

What cognitive processes underlie inter-brain synchronization during tacit coordination?

J. A. Blankestijn

University of Groningen

Supervisor: M. K. Van Vugt, Dr.

Date: 18-02-2020

Abstract

Contemporary research found that neural signals tend to synchronize during coordination. This study investigated cognitive processes underlying inter-brain synchrony while coordinating. During a tacit coordination task electroencephalography (EEG) data was simultaneously recorded for paired participants. Their goal was to choose matching images without talking nor seeing each other, only using each other's choices as feedback. Pairs succeeded in matching more often than shuffled participants. Moreover, participants learned to coordinate better over time. Namely, matching performance increased significantly over trials. Successful coordination requires thinking about each other's beliefs and intentions (theory of mind; ToM). Therefore, it was hypothesized that inter-brain synchrony in the alpha band (9-14 Hz) reflected ToM processing. Overlapping attentional resources with working memory might impair ToM processing. Consequently, it was expected that coordination and synchrony decrease with higher working memory load. In this study a high load n-back task decreased coordination performance, but not inter-brain synchrony. Due to limited EEG (one session) and behavioral (four sessions) data, results should be interpreted lightly. However, coordination performance and right parieto-occipital phase locked inter-brain synchrony might be related. This regional synchrony potentially reflects that people learn to attend and integrate similar stimulus features during the task in order to coordinate.

Introduction

According to definition, being on the same wavelength means: “to think or behave similarly” (Farlex Dictionary of Idioms, 2015). Whilst the saying itself does not refer to brainwaves, cooperation might require brain signals to be on the same wavelength. The empirical phenomenon where two brains show similar activity during a task is called inter-brain synchrony (Hasson, Ghazanfar, Galantucci, Garrod, & Keysers, 2012). To measure synchrony neural activity from two brains is recorded simultaneously, which is called ‘hyperscanning’ (Astolfi et al., 2011). Inter-brain synchrony is hypothesized to be a neural measure for cooperative behavior (Alstolfi et al., 2011).

Hasson et al. (2012) define inter-brain synchrony as brain-to-brain coupling. Synchronous neural patterns could be interpreted as the coupling of two brains through a physical stimulus, which can be sound (auditory), light (visual), pressure (tactile) or a chemical (olfactory) compound (Hasson et al., 2012). Inter-brain synchrony could be caused by several things, like having the same neural response to the same stimulus input (Szymanski et al., 2017). However, contemporary literature investigated social coordination tasks, and found that brainwaves of two cooperating participants show increased synchrony (Astolfi et al., 2011). For example, Toppi et al. (2016) showed that inter-connections between brains of two pilots were denser during the cooperation intensive takeoff and landing phases compared to cruising. Moreover, inter-brain synchrony has been observed in many different contexts. These will be discussed in the following sections on communication, movements, coordination and cooperative games.

Inter-brain synchrony in social contexts

First, during communication, seeing mouth movements of a speaker was shown to amplify brain signals of a listener, predicting speech and making speech more comprehensible (Schroeder et al., 2008; Stephens, Silbert and Hasson, 2010). More specifically, Stephens et

al. (2010) performed an inter-subject correlation analysis on functional magnetic resonance imaging (fMRI) data. They found that during successful communication, speakers' and listeners' neural response patterns were spatially and temporally coupled. Particularly in auditory and parietal areas, the temporoparietal junction (TPJ), and inferior frontal gyrus (IFG). Additionally, it was concluded that more coupling and greater anticipatory neural responses were associated with better comprehension (Stephens et al., 2010).

Second, synchrony was shown to be related to (coordinated) movements as well. Namely, inter-brain synchrony as measured by between-brain Granger Causality was related to interpreting gestures ('charades') in a fMRI machine (Schippers et al., 2010). During fMRI people cannot move. Therefore, hyperscanning studies on movement have generally been performed using EEG. Phase locked alpha (9-14 Hz) synchrony in the right centro-parietal region was found to be related to coordinated hand movements (Dumas, Nadel, Soussignan, Martinerie, & Garnero 2010; Dumas, Chavez, Nadel, & Martinerie 2012). Also, synchrony in the alpha band was related to finger movements (Naeem, Prasad, Watson, & Kelso, 2012) as well as synchronously swinging a pendulum (Fitzpatrick, Mitchell, Schmidt, Kennedy, & Frazier, 2019). Therefore, coordinated movements were shown to elicit synchrony in the alpha band.

Apart from communication and movements, other coordination tasks elicited synchrony as well. Using EEG, Babiloni et al. (2011; 2012) found a correlation between alpha waves (9-14 Hz) in the IFG and empathy during joint music making. In addition, Sanger, Muller and Lindenberger (2013) found a relation between phase locking synchrony and joint music making in central and frontal electrodes in the delta (1-4 Hz) and theta (5-8 Hz) frequency bands. Moreover, delta band phase locking synchrony in frontal and parietal electrodes was related to better task performance during joint visual search (Szymanski et al., 2017). Furthermore, better coordination during threat detection was associated with greater

phase locking synchrony in the gamma band (Mu, Han, & Gelfand, 2017). In short, communication, coordinated movements and coordination have been associated with inter-brain synchrony. However, it remains to be shown what cognitive processes underlie synchrony during social interactions.

Cooperative games

Cooperative games are generally used to study social interactions in a more formal way (Babiloni & Astolfi, 2014; De Vico Fallini et al., 2010). Multiple hyperscanning EEG studies have investigated the neural basis of social interaction using cooperative games (De Vico Fallini et al., 2010; Astolfi et al., 2010a, 2011; Jahng, Kralik, Hwang, & Jeong, 2017). The Prisoner's dilemma task is such a two-player, multiple round game. Each round, players can either choose to cooperate or defect. When both players cooperate, both gain a reward and if both defect, no-one gets a reward. However, if one cooperates while the other defects, the defector gets a reward. To successfully perform this task, people have to reason about each other's intentions (Jahng et al., 2017). Reasoning about beliefs, intentions and desires of others is called Theory of Mind (ToM; Bock, Gallaway, & Hund, 2015). ToM is an important cognitive process for social interactions (Babiloni & Astolfi, 2014). The structures underlying ToM have been called the mentalizing network (Babiloni & Astolfi, 2014). These are the (ventro-)medial prefrontal cortex (mPFC; Schippers et al., 2011; Babiloni & Astolfi, 2014), the TPJ (Frith & Frith, 2006; Keysers & Gazzola, 2007; Babiloni & Astolfi, 2014) and the anterior cingulate cortex (ACC; Babiloni & Astolfi, 2014; Schnell, Bluschke, Konradt, & Walter, 2011; De Fico Fallini et al., 2010).

Parts of the mentalizing network seem to be synchronize during the Prisoner's dilemma. De Vico Fallini et al. (2010) found more inter-brain links during cooperation versus defecting in the PFC (see also Chung, Yun, & Jeong, 2008) and the ACC in multiple frequency bands. Moreover, they showed that double defecting could be predicted in 90% of

cases by investigating hyperconnections. What is more, in a Prisoner's dilemma task, using phase locking synchrony, Jahng et al. (2017) showed greater alpha and beta synchrony when people were face-to-face with each other compared to when they could not see each other. Results showed greater frontal and frontocentral (PFC) alpha synchrony when both players cooperated. Moreover, there was greater alpha synchrony in the right (temporo-)parietal area (which overlaps with the TPJ) when both defected compared to when both cooperated. However, Astolfi et al (2010a; 2011) used partial directed coherence to show greater beta and theta band synchrony in pre- and orbitofrontal regions during defection. Also, prefrontal and orbitofrontal theta synchrony was greater compared to rest. However, the bilateral anterior PFC showed greater theta band synchrony during cooperation. Lastly, PFC alpha band connectivity was greater during success compared to defeat in a cooperative card game (Astolfi et al., 2010b). In short, inter-brain synchrony in the PFC, ACC and TPJ, mainly in the alpha frequency band, seems to be related to tasks that involve thinking about each other's intentions (ToM).

