between the coordination and control tasks in male participants. Thus it is unknown whether the task modulation of the alpha band inter-brain synchrony can be observed in a large sample. Moreover, although the OT effect on inter-brain synchrony during coordination was observed in our sample, this should also be confirmed in a large sample. Third, the spatial resolution of EEG makes it difficult to localize the brain regions

involved in the coordination task employed in our work. Future research calls for integration of different imaging techniques (e.g. hyperscanning fMRI-EEG) to identify the neural circuit that is sensitive to OT effects during the social coordination task. Finally, as pointed out by Burgess (2013), the alpha band results are more likely to be challenged by spurious coupling. To avoid this, our study included the control task which was identical to the coordination task except that participants had to synchronize with a computer. The coordination and control tasks were matched in stimuli and motor responses so as to reduce spurious EEG coupling to a minimum degree. Future studies should develop other paradigms to measure inter-brain synchrony that can exclude the effect of spurious hyperconnectivity.

In conclusion, our EEG findings cast new light on the neural and molecular mechanisms that facilitate the coupling of two agents' mind and improve interpersonal behavioral coordination. These mechanisms may assist the processes underlying social cooperation when body signals and verbal information are not available for two individuals to coordinate with each other. Given the increasing evidence for OT influences on social cognition and behavior, future research should clarify the functional role of OT-promoted inter-brain synchrony in complicated social interactions such as social cooperation and intergroup conflict.

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Supplementary data

Supplementary data are available at *SCAN* online.

Conflict of interest. None declared.

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