



Inter-brain synchronization occurs without physical co-presence during cooperative online gaming

Valtteri Wikström^{a,b,*}, Katri Saarikivi^{a,b}, Mari Falcon^{a,b}, Tommi Makkonen^a,
Silja Martikainen^{a,b}, Vesa Putkinen^{c,d}, Benjamin Ultan Cowley^{b,e}, Mari Tervaniemi^{a,b}

^a Cognitive Brain Research Unit, Faculty of Medicine, University of Helsinki, P.O. Box 21, Helsinki, 00014, Finland

^b Department of Education, Faculty of Educational Sciences, University of Helsinki, P.O. Box 9, Helsinki, 00014, Finland

^c Turku PET Centre, University of Turku, P.O. Box 52, Turku, 20521, Finland

^d Turku University Hospital, P.O. Box 52, Turku, 20521, Finland

^e Cognitive Science, Department of Digital Humanities, Faculty of Arts, University of Helsinki, P.O. Box 24, Helsinki, 00014, Finland

ARTICLE INFO

Keywords:

Hyperscanning
Inter-brain
Synchrony
Synchronization
EEG
Cooperation
Collaboration
Performance
Multiplayer
Online
Video game

ABSTRACT

Inter-brain synchronization during social interaction has been linked with several positive phenomena, including closeness, cooperation, prosociality, and team performance. However, the temporal dynamics of inter-brain synchronization during collaboration are not yet fully understood. Furthermore, with collaboration increasingly happening online, the dependence of inter-brain phase synchronization of oscillatory activity on physical presence is an important but understudied question. In this study, physically isolated participants performed a collaborative coordination task in the form of a cooperative multiplayer game. We measured EEG from 42 subjects working together as pairs in the task. During the measurement, the only interaction between the participants happened through on-screen movement of a racing car, controlled by button presses of both participants working with distinct roles, either controlling the speed or the direction of the car. Pairs working together in the task were found to have elevated neural coupling in the alpha, beta, and gamma frequency bands, compared to performance matched false pairs. Higher gamma synchrony was associated with better momentary performance within dyads and higher alpha synchrony was associated with better mean performance across dyads. These results are in line with previous findings of increased inter-brain synchrony during interaction, and show that phase synchronization of oscillatory activity occurs during online real-time joint coordination without any physical co-presence or video and audio connection. Synchrony decreased during a playing session, but was found to be higher during the second session compared to the first. The novel paradigm, developed for the measurement of real-time collaborative performance, demonstrates that changes in inter-brain EEG phase synchrony can be observed continuously during interaction.

1. Introduction

Interpersonal synchronization occurs when individuals perform simultaneous or closely timed actions together. Research has shown that engaging in activities inducing interpersonal synchronization increases prosocial behavior and social bonding (Wiltermuth and Heath, 2009; Valdesolo and DeSteno, 2011; Pearce et al., 2015; Good and Russo, 2016; Mogan et al., 2017; Tarr et al., 2016; Dunbar et al., 2012). Such activities exist across cultures, and they are often used in rituals which increase group cohesion (Tonina et al., 2019). A form of synchronization which exists between the neural activity of interacting people has also

been observed, and it is a possible mechanism behind the effects of interpersonal synchronization (Nozawa et al., 2019). With social interaction increasingly happening through new forms of digital media, it is an open question whether such fundamental social cohesion is still facilitated when humans are not able to observe each other directly, and instead the interaction is mediated by a computer interface. We studied this question with an electroencephalography (EEG) experiment, in which pairs of subjects played a cooperative online multiplayer game. The subjects were located in different rooms and unable to communicate with each other aside from the actions performed in the game, essentially removing the rich medium of face-to-face social interaction and

* Corresponding author. Cognitive Brain Research Unit, Faculty of Medicine, University of Helsinki, P.O. Box 21, Helsinki, 00014, Finland.

E-mail address: valtteri.wikstrom@helsinki.fi (V. Wikström).

<https://doi.org/10.1016/j.neuropsychologia.2022.108316>

Received 19 November 2021; Received in revised form 1 July 2022; Accepted 2 July 2022

Available online 8 July 2022

0028-3932/© 2022 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

replacing it with a simple and controlled environment.