Tacit coordination

As aforementioned, communication (Stephens et al., 2010) as well as being face-to-face with each other (Jahng et al., 2017) can increase synchrony in the PFC as well as the TPJ. If inter-brain synchrony in the alpha band is related to ToM processes, then synchrony should increase when people coordinate successfully, but cannot see nor talk to each other. This is called tacit coordination (Alberti, Sugden, & Tsutsui, 2012). During tacit coordination tasks, people will have to take each other's perspective (ToM) in order to perform well (Alberti et al., 2012). Alberti et al. (2012) investigated such a task, in which participants need to choose matching images. The images can be chosen based on a number of different dimensions (e.g. color, contrast, prettiness, etc.). Participants only receive feedback on whether they chose matching or non-matching images but cannot see nor communicate with each other.

Coordination performance (i.e. matching frequency) was significantly better than chance (Alberti et al., 2012). As mentioned, tacit coordination requires ToM and cooperative games showed increased frontal alpha synchrony (Astolfi et al., 2010b; 2011; Jahng et al., 2017; De Vico Fallani et al., 2010). Therefore, successful tacit coordination performance might be related to frontal alpha synchrony. But how can we show that ToM is the cognitive process underlying synchrony? One way is to manipulate ToM processing.

Theory of mind impaired during higher working memory load

A factor that affects people's ability to engage in ToM reasoning is executive functioning (Bock et al., 2015). Executive functioning is a broad term used to describe goal directed thoughts and behaviors. Research indicates that executive functioning influences the ability to reason about another's mental states (Bock et al., 2015). Executive functioning has often been linked to the emergence of ToM in early childhood, since both show related developmental progress (Bock et al., 2015). In addition, Bock et al. (2015) showed that even in middle childhood executive functioning predicted performance on a "social stories" ToM task.

One of the main executive functioning components is working memory; the ability to keep information in mind or manipulate it for a global task goal (Bock et al., 2015). A higher working memory load causes interference in ToM processes (Bull, Phillips, & Conway, 2008; Qureshi, Apperly, & Samson, 2010; Schneider, Lam, Bayliss, & Dux, 2012). Schneider et al. (2012) investigated an implicit ToM task, where participants concurrently counted sounds in a high load condition. In it, people observed a videotaped person who was looking for an object. In control conditions, observers generally look at the place where the videotaped person thinks an object is. However, during higher load, observers eye movements did not (Schneider et al., 2012). Moreover, Bull et al. (2008) found that interpreting stories (ToM task) while concurrently performing an n-back task (working memory task) reduces

performance in both tasks. Furthermore, Qureshi et al. (2010) found that concurrently performing an n-back task interfered with reaction times and accuracy in perspective taking. So, working memory and ToM are related and might compete for limited overlapping attentional resources (Bull et al., 2008). Since tacit coordination requires taking the each other's perspective (ToM) to match, coordination performance should be disrupted when working memory load is increased.

Research question

Our study investigated what the underlying cognitive processes of inter-brain synchrony are by performing a tacit coordination task (adapted from Alberti et al., 2012), while manipulating working memory load. The question is: does inter-brain synchrony underlie successful tacit coordination performance? Furthermore, does working memory load disrupt coordination performance and synchrony?

To address these questions, firstly it needs to be known whether people can successfully coordinate on this task. It is expected that picture matching performance within paired participants will be higher than randomly shuffled participants. Also, it is expected that if people can coordinate successfully during this task, matching performance should increase over trials. Secondly, if inter-brain synchrony reflects synchronous cognitive processes within pairs, coordination performance and inter-brain synchrony should be associated with each other (Szymanski et al., 2017). Lastly, ToM processes are required for successful tacit coordination (Alberti et al., 2012). Therefore, if ToM processes underlie inter-brain synchrony, then matching performance and inter-brain should decrease with higher working memory load.

Methods

Participants and design

In this study eight men were recruited who reported no previous history of neurological injury or illness and had normal or corrected-to-normal vision. They were divided into four pairs. Only males were recruited due to sex differences in coordination and inter-brain synchrony (Baker et al., 2016; Cheng, Xiaojun, Li, & Hu, 2015; Mu, Guo, & Han, 2016). All participants were students from the University of Groningen. They were aged between 20 and 28 years old ($M_{\text{age}} = 23.25$, $SD_{\text{age}} = 3.49$). The participants were compensated for the study with eight euros per hour. To motivate participants, they received extra compensation (with a maximum of eight euros) based on task performance. An average session took roughly two hours. The study was approved by the local ethics committee.

To recruit participants, a recruitment poster was posted in a Facebook group and emailing list for researchers in Groningen seeking participants. After signing up participants received a form with a color blindness test (<https://enchroma.com/pages/color-blindness-test>) and general demographic questions (i.e. age, nationality, study). Before the experiment began questionnaires were filled in. The following questionnaires were set up in Google Forms: an empathy test (the Interpersonal Reactivity Index; Davis, 1980), a social anxiety test (Interaction Anxiousness Scale; Leary, 1983) and a Autism Spectrum Quotient test (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001).

EEG recording

During the experiment, participant pairs sat on two chairs in a room behind two monitors which were set to the same resolution (see Figure 1). To avoid the possibility of verbal or nonverbal communication, their view of each other was obstructed by a closet in between them. The behavioral task was created in OpenSesame (Mathôt, Schreij, & Theeuwes, 2012). Pairs were individually hooked up to a Biosemi electroencephalography

(EEG) system. Therefore, there were two EEG systems, with data from the ‘slave’ AD-box fed to the ‘master’ via a fiber optic cable using daisy chain technology. The master sent data via this fiber optic cable to a USB receiver connected to the EEG data acquisition machine. The stimulus presentation machine displayed the behavioral computer-based task to two separate monitors and sent EEG triggers via parallel port to the USB receiver. These EEGs had 32 electrodes for the scalp and six external electrodes. The electrodes were placed according to the international 10/20 system and recorded in the ActiView program (for more information on hyperscanning setup see; Barraza, Dumas, Liu, Blanco-Gomez, van den Heuvel, Baart, & Pérez, 2019). Four external electrodes were placed besides the outer side of the eyes and above and below the left eye to detect eye blinks and movement. Also, two reference electrodes were placed behind the ears on the mastoids. These locations are preferred since they are close to the other electrodes, but do not record as much signal from the brain. Therefore, they can be used as indicators of noise.

Procedure

First, the task was explained to participants. Then they then signed an informed consent form. Afterwards the aforementioned questionnaires were filled out. Finally, the EEG was set up in roughly 30 minutes, and then the task began.

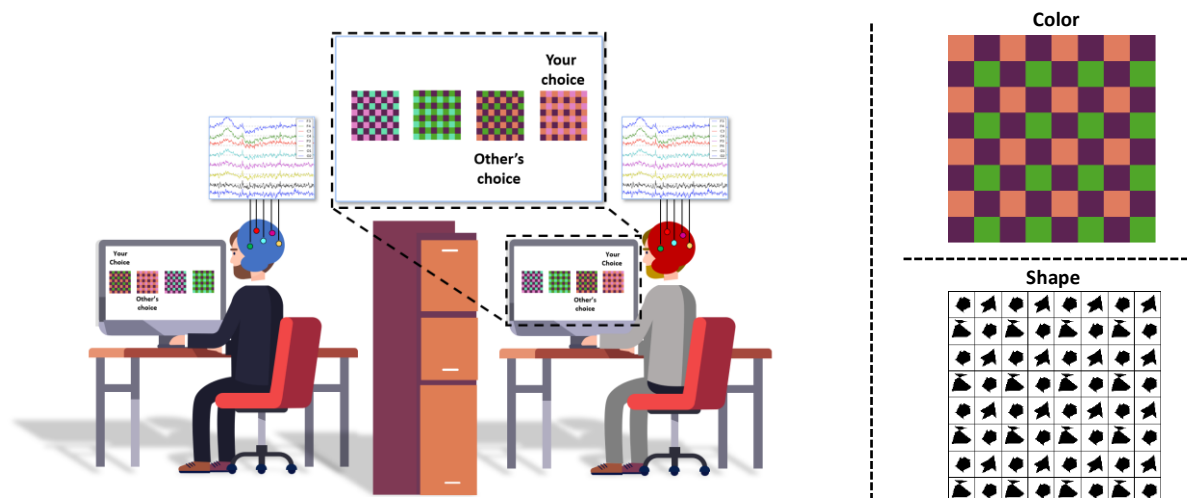


Figure 1. Example of the tacit coordination task (left). After both participants have chosen an image, their choice and the other's shows on their screens. The choice stimuli were either color matrices (top-right) or shape matrices (bottom-right).

Task. The tacit coordination task was adapted from Alberti et al. (2012). The goal for the participants was to choose the same picture as their assigned partner in a row of four pictures each trial (see Figure 1). Also, they had to indicate a second choice, given their first choice might not match with their partner. This study used a 2 x 2 (*high-load* versus *low-load* x *shapes* versus *colors*) design. The factor combinations (*high load color* + *low-load shape* versus *low-load shape* + *high-load color*) were randomly counterbalanced.

The first factor was working memory load, with a *high-load* condition and a *low-load* condition (90 trials each). Participants could take a short self-paced break between the two conditions. In both conditions numbers were shown for 3000 ms, in-between picture matching. Before images or numbers were visible a fixation cross was present for 1000 ms. In the low-load condition, participants needed to indicate whether a number was odd or even, in-between picture matching. In contrast, during high-load, participants indicated whether the number on screen was the same as the number they saw two trials back. This is an n-back task. It is commonly used to test working memory performance, and therefore imposes a load on working memory processes (Kirchner, 1958).

To observe a fresh learning process for each condition, we manipulated stimulus type (*colors* versus *shapes*; see Figure 1). This prevented decision rules from establishing during the first block that would render the second block trivial. For example people can learn matching rules during the first block, e.g. choose the most “purplish” image, but new rules during the second block, e.g. choose the image with the most “edgy” shapes.

The stimuli were square matrices of 64 smaller squares. These smaller squares contained either shapes or colors. In total, ten colors and ten shapes were used to create the stimuli. The small shapes consisted of a few connecting nodes and edges to create a figure.

Shapes were randomly generated patterns, chosen for distinguishability. We chose the similarity of shape and color matrices to be as equal as possible, such that performance would be equalized. Three colors or shapes alternated in a checkerboard pattern, such that within each trial two colors or shapes were present in all four images while one color or shape varied between each image. Finally, stimuli were created such that each color and shape appeared an equal number of times.

EEG. Behavioral piloting began earlier than EEG piloting, therefore data was collected in four behavioral sessions and only one EEG session. In this session, EEG caps were strapped on, which were confirmed to be in the correct position by verifying if the central electrode was at the vertex of the head, i.e. between the Nasion and Inion and between two similar points of the ears. After everything was in place, the quality of participants' EEG signals was checked using ActiView software. First, it was inspected that none of the electrodes were noisy, did not contain any bridges nor large drifts, or if there were any other abnormalities. Second, it was inspected whether vertical and horizontal eye movements and eye blinks were visible. These simple signals confirm that the electrodes are in fact transmitting actual data. Also, it was checked whether there was not too much high frequency noise. Lastly, we examined whether none of the electrodes were unstable, nor had an impedance higher than 20 μ V. If this was the case, those particular electrodes were removed and reattached.

Statistical analysis

Most of the statistical analyses were performed in R version 3.6.1 (R Core Team, 2019), while the EEG analysis was carried out in Matlab (MATLAB, 2018) using the Fieldtrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011).

Bootstrap matching proportion. It is important to compare whether matching performance of interacting pairs is significantly different from that of non-interacting

randomly shuffled participant pairs. Therefore a bootstrap procedure was performed. The coordination index is the proportion of shuffled participants' overlapping choices. It was calculated by randomly selecting an image set and two random participants' choices on that image set 10,000 times. There are 180 different image sets (90 shape sets, 90 color sets). In other words, there are 90 configurations of four images per stimulus type. Shuffled pairs were created by randomly selecting two different sessions. Then, from each of these sessions one participant was chosen to create a random pair.

To find out whether this matching frequency is significantly greater than the coordination index ($H_0: \bar{x}_{\text{matching}} > \bar{x}_{\text{coordination index}}$), a bootstrap test was executed. The original sample consisted of $N = 1440$ data points (*number of image sets * participants = 180 * 8*). For all image sets, eight random participants were sampled with replacement, which created an entire sample of simulated data. Then, the randomly sampled data were divided into four sessions for which the matching frequencies were calculated. This procedure was repeated $k = 1000$ times (1000 samples) to create a simulated population distribution. Then the pseudo distribution was shifted by adding the difference between the coordination index and the mean of the pseudo distribution to each pseudo observation, according to the shift method: *pseudo distribution + (coordination index - Mpseudo dist)*.

Generalized linear models. Generalized linear models were then calculated to perform logistic regression analyses on the relation between matching performance, load and synchrony. In the purely behavioral datasets a generalized linear mixed effects model was performed. Namely, these have more power and are less prone to false positives than ANOVAs. Moreover, they account for idiosyncratic session by session and item-by-item variation (Baayen, Davidson, & Bates, 2008). To assess whether alpha synchrony differed between load conditions, paired t-tests were executed.

EEG Preprocessing. After collection of the single EEG session, channels were re-referenced to Mastoids separately for each subject. Then a band-pass filter [0.5 - 50 Hz] was applied to remove slow drifts and high-frequency noise. Afterwards, 180 trials, or epochs, were defined with 1000 ms pre-stimulus onset, which corresponds to the time a fixation point was shown pre-stimulus onset, and 1500 ms post-stimulus onset. This epoching was done after filtering to prevent edge artifacts. Of note is that the period up to 1500ms is the time that participants only see the stimuli. At this time people are not prompted to, and cannot, give a response. We chose this window to prevent movement artifacts to influence the EEG data.

Following this .022% of trials were rejected based on visual artifact inspection. These were rejected for both participants, since data for both participants is needed to compute synchrony. Afterwards, the average of the pre-stimulus period was subtracted from each trial (baseline correction), and linear trends were removed for each trial (detrending). Then an Independent Component Analysis was performed to identify the largest sources of variation in the EEG signals. The most likely sources of noise (e.g., eye blinks and muscle movement) were selected and rejected manually. On average 6.5 components were rejected per participant. Finally, the pre-stimulus baseline was dropped (which resulted in trials ranging from stimulus onset to post-stimulus time of 1500 ms).

EEG data analysis. Next, data was time-frequency transformed by means of convolution, using a Hanning taper with a window length of four cycles. The frequency band of interest, the alpha band, was defined as 9-14 Hz as in previous studies (van Vugt, Sederberg, & Kahana, 2007). For each trial the average phase angle across time was calculated: trials x channel combination x frequency. After this, paired synchrony values were calculated for analogous electrode pairs across the two participants (e.g. [Fz₁ Fz₂], [Cz₁ Cz₂]).