Multiplayer gaming is already a widespread form of social interaction: it has been estimated that in the USA, 77% of all gamers, or around 53% of the whole population plays video games with others (Entertainment Software Association, 2021). Meanwhile, virtual worlds, in which users are represented as spatial avatars, are receiving ever growing attention and market share, not least because of the recent efforts and investments of the social media giant Meta, formerly Facebook, to create a virtual social world dubbed the Metaverse (Kastrenakes and Heath, 2021). Virtual environments can provide wholly different kinds of experiences to the physical world, and users do not need to be represented in a format resembling their physical selves, which calls for investigation of the types of information that are required for interpersonal and inter-brain synchronization to occur in this environment. This question is even more important since online professional and personal interaction, as well as online gaming, have become increasingly common due to the COVID-19 pandemic, a trend which may well continue after the pandemic is over (Brynjolfsson et al., 2020; Entertainment Software Association, 2021).

Biosignal synchronization of groups of people engaged in social interaction can be observed in heart rate variability, respiratory rate, and skin conductance (Palumbo et al., 2017), as well as in hemodynamic and oscillatory activity of the brain (Czeszumski et al., 2020). In hyperscanning studies, inter-brain synchrony typically refers to similarity in the temporal pattern of simultaneous measurements obtained from test subjects using neuroimaging methods, such as EEG, magnetoencephalography (MEG), functional magnetic resonance imaging (fMRI), and functional near infrared spectroscopy (fNIRS) (Czeszumski et al., 2020). Most hyperscanning studies of interacting individuals place participants in a face-to-face situation or at minimum in the same room, making it possible to observe each other's bodily and facial expressions, or hear vocalizations, breathing, and movement. As expected, inter-brain synchronization depends on such cues, with face-to-face interaction producing higher synchronization than face-blocked interaction (Jahng et al., 2017). In one study, synchronization of the brain's hemodynamic signal over areas related to communication was observed during interaction while the participants were in separate rooms (Stolk et al., 2014). However, this study utilized a turn-taking task without real-time interaction, where the explicit movement of puzzle pieces on a grid was used by participants to communicate intentions to another player. Also, no studies of phase synchronization of oscillatory activity have been conducted with interacting individuals in separate rooms. Therefore, whether inter-brain phase synchronization of oscillatory activity depends on physical co-presence is not yet understood.

Increased inter-brain synchrony has been linked with social closeness (Kinreich et al., 2017), rapport (Nozawa et al., 2019), agreement (Richard et al., 2021), sense of joint agency (Shiraishi and Shimada, 2021), prosociality (Hu et al., 2017), similarity of flow states (Nozawa et al., 2021), shared meaning-making (Stolk et al., 2014), and cooperation (Cui et al., 2012; Toppi et al., 2016; Szymanski et al., 2017; Cheng et al., 2019). Phase-coupled brain stimulation has led to increased interpersonal synchrony (Novembre et al., 2017), as well as improved interpersonal learning (Pan et al., 2020b). Furthermore, preceding a learning task with synchronized physical activity led to both better rapport and increased inter-brain synchrony, although task performance was unaffected (Nozawa et al., 2019). Nonetheless, learning outcomes (Pan et al., 2020a) and team performance in a variety of tasks (Szymanski et al., 2017; Reiner et al., 2020) can be predicted with the amount of inter-brain synchrony occurring between interacting individuals. Even though collaboration is a dynamic phenomenon, previous studies reporting connections between positive social outcomes and inter-brain synchronization have not explored the temporal aspects of this phenomenon, as recently pointed out by Li et al. (2021). Their fNIRS study revealed differences in the time courses of inter-brain synchronization during two different cooperative tasks. The connection between temporal changes in inter-brain synchronization and the success of

collaboration is, however, still not clear.

EEG and fNIRS allow freer movement and more natural interaction compared to magnetic imaging such as fMRI and MEG, arguably lending themselves most easily to actual interactive situations. However, interpersonal synchronization and mirroring between people engaged in social interaction involve quite fast timing precision. For example, participants' movements were synchronized to less than 40 ms in the mirror game, in which participants improvise motion together (Noy et al., 2011). As EEG measures the electrical activity of the brain, it represents a faster changing signal than hemodynamic measurement, i. e. measures of blood flow, such as fNIRS. This makes EEG a suitable method for investigating fast changes in phase synchronization of oscillatory activity during dynamic social interaction, when taking into account the limitations of the method in regards to signal-to-noise ratio.

In this study, we wanted to investigate whether cooperative action of physically isolated participants would lead to inter-brain phase synchronization. We were especially interested in the temporal dynamics of inter-brain synchrony and its connection to performance in a collaborative task. We attempted to create an experimental setup which would facilitate the occurrence of inter-brain synchrony, while removing any bodily cues and controlling, as much as possible, for spurious synchronization. We also wanted to create a granular performance measure that could be calculated for any segment of the data, to make it possible to investigate dynamic changes in synchrony during the measurement and their connection to dynamic changes in collaborative success during the task.