The inter-brain synchrony measure used was the Phase Locking Value (PLV; Lachaux, Rodriguez, Martinerie, & Varela, 1999). PLV computes how consistent the phase

difference between two signals is at a given frequency. High synchrony is reflected in a consistent phase difference. The PLV was calculated between all pairs of equal electrodes between the two participants for all trials N and all frequencies f within the alpha frequency band (9 – 14 Hz).

$$PLV_t = \frac{1}{T} \left| \sum_{n=1}^T \exp(j \theta(t, n)) \right|, j = \sqrt{-1}$$

Where t is time, T is the number of timesteps in a single trial, and $\theta(t, n)$ is the phase difference $\varphi_{participant\ 1}(t, n) - \varphi_{participant\ 2}(t, n)$. This results in five PLVs, one for each frequency. These five were average to get one PLV per trail for each electrode pair.

Many previous hyperscanning studies found (pre)frontal or central frontal synchrony in the alpha band during cooperation (Toppi, et al., 2016; Jangh et al., 2017; Astolfi et al., 2010; Babiloni et al., 2011). Therefore all frontal electrodes were investigated {Fz, FC1, FC2, F3, F4, AF3, AF4, Fp1, Fp2, F7, F8}. In addition, increased alpha synchrony during inter-personal coordination tasks has previously been found in right temporo-parietal {CP6}, right parietal {PO4, P8, P4} (Jangh et al., 2017), centro-parietal {CP1, CP2, Pz} (Dumas et al., 2012; Toppi et al., 2016), left parieto-occipital {PO3} (Lachat, Hugueville, Lemaréchal, Conty, & George, 2012), and right occipital {PO4, O2} (Jangh et al., 2017) areas. Therefore, in total 21 electrodes were included in the EEG analysis. The p-value threshold was corrected with Bonferroni adjustment, $\alpha/21 = .05 / 21 = .0024$.

Results

Paired matching frequency greater than chance

First, we examined whether paired participants match more often on picture matching trials, than randomly shuffled participants. Pair-specific picture matching proportion .55 ($SD = .12$) was higher than that of non-paired participants .48 ($SD = .016$) across all trials. The null hypothesis tests whether matching proportion of the real sample is greater than the

coordination index ($H_0: 0.55 > 0.48$). Therefore, the pseudo-distribution generated by a bootstrap analysis was shifted using the shift method. After shifting, the chance to obtain the current sample's matching frequency was $p = 0.039$. Therefore, the matching frequency is significantly greater than the coordination index.

Matching frequency improves over time and decreases with working memory load

Second, we predicted that people get better at this task over time, because decision rules for pictures should develop. So, we analyzed matching over trials, using logistic regression with matching (*match* versus *no-match*) as the dependent variable, as predicted by all main effects and interactions between trial number, load condition and stimulus type.

To find the simplest yet best fitting model, we performed backward fitting with Chi-square tests. From this a model was found that was a significantly better fit ($\chi^2(4) = 114.21, p < .001$) than the null model, i.e. a model with no predictors. This model had an intercept of $\beta_0 = -1.10, p = .0011$. It included significant main effects for load condition ($\beta_{low\ load} = .72, p < .001$) and trial ($\beta_{trial} = .032, p < .001$), a nonsignificant effect of stimulus type ($\beta_{shape\ stimulus} = -.28, p = .38$), and a significant interaction of trial by stimulus type ($\beta_{stimulus*trial} = -.015, p = .02$; see Figure 2).

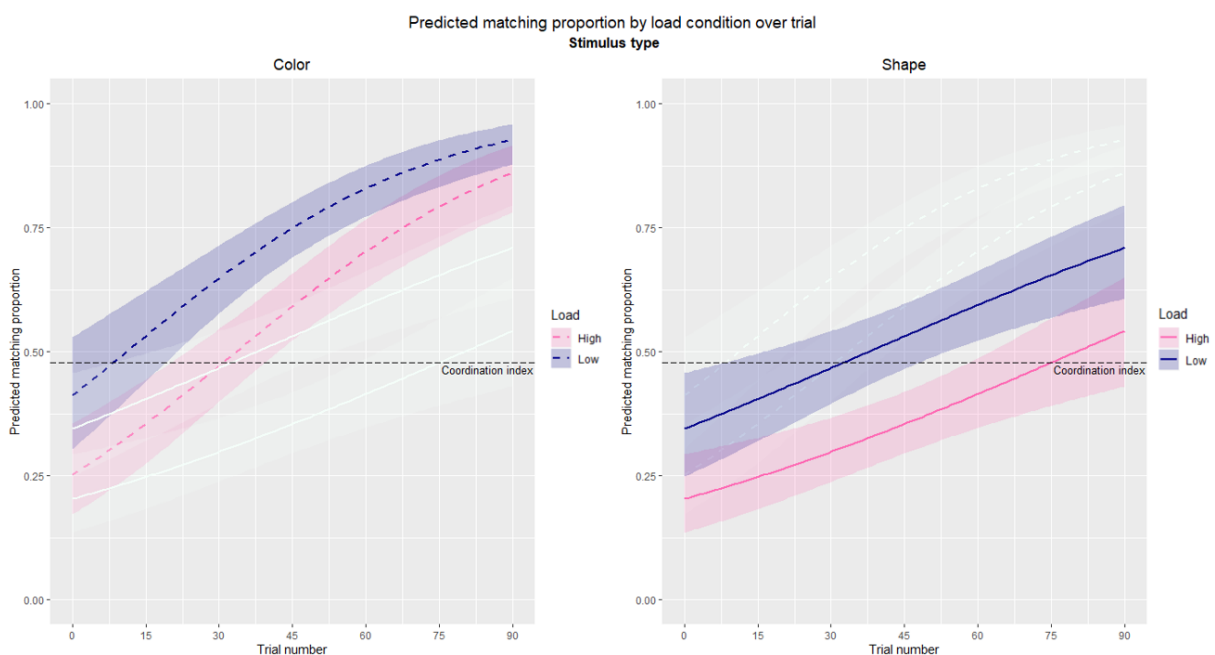


Figure 2: Predicted matching proportion (y-axis) over trials (x-axis) by stimulus type (left: color, right: shape) and load condition (blue: low, pink: high), derived from a logistic regression model. Shaded areas represent 95% confidence intervals of the model's predictions. Coordination index: the matching proportion of randomly shuffled data.

After converting log-odds to proportions, the predicted matching proportion over trials can be viewed in Figure 2 more clearly. An average increase of matching proportion with .0068 per trial is predicted during high load, while during low load it increases with .0057 per trial. These numbers correspond to a proportion increase of .61 (*high load*) and .52 (*low load*) from trial 1 to 90. More importantly, on average low load increases predicted matching proportion on by .14 with respect to high load.

Moreover, matching performance on shape stimuli was worse than color stimuli, as indicated by the trial*stimulus interaction and negative main effect for stimulus. On average, predicted matching proportion is .22 lower on shape than color trials. Furthermore, matching proportion in the low load condition on color trials increases by .00574 per trial on average, while in the shape trials it increases by .00406. In the high load condition matching proportion increases nearly twice as fast on color trials. A predicted increase of .00676 per color trial, compared to .00377 per shape trial.

Lastly, since this was a repeated measures design, there are dependencies between the trials of a single participant pair. Therefore, after determining the fixed effects structure, random intercepts for participant pair number and image set were added to the model. The model with image set included fitted significantly better than when it was removed, $\chi^2(1) = 3.94, p = .047$. It did not change the model's coefficients much, $\beta_0 = -1.15, p = .0015, \beta_{low\ load} = .76, p < .001, \beta_{trial} = .035, p < .001, \beta_{shape\ stimulus} = -.38, p = .29, \beta_{s*t} = -.015, p = .035$. In conclusion, predicted matching proportion decreases with higher load and increases over trials, confirming the aforementioned hypotheses.

Matching frequency's association with inter-brain synchrony

Thirdly, it was expected that matching proportion was associated with inter-brain synchrony in the alpha frequency band. Using the data from a single session, phase locking values (PLV) - which quantify synchrony - were calculated for equal pairs of electrodes between paired participants for each trial. For each pair a logistic regression model was calculated with main effects for load condition and synchrony, and their interaction. Only the model for the right parieto-occipital (PO4) electrodes fit significantly better than the null model, $\chi^2(3) = 7.87$, $p = .049$. After backward fitting, the best PO4 model ($\chi^2(1) = 4.94$, $p = .0026$) was slightly above the Bonferroni corrected p-value ($p_{Bonferroni} = 0.0024$). It included only a significant main effect for synchrony ($\beta = .72$, $p < .001$). As can be seen in Figure 3 synchrony in the PO4 electrodes increases with matching proportion. This provides marginal support for our hypothesis that synchrony and matching are related for only one electrode.

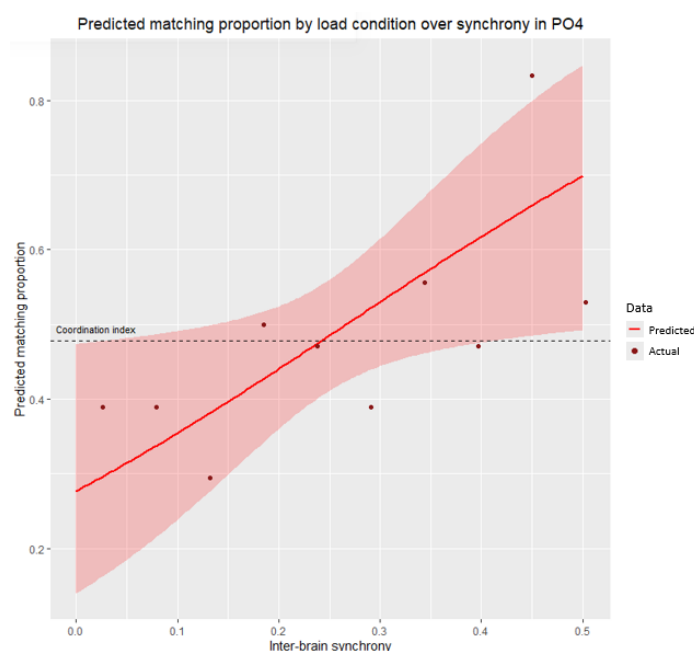


Figure 3. Predicted matching proportion (y-axis) over inter-brain synchrony (x-axis), as per a logistic regression model. Actual data points are average matching proportions calculated over ten synchrony intervals of .05, i.e. [0 to .05], [.05 to .1], ..., [.45 to .50]. Shaded areas represent 95% confidence intervals around the model's predictions. Coordination index: the matching proportion of randomly shuffled data.

Load did not decrease synchrony

Lastly, there was no support for the hypothesis that synchrony decreased with higher load. A paired samples t-tests to compare synchrony in high- and low load conditions. It indicated that in one parietal electrode (P8) there was more synchrony during low than high load, $t(87) = 2.45$, $p = .016$, $CI = [.0060; .0062]$. Since $p > p_{Bonferroni}$, this should be interpreted as false positive.

This non-difference in load can be explained by the stimulus type and load condition combination this particular session had. Namely, a *low load shape* versus a *high load color* block. Looking at Figure 2 indicates that matching proportion in *low load shape* versus *high load color* blocks does not differ much over trials. Consequently, there was no significant overall difference in accuracy on matching shapes ($M = 0.45$, $SD = 0.19$) compared to colors ($M = 0.65$, $SD = 0.12$), $t(5.22) = 1.85$, $p = .12$.

There were four sessions with two possible session configurations: *high load shape* and *low load color* or *high load color* and *low load shape*. To further investigate these configurations, t-tests for individual sessions determined that there were matching proportion differences between *high load shape* and *low load color* ($t_{\text{session 1}}(173.86) = 7.32$, $p < .001$; $t_{\text{session 2}}(177.12) = 3.40$, $p < .001$). In contrast, there were no significant differences in matching proportion between *high load color* and *low load shape* ($t_{\text{session 3}}(173.86) = -.30$, $p = .77$; $t_{\text{session 4}}(175.34) = 1.81$, $p = .073$).

This was further confirmed by performing a follow-up logistic regression analysis on the two sessions with block (*low load shape* versus a *high load color*) and trial as predictors. Block turned out to be an insignificant main effect, $p = .30$. Contrarily, a model with only a main effect of trial ($\beta = .030$, $p < .001$) was the best fit, $\chi^2(1) = 48.80$, $p < .001$. In short, the particular factor combination and little data made it unlikely to detect an effect for load on synchrony.

Discussion

This study investigated whether inter-brain synchrony underlies successful tacit coordination performance, and whether working memory load disrupts coordination performance and synchrony. In conclusion, paired participants coordinated better randomly shuffled participants, coordination performance increased over time and decreased with higher working memory load. Furthermore, results suggest a positive association between right parieto-occipital phase synchrony and coordination performance, however whether synchrony decreases with load remains inconclusive.

Matching proportion versus randomly shuffled performance

The first finding was that paired participants chose matching pictures more often than randomly shuffled participants. In addition, people matched more frequently over time in both load conditions. This leads us to conclude that the tacit coordination task creates a successful social coordination setting where people are able to coordinate their answers without verbal, facial or gestural communication. Importantly, paired participants matched on 55% of trials, which is significantly higher than randomly shuffled performance. The question is how participants succeeded in making the same decision. Interestingly, it seems there are general preferences for certain strategies or pictures, because randomly shuffled participants chose the same images quite often, namely 47% of the time. It could be that a lot of pairs thought of a similar strategy, for example: “choose the image that looks the most purple”. A potential reason for this is that certain colors or shapes are more salient than others, i.e. they capture attention more easily (Wolfe & Horowitz, 2017). Another, potentially connected, explanation is that people like certain images initially which creates similar strategies. Namely, Alberti et al. (2012) showed that during a similar tacit coordination task some people employ a “liking strategy”. Therefore, these pictures’ features (e.g. rounder shapes) could end up in pairs

shared target representation. However, pairs do find original successful decision rules, since otherwise their matching performance wouldn't differ from random choices.

Effect of working memory load on coordination

During higher working memory load, people's ability to form shared decision rules seems to decrease. Namely, results indicate that during the high working memory load condition coordination performance drops. Thus, matching performance decreased with higher working memory load (even after controlling for stimulus type). A possible reason for this is that working memory load decreases the ability to employ theory of mind (ToM) processes (Bull et al., 2008; Qureshi et al., 2010; Schneider et al., 2012). Successful coordination during this task requires participants to use ToM, since they have to think about each other's beliefs, actions and intentions to be able to choose the same stimulus (Alberti et al., 2012). These results indicated that working memory load interferes with coordination performance. Hence, it replicates that working memory processes employ similar attentional resources as ToM (Bull et al., 2008).

Inter-brain phase synchrony

As elaborated on before, people showed they can successfully coordinate without talking nor seeing each other. In order to determine what cognitive processes underlie synchrony during coordination, it is important that synchrony due to other cognitive processes cannot interfere with the results. Previous studies determined that inter-brain synchrony was enhanced during verbal communication (Bevilacqua et al., 2019; Dikker, Silbert, Hasson, Zevin, 2014; Dikker et al., 2017; Stephens et al., 2010), when people are face-to-face compared to not seeing each other (Jahng et al., 2017) and when performing or observing movements (Schippers et al., 2010; Dumas et al., 2010; 2012; Naeem et al., 2012). Thus, the tacit coordination task should be able to isolate people's neural signals during coordination from neural signals due to other social cues.