We chose a task which requires joint coordination and simultaneous real-time action facilitating a continuous interactive feedback loop between the participants. We expected that a task which requires interpretation and prediction of the partner's actions and intentions would be most likely to engage neural coupling relevant to collaborative performance. Although synchronized or mimicked physical action, which could be achieved for example by deploying a version of the mirror game (Noy et al., 2011), would certainly be a potential way of inducing neural synchrony online, the simultaneous motor activity required to perform in the task could produce a similar pattern of muscular artefacts and similar action in itself causing similarity in the EEG signals of the participants, which would confound the results of the synchrony analysis.

Because of this, we developed a joint coordination task in the form of an online game, in which two participants work together, with distinct roles of *accelerator* and *steerer*, to control continuously the movements of an on-screen racing car (see Section 2.3). This task requires joint coordination and joint action, but the distinct roles do not require the same physical movements for the participants to perform well, reducing the risk of simultaneous muscle artefacts confounding the EEG synchrony analysis, as well as controlling for similar brain activity arising simply from simultaneous and similar action. We were also interested in measuring synchrony on a more granular level than comparisons between pairs or groups. To this end, we created a method to quantify momentary performance in the task based on relative task progression. This allowed us to investigate the possible link between performance and momentary synchrony.

We hypothesized that shared attention, interaction, and cooperation in the real-time online game would produce inter-brain synchrony, measured here using the circular correlation coefficient (CCorr) of different frequencies within electrodes representing the frontal, fronto-central, central, temporoparietal, parietal, and occipital regions. The comparison was done between real pairs and performance-matched false pairs (see Section 2.6). Based on testing this hypothesis, we made exploratory analyses of the relationship between inter-brain synchrony and task performance, expecting to find positive links in line with previous research.

2. Material and methods

2.1. Participants

44 volunteers were recruited through email lists and social media in pairs of friends or romantic couples among students of the University of Helsinki and others interested in participating in the study. One pair was excluded from all analyses due to EEG measurement device malfunction. This resulted in 42 subjects (9 female-female, 5 female-male, 7 male-male pairs). Subjects were all right-handed and reported no visual impairments or neurological disorders. The participants' ages varied between 20 and 45 years with the average age of 27 years ($SD = 5.42$). The mean age difference between the subjects within a dyad was 1.86 years ($SD = 1.74$) with a minimum of 0 years and a maximum of 7 years. The participants were rewarded two movie tickets for taking part in the study.

Before the experiment, written informed consent was obtained from the participants. The study was conducted according to the guidelines of the Declaration of Helsinki, and it was approved by the Ethical Review Board in the Humanities and Social and Behavioural Sciences of the University of Helsinki, Finland.

2.2. Pre-task measures

Subjects completed tests designed to measure individual IQ and empathy, and filled in a background questionnaire. Additionally, the participating pair was asked to provide the researchers with an instant messaging thread between the participants, after which they completed a questionnaire related to their communication. Results concerning the empathy measures and the pair's ratings of their instant messaging history will be reported separately.

2.2.1. IQ

We expected that performance in the task would rely on visuospatial skills, which was measured with the block design subtest of the Wechsler Adult Intelligence Scale (WAIS-IV) (Wechsler, 2012). The WAIS-IV Vocabulary test was also carried out in order to examine associations between task performance and a measure reflecting a different dimension of IQ. The mean among all subjects was 56.33 ($SD = 6.80$) out of 68 (82%) for the block design subtest score and 36.5 ($SD = 6.27$) out of 64 (58%) for the vocabulary subtest. This indicates that the subjects performed better in the visuospatial block design subtest, and received slightly lower scores in the vocabulary subtest, compared to the Finnish norm (Wechsler, 2012).

2.2.2. Social closeness

Previous research suggests higher synchrony of biosignals between subjects reporting higher levels of social closeness with one another (Dikker et al., 2017) and differences in patterns of synchronization depending on familiarity (Dikker et al., 2021; Kinreich et al., 2017). Because the effect of familiarity or closeness was not a target in this study, we decided to recruit a participant pool of only familiar participants: Pairs of either friends or romantic partners were recruited. To make sure that our sample consisted of socially close pairs, we asked subjects to rate how socially close they felt to their partner on a scale from 1 to 5, with 1 indicating the lowest and 5 indicating the highest amount of closeness. The mean rating was 4.52 ($SD = 0.92$).