The results indicate a positive relation between matching frequency and right parieto-occipital inter-brain synchrony in the alpha band. The expectation was that synchrony would be mainly present in the frontal areas of the brain, since previous coordination research mainly found alpha synchrony in frontal electrodes (Toppi, et al., 2016; Jangh et al., 2017; Astolfi et al., 2010; Babiloni et al., 2011). Moreover, brain activity during ToM processes, or ‘mentalizing’, has been consistently observed in the temporo-parietal junction (TPJ) connected to the medial prefrontal cortex (mPFC; Babiloni & Astolfi, 2014). However, Lachat et al. (2009) also found increased (left) parieto-occipital synchrony during joint attention and Jangh et al. (2017) found increased right occipital and parietal synchrony during defection in the Prisoner’s Dilemma task. So, some evidence of right parieto-occipital synchrony was found before.

Right parieto-occipital activity was shown to be related to spatial attention (Learmonth, Benwell, Thut, & Harvey, 2017; Banerjee, Frey, Molholm, & Foxe, 2015; Bodenburg, 2000). Therefore, one might suspect the spatial location of the images on screen to influence participants’ decisions. Pairs both saw four similar images, but in different randomized orders. Consequently, the synchrony and matching relation does not seem to stem from spatial attention similarities.

Potentially, synchrony might occur because pairs attend to the same non-spatial features (e.g. purple) of the stimuli when they choose the same picture. Namely, previous researchers investigated attentional tasks in which people had to detect a certain target color in a series of flashing colors. Shortly after stimulus onset (150 ms), event-related potentials in parieto-occipital electrodes showed a continuous negative wave for target non-target colors compared to target colors (Purves et al., 2017). In our tacit coordination task, pairs might have formed decision rules for certain target shapes and colors (e.g. choose the most “purplish” looking image). Therefore, a possible explanation for phase locked parieto-occipital

synchrony during matching could be that people are attending to the same non-spatial features.

In addition, inter-brain synchrony might reflect people integrating the same visual features into a representation. Sensory input, like the tacit coordination task images, is generally compressed in the perceptual system so it can be represented and stored more efficiently (Ronconi, Oosterhof, Bonmassar, & Melcher, 2017). This is called integration. In our task an example would be the integration of two features, e.g. two colors. This integrated representation could be used as a decision rule. For example, “when there is a picture with *red* and *purple*, choose that picture”. Ronconi et al. (2017) showed that integration versus segregation of a two-flash fusion task was reliably predicted by the phase of alpha oscillations (8-10 Hz) in the right parieto-occipital electrode. Therefore, increased phase synchrony in this electrode during successful coordination potentially indicates that people are integrating similar features of the stimuli.

Limitations

This study had a few limitations. First, this study intended for color and shape stimuli to be equally difficult. This way, they could be used interchangeably in the two load conditions, so decision rules that developed in the first block could not be used in the second. However, color trials were significantly easier to match on than shape trials. It can be more difficult to find regularities in shape matrices than in color matrices, as Yu, Luo, Osherson and Zhao (2019) showed. If it is more difficult to find a regularity between two different shapes, then it should also be more difficult to find a consistent decision rule involving multiple shapes. Additionally, colors guide attention more easily than shapes. Namely, color is deemed to be a more salient feature of an object than shape (Wolfe & Horowitz, 2017). In other words, colors pop-out more than shapes. Therefore, it might be easier to choose among color matrices than shape matrices.

Furthermore, there were only four behavioral sessions and a singular EEG pair, so results should be interpreted with caution. Moreover, the EEG pair performed a *high load color* and *low load shape* block. No evidence was found for a difference in synchrony between blocks. Maybe this indicates that equal amounts of attentional resources were required in both of these block configurations. In other words, digit memorization (the working memory task) and shape trials might require equal amounts attentional effort. ToM processes were shown to require similar attentional resources as working memory (Bull et al., 2008; Qureshi et al., 2010; Schneider et al., 2012). This might explain why synchrony did not differ between working memory load conditions. Additionally, since ToM might have been partly disrupted, block configuration possibly explains why there were no associations between coordination and synchrony in the frontal areas nor in the temporo-parietal junction (TPJ), where ToM processes, or ‘mentalizing’, is generally observed (Babiloni & Astolfi, 2014).

Another limitation of this study is that one generally wishes to distinguish individual non-social task performance from paired social task performance using a control condition. One critique on inter-brain synchrony studies has been that there was no control condition that varied only on the social dimension, but not on the perceptual input (Szymanski et al., 2017). Firstly, the current coordination task could also be performed with one participant trying to coordinate with a computer. Secondly, this study only used one session for the inter-brain synchrony results. However, when more data is collected a bootstrap test can be executed, like was done for matching performance. Then participant’s EEG signals can be randomized to see whether paired participants show increased synchrony compared to non-paired participants.

A final limitation of this study is the inter-brain synchrony measure we used; the phase locking value (PLV). It measures the consistency of the phase difference between two

electrodes (Lachaux et al., 1999). However, it cannot distinguish between coincidental and “true” phase synchronization, i.e. it can detect non-existent synchronization/hyperconnectivity (Burgess, 2013). Consequently, Burgess (2013) compared different synchrony measures. They simulated EEG data with an alpha rhythm to manipulate phase coupling artificially. First, during their human data rest condition, PLVs identified more spurious hyperconnections in the low frequency alpha and theta band than other measures of synchrony, even after correcting for family-wise Type-1 errors. They showed that high synchrony, as measured by PLV, does not necessarily imply high signal covariance, i.e. that signals are systematically related. In contrast, the Circular Correlation Coefficient measures the signal covariance instead of the consistency of phase difference (Burgess, 2013). Therefore, future studies that want to investigate whether two brain signals are related might better use a good control condition or another less biased measure.

Future directions and conclusion

Relevant brain regions that are located deeper inside the brain are not reachable with EEG measures nor does EEG have a good spatial resolution. However, the tacit coordination task lends itself well to fMRI research, since there is neither a need to communicate nor to move. This way future research could look at which structures exactly are involved. However, two fMRI scanners would be needed, which are not readily available in most research labs (Babiloni & Astolfi, 2014). There is a research lab which developed and tested an MRI dual-head volume coil for simultaneously measuring brain signals (Lee, Dai, & Jones, 2012). It would be interesting to see if this technology will be incorporated more often as hyperscanning continues to give neuroscientific explanations for social interactions.

Next, it would be fascinating to stimulate two brains to see whether one can manipulate synchrony. For example, Transcranial Magnetic Stimulation (TMS) has been used to demonstrate that ToM learning processes are impaired when stimulating the vmPFC (Lev-

Ran, Shamay-Tsoory, Zangen, & Levkovitz, 2012). Therefore, for the current tacit coordination task it would be expected that stimulating the vmPFC will result in decreased matching performance as well as decreased inter-brain synchrony.

Lastly, researchers have suggested that inter-brain synchrony could be used as a tool for detecting social problems in psychiatric disorders, like schizophrenia or autism (Schilback, 2016). Since symptoms of autism include difficulties with ToM (Schilback, 2016) and our study looks at this as well, the relation between performance on this task and autistic or psychotic symptoms should be further investigated. In particular, decreased synchrony might predict social problems neurologically.

In short, this study showed that people can coordinate without conventional social cues like speech, facial cues or gestures. Moreover, some evidence showed a relation between coordination and inter-brain synchrony in the right parieto-occipital region, which might indicate people are attending and integrating the same stimulus features better when they match.