2.3. Real-time joint coordination task

Inspired by an episode of the British television series Top Gear (Churchward and Doyle, 2008), in which participants were tasked to drive double-decked cars, with the person on top turning the steering wheel and the person on bottom operating the pedals, we implemented a joint coordination task as a car racing game (Fig. 1a) in the PsychoPy (Peirce et al., 2019) environment. In this custom-built game, the goal of the pair was to drive a racing car on a track as fast as possible, while one of the subjects steered and the other accelerated and decelerated the vehicle. Driving the car out of the track would either slow down the car, or stop it in case of obstacles, which were placed in the middle of each track to avoid shortcuts. There were four different tracks (see Appendix A), and the participants took turns to drive each track in both roles. The participants used two letter keys (either U and H or O and K) of a regular QWERTY computer keyboard to control the car. The functions of the keys depended on, and changed according to the subject's role: they were either used for accelerating and decelerating or for turning left and right. The length of button presses mattered, in the way that a prolonged press would lead to continued turning or sustained acceleration. Statistics about the timing of the button presses in the two different roles can be found in Appendix B.

The task type was chosen based on several criteria. First of all, we considered a task involving movement, coordination, and prediction of the partner's intentions to have the potential for inducing inter-brain synchrony, but at the same time we wanted to avoid synchronization of participants' motor actions to avoid the possibility of simultaneous motor artefacts confounding the analysis. Also, to minimize the amount of muscle artefacts, we ruled out any vocal communication between the two isolated, shielded and sound proofed rooms and we instructed the participants to move as little as possible apart from the finger movements required for the task. We also wanted to avoid any large sudden onset visual stimuli in the form of rapid scene changes, which might also

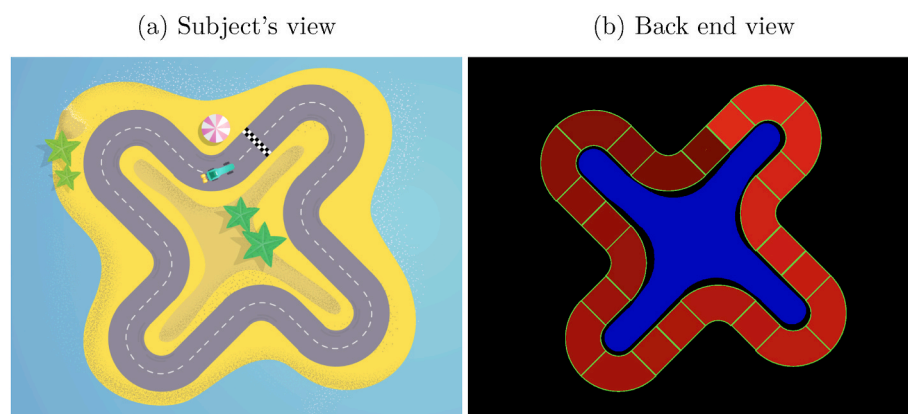


Fig. 1. On the left is the view shown to the participants during the task execution, and on the right is the back end representation of the track showing the division into different segments for granular performance comparison, with different values of red (0–255) on the RGB scale corresponding with the triggers sent to the EEG recording equipment. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

cause spurious synchronization. Finally, we required granular measurement of task performance for the momentary analysis of EEG synchrony. Distinct roles of steerer and accelerator during the task, restricting the movement necessary to perform the task to two fingers pressing buttons, continuous visual movement, and granular measurement of progression on the track fulfilled these criteria.

Practically, the granular measurement of progression on the track was achieved by sending triggers to the EEG recording device when the car entered each segment of the track (shown in Fig. 1b as varying levels of red separated by yellow lines). This allowed us to take any arbitrary range in the dyadic EEG data and give it a performance value based on the timing of entering the preceding and succeeding track segments compared to the mean timing of all the other instances of progression between those segments for all the dyads, following the formula:

$$p' = \frac{t'_2 - t'_1}{T_2 - T_1},$$

where p' is the current performance value, t'_1 is the time of entering the track segment preceding the current time window, t'_2 is the time of entering the track segment succeeding the current time window and $T_2 - T_1$ is the average time between entering the two corresponding segments on the track across all trials and dyads.

Due to the nature of the track segment comparison, each performance value reflected a longer duration than the actual EEG data used in the analysis. There were some instances, in which the triggers were not registered correctly by the recording system, leading to possibly erroneous and excessively long segments for performance calculation. To clean the data from these instances, any segment with a $t'_2 - t'_1$ exceeding 9 s was excluded from the momentary EEG analysis, leading to an average of 4.0% (SD = 3.9%) exclusions per pair. The remaining performance values were calculated for an average duration of 4.2 s (SD = 0.97 s) per 3 s of EEG data.