References

- Alberti, F., Sugden, R., & Tsutsui, K. (2012). Salience as an emergent property. *Journal of Economic Behavior & Organization*, 82(2–3), 379–394. <https://doi-org.proxy-ub.rug.nl/10.1016/j.jebo.2011.10.016>
- Astolfi, L. et al., (2010a). Imaging the social brain: multi-subjects EEG recordings during the “Chicken's game”, *2010 Annual International Conference of the IEEE Engineering in Medicine and Biology*, 1734-1737. doi: 10.1109/IEMBS.2010.5626708
- Astolfi, L., Toppi, J., De Vico Fallani, F., Vecchiato, G., Salinari, S., Mattia, D., Cincotti, F., & Babiloni, F. (2010b). Neuroelectrical hyperscanning measures simultaneous brain activity in humans. *Brain topography*, 23, 243-56
- Astolfi, L., Toppi, J., De Vico Fallani, F., Vecchiato, G., Cincotti, F., Wilke, C., Han Yuan Mattia, D., Salinari, S., He, B., Babiloni, F. (2011) Imaging the Social Brain by Simultaneous Hyperscanning during Subject Interaction. *IEEE Intelligent Systems*, 26(5), 38–45.
- Baayen, R. H., Davidson, D. J., & Bates, D. M. (2008). Mixed-effects modeling with crossed random effects for subjects and items. *Journal of Memory and Language*, 59(4), 390–412. <https://doi.org/10.1016/j.jml.2007.12.005>
- Babiloni, C., Buffo, P., Vecchio, F., Marzano, N., Del Percio, C., Spada, D., Rossi, S., Bruni, I., Rossini, P. M., Perani, D. (2011). Brains “in concert”: Frontal oscillatory alpha rhythms and empathy in professional musicians. *NeuroImage*. 60(1):105-16. doi: 10.1016/j.neuroimage.2011.12.008
- Babiloni, C., Vecchio, F., Infarinato, F., Buffo, P., Marzano, N., Spada, D., Rossi, S., Bruni, I., Rossini, P. M., Perani, D. (2012). Simultaneous recording of electroencephalographic data in musicians playing in ensemble. *Cortex*. 47(9):1082-90. doi: 10.1016/j.cortex.2011.05.006.

- Babiloni, F., & Astolfi, L. (2014). Social neuroscience and hyperscanning techniques: Past, present and future. *Neuroscience and Biobehavioral Reviews*, *44*, 76–93. <https://doi-org.proxy-ub.rug.nl/10.1016/j.neubiorev.2012.07.006>
- Baker, J. M., Liu, N., Cui, X., Vrticka, P., Sagar, M., Hosseini, S. M. H., & Reiss, A. L. (2016). Sex Differences in Neural and Behavioral Signatures of Cooperation Revealed by FNIRS Hyperscanning. *Scientific Reports* *6*(1): 26492.
- Banerjee, S., Frey, H., Molholm, S., & Foxe, J. J. (2015). Interests shape how adolescents pay attention: The interaction of motivation and top-down attentional processes in biasing sensory activations to anticipated events. *European Journal of Neuroscience*, *41*(6), 818–834. <https://doi-org.proxy-ub.rug.nl/10.1111/ejn.12810>
- Barraza, P., Dumas, G., Liu, H., Blanco-Gomez, G., van den Heuvel, M. I., Baart, M., & Pérez, A. (2019). Implementing EEG hyperscanning setups, *MethodsX*, *6*, 428 - 436
- Baron-Cohen, S., Wheelwright, S., Skinner, R., Martin, J., & Clubley, E. (2001). The Autism-Spectrum Quotient (AQ): Evidence from Asperger syndrome/high-functioning autism, males and females, scientists and mathematicians. *Journal of Autism and Developmental Disorders*, *31*(1), 5–17. <https://doi-org.proxy-ub.rug.nl/10.1023/A:1005653411471>
- Be on the same wavelength. (n.d.) Farlex Dictionary of Idioms. (2015). Retrieved February 5 2020 from <https://idioms.thefreedictionary.com/be+on+the+same+wavelength>
- Bevilacqua, D., Davidesco, I., Wan, L., Chaloner, K., Rowland, J., Ding, M., ... Dikker, S. (2019). Brain-to-brain synchrony and learning outcomes vary by student–teacher dynamics: Evidence from a real-world classroom electroencephalography study. *Journal of Cognitive Neuroscience*, *31*(3), 401–411. https://doi-org.proxy-ub.rug.nl/10.1162/jocn_a_01274

- Bock, A. M., Gallaway, K. C., & Hund, A. M. (2015). Specifying links between executive functioning and theory of mind during middle childhood: Cognitive flexibility predicts social understanding. *Journal of Cognition and Development, 16*(3), 509–521.
<https://doi-org.proxy-ub.rug.nl/10.1080/15248372.2014.888350>
- Bull, R., Phillips, L. H., & Conway, C. A. (2008). The role of control functions in mentalizing: Dual-task studies of Theory of Mind and executive function. *Cognition, 107*(2), 663–672.
<https://doi-org.proxy-ub.rug.nl/10.1016/j.cognition.2007.07.015>
- Burgess, A. P. (2013). On the interpretation of synchronization in EEG hyperscanning studies: A cautionary note. *Frontiers in Human Neuroscience, 7*. <https://doi-org.proxy-ub.rug.nl/10.3389/fnhum.2013.00881>
- Cheng, X., Li, X., & Hu, Y. (2015). Synchronous Brain Activity during Cooperative Exchange Depends on Gender of Partner: A FNIRS-Based Hyperscanning Study. *Human Brain Mapping 36*(6): 2039–48
- Chung, Dongil & Yun, Kyongsik & Jeong, Jaeseung. (2008). Neural Mechanisms of Free-riding and Cooperation in a Public Goods Game: An EEG Hyperscanning Study. International Conference of Cognitive Science; Seoul, 2008. Korea.
- Davis, M. H. (1980). A multidimensional approach to individual differences in empathy. *JSAS Catalog of Selected Documents in Psychology, 10*, 85.
- De Vico Fallani, F., Nicosia, V., Sinatra, R., Astolfi, L., Cincotti, F., Mattia, D., ... Babiloni, F. (2010). Defecting or Not Defecting: How to “Read” Human Behavior during Cooperative Games by EEG Measurements. *PLoS ONE, 5*(12), e14187.
<https://doi.org/10.1371/journal.pone.0014187>

- Dikker S., Silbert L.J., Hasson U., Zevin J.D. (2014). On the same wavelength: predictable language enhances speaker–listener brain-to-brain synchrony in posterior superior temporal gyrus. *Journal of Neuroscience*, *34*(18), 6267–72.
- Dikker, S., Wan, L., Davidesco, I., Kaggen, L., Oostrik, M., McClintock, J., et al. (2017). Brain-to-brain synchrony tracks real-world dynamic group interactions in the classroom. *Curr. Biol.* *27*, 1375–1380. doi: 10.1016/j.cub.2017.04.002
- Dumas, G., Nadel, J., Soussignan, R., Martinerie, J., & Garnero, L. (2010). Inter-brain synchronization during social interaction. *Plos One*, *5*(8), 12166. doi:10.1371/journal.pone.0012166
- Dumas, G., Chavez, M., Nadel, J., & Martinerie, J. (2012). Anatomical connectivity influences both intra- and inter-brain synchronizations. *Plos One*, *7*(5), 36414. doi:10.1371/journal.pone.0036414
- Fitzpatrick, P., Mitchell, T., Schmidt, R., Kennedy, D., & Frazier, J. (2019). Alpha band signatures of social synchrony. *Neuroscience Letters*, *699*, 24-30. doi:10.1016/j.neulet.2019.01.037
- Frith, C. D., & Frith, U. (2006). The Neural Basis of Mentalizing. *Neuron*, *50*(4), 531–534. <https://doi.org/10.1016/J.NEURON.2006.05.001>
- Hasson, U., Ghazanfar, A. A., Galantucci, B., Garrod, S., & Keysers, C. (2012). Brain-to-brain coupling: a mechanism for creating and sharing a social world. *Trends in Cognitive Sciences*, *16*(2), 114–121. <https://doi.org/10.1016/j.tics.2011.12.007>
- Jahng, J., Kralik, J. D., Hwang, D.-U., & Jeong, J. (2017). Neural dynamics of two players when using nonverbal cues to gauge intentions to cooperate during the Prisoner’s Dilemma Game. *NeuroImage*, *157*, 263–274. <https://doi-org.proxy-ub.rug.nl/10.1016/j.neuroimage.2017.06.024>

- Keyesers, C., & Gazzola, V. (2007). Integrating simulation and theory of mind: From self to social cognition. *Trends in Cognitive Sciences, 11*(5), 194-196.
- Kirchner, W. K. (1958). Age differences in short-term retention of rapidly changing information. *Journal of Experimental Psychology, 55* (4): 352–358. doi:10.1037/h0043688.
- Lachat, F., Hugueville, L., Lemaréchal, J.-D., Conty, L., & George, N. (2012). Oscillatory Brain Correlates of Live Joint Attention: A Dual-EEG Study. *Frontiers in Human Neuroscience, 6*, 156. <https://doi.org/10.3389/fnhum.2012.00156>
- Lachaux, J. P., Rodriguez, E., Martinerie, J. & Varela, F. (1999). Measuring phase-synchrony in brain signals. *Human Brain Map, 8*. 194-208.
- Learmonth, G., Benwell, C. S. Y., Thut, G., & Harvey, M. (2017). Age-related reduction of hemispheric lateralisation for spatial attention: An EEG study. *NeuroImage, 153*, 139–151. <https://doi-org.proxy-ub.rug.nl/10.1016/j.neuroimage.2017.03.050>
- Leary, M. R. (1983). Social anxiousness: The construct and its measurement. *Journal of Personality Assessment, 47*, 66-75.
- Lee, R. F., Dai, W., & Jones, J. (2012). Decoupled circular-polarized dual-head volume coil pair for studying two interacting human brains with dyadic fMRI. *Magnetic resonance in medicine, 68*, 1087-96
- Lev-Ran, S., Shamay-Tsoory, S. G., Zangen, A., & Levkovitz, Y. (2012). Transcranial magnetic stimulation of the ventromedial prefrontal cortex impairs theory of mind learning. *European Psychiatry, 27*(4), 285–289. <https://doi-org.proxy-ub.rug.nl/10.1016/j.eurpsy.2010.11.008>
- MATLAB. (2018). version 9.5.0.944444 (R2018b). Natick, Massachusetts: The MathWorks Inc.

- Mathôt, S., Schreij, D., & Theeuwes, J. (2012). OpenSesame: An open-source, graphical experiment builder for the social sciences. *Behavior Research Methods*, *44*(2), 314–324. doi:10.3758/s13428-011-0168-7
- Mu, Y., Guo, C., Han, S. (2016). Oxytocin enhances inter-brain synchrony during social coordination in male adults. *Social Cognitive and Affective Neuroscience*, *11*, 1882–93.
- Mu, Y., Han, S., & Gelfand, M. (2017). The role of gamma interbrain synchrony in social coordination when humans face territorial threats. *Social Cognitive and Affective Neuroscience*, *12*(10), 1614–1623. doi:10.1093/scan/nsx093
- Naeem, M., Prasad, G., Watson, D., & Kelso, J. (2012). Functional dissociation of brain rhythms in social coordination. *Clinical Neurophysiology*, *123*(9), 1789–1797. doi:10.1016/j.clinph.2012.02.065
- Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J. M. (2011). FieldTrip: Open Source Software for Advanced Analysis of MEG, EEG, and Invasive Electrophysiological Data. *Computational Intelligence and Neuroscience*, *2011*, 156869. <https://doi.org/10.1155/2011/156869>
- Purves, D., Cabeza, R., Huettel, S. A., LaBar, K. S., Platt, M. L., Woldorff, M. G. (2017). *Principles of Cognitive Neuroscience*. Sunderland, MA: Sinauer Associates, Inc. Publishers.
- Qureshi, A. W., Apperly, I. A., & Samson, D. (2010). Executive function is necessary for perspective selection, not level-1 visual perspective calculation: Evidence from a dual-task study of adults. *Cognition*, *117*(2), 230–236.
- R Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>

- Ronconi, L., Oosterhof, N. N., Bonmassar, C., & Melcher, D. (2017). Multiple oscillatory rhythms determine the temporal organization of perception. *PNAS Proceedings of the National Academy of Sciences of the United States of America*, *114*(51), 13435–13440. <https://doi-org.proxy-ub.rug.nl/10.1073/pnas.1714522114>
- Sanger, J., Muller, V., & Lindenberger, U. (2013). Directionality in hyperbrain networks discriminates between leaders and followers in guitar duets. *Frontiers in Human Neuroscience*, *Jun*(Jun). doi:10.3389/fnhum.2013.00234
- Schilbach, L. (2016). Towards a second-person neuropsychiatry. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *371*(1686), 20150081–20150081. doi:10.1098/rstb.2015.0081
- Schippers, M., Roebroek, A., Renken, R., Nanetti, L., Keysers, C., & Hari, R. (2010). Mapping the information flow from one brain to another during gestural communication. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(20), 9388–9393.
- Schneider, D., Lam, R., Bayliss, A. P., & Dux, P. E. (2012). Cognitive load disrupts implicit theory-of-mind processing. *Psychological Science*, *23*(8), 842–847. <https://doi-org.proxy-ub.rug.nl/10.1177/0956797612439070>
- Schnell, K., Bluschke, S., Konradt, B., & Walter, H. (2011). Functional relations of empathy and mentalizing: An fMRI study on the neural basis of cognitive empathy. *NeuroImage*, *54*(2), 1743–1754. <https://doi.org/10.1016/J.NEUROIMAGE.2010.08.024>
- Schroeder, C. E., Lakatos, P., Kajikawa, Y., Partan, S., & Puce, A. (2008). Neuronal oscillations and visual amplification of speech. *Trends in Cognitive Sciences*, *12*(3), 106–113. <https://doi-org.proxy-ub.rug.nl/10.1016/j.tics.2008.01.002>

- Stephens, G. J., Silbert, L. J., & Hasson, U. (2010). Speaker-listener neural coupling underlies successful communication. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(32), 14425–14430. <https://doi-org.proxy-ub.rug.nl/10.1073/pnas.1008662107>
- Szymanski, C., Pesquita, A., Brennan, A., Perdikis, D., Enns, J., Brick, T., . . . Lindenberger, U. (2017). Teams on the same wavelength perform better: Inter-brain phase synchronization constitutes a neural substrate for social facilitation. *Neuroimage*, *152*, 425-436. doi:10.1016/j.neuroimage.2017.03.013
- Toppi, J., Borghini, G., Petti, M., He, E. J., De Giusti, V., et al. (2016). Investigating Cooperative Behavior in Ecological Settings: An EEG Hyperscanning Study. *PLOS ONE* *11*(4): e0154236. <https://doi.org/10.1371/journal.pone.0154236>
- van Vugt, M. K., Sederberg, P. B., & Kahana, M. J. (2007). Comparison of spectral analysis methods for characterizing brain oscillations. *Journal of Neuroscience Methods*, *162*(1–2), 49–63.
- Wolfe, J. M., & Horowitz, T. S. (2017). Five factors that guide attention in visual search. *Nature Human Behaviour*, *1*(3), 1-8
- Yu, R. Q., Luo, Y., Osherson, D., & Zhao, J. (2019). Perception of multi-dimensional regularities is driven by salience. *Attention, Perception, & Psychophysics*, *81*(5), 1564–1578. <https://doi-org.proxy-ub.rug.nl/10.3758/s13414-019-01667-x>