2.4. Task execution

Each pair completed two sessions with the collaborative driving task. One session consisted of 8 runs, each lasting 90 s. During one 90 s run, the task of the pair was to complete as many laps as possible on a track, and the lap time in seconds was presented to the subjects after each lap. After each run, the subjects' roles switched, so that each subject completed the same track in both roles (accelerator and steerer). After two runs on the same track, the track would change as a new run began and the roles of the subjects would switch back to the original ones. All-in-all, there were four different tracks that were each played as described. With four tracks, and each track being played in two different roles, this amounted to eight runs per session.

2.5. Procedure

Upon arriving at the research facilities, the two participants were asked to fill in the consent form. After this, the subjects were separated and no longer able to communicate with one another. The subjects were then randomly assigned to either first complete the IQ tests with a researcher and then fill in the background, empathy, and social closeness questionnaires, and the questionnaire concerning text-based communication, while the other subject was assigned to carry out these tasks in the opposite order. EEG electrode caps were then placed on both participants.

During the experiment, subjects were seated in separate electrically and acoustically shielded rooms. The subjects were then individually introduced to the joint coordination task. Subjects were informed that they would be playing the game with their pair, and that they would not be able to interact with each other in other ways. They were instructed to work together and to finish as many laps as possible. Other than driving the car together, no other form of interaction between the

subjects was possible during the experiment.

Altogether, the tests and questionnaires took approximately 45 min to complete and placing the EEG electrodes took around 15 min. Each session of the experiment lasted for 15 min. In the beginning of each session a fixation cross was presented to the subjects for 90 s. After finishing the first session, the subjects were given a 10 min break. The break was followed by another identical session, in which the subjects alternated roles in the same order through the 4 different tracks.

2.6. Control pairs

In order to examine which components of inter-brain synchrony, if any, were specific to collaboration, pair-specific synchronization values were compared to values obtained by analysing the data of two selectively chosen subjects that were not playing together. These false pairs were selected by matching two pairs in the study based on their level of performance in the task, so that the difference in the average lap times during the gaming sessions was as low as possible. This minimal difference was calculated on a group level to avoid pairs being matched into more than one false pair. As the data contained an uneven number of pairs, one pairs' data was used twice in the false pairs analysis to include all the participants. Within the false pairs, the subjects' data were matched to correspond with the same order of the roles (accelerator or steerer) between subjects and the order of the rounds were kept consistent, thus controlling for possible effects arising from the temporal progression of the experiment.

2.7. EEG recording

During the task, the brain activity of the subjects was simultaneously recorded using two EEG systems (Biosemi ActiveTwo, BioSemi B.V., The Netherlands) with 64 active scalp electrodes (in addition to the CMS and DRL reference electrodes) and a sampling rate of 512 Hz. Triggers for the beginning of the session, track changes, and those generated from the coordinates of the car on the track were sent simultaneously to both of the subjects' EEG systems, enabling precise temporal matching of the two EEG data sets. Two additional electrodes were placed on the right and left mastoid. Two electrodes for measuring electrooculogram (EOG) were placed under and on the outer canthus of the left eye. In addition, ECG was measured, but it is not part of this analysis. The data for each gaming session were saved as separate data sets, resulting in two data sets per subject, and four data sets per pair.

2.7.1. Data preprocessing

The preprocessing of the EEG data was carried out using EEGLAB 2019.1 (Delorme and Makeig, 2004) and custom scripts in MATLAB 2020b (MathWorks Inc., USA). Each data set was set to begin from the starting point of the first race track and end 5 s after the endpoint of the last track of the session. Channel locations were added using the Biosemi 64 electrode layout for the EEG channels, appended with the two EOG channels. Data from all channels were visually inspected, and flat or highly noisy channels were marked in order to be excluded in the following steps. The data were referenced to channel Cz. After this, a low-pass filter at 0.5 Hz (-6 dB cutoff at 0.25 Hz) was first applied, followed by the application of a high-pass filter at 48 Hz (-6 dB cutoff at 49.056 Hz).

The data were then divided into 3-s segments for exclusion of segments with artefacts. This resulted in 270 segments for each of the two sessions, equalling a total of 540 segments per subject. The threshold for segment rejection was set to ± 500 μV . Prior to rejection, segments set for removal as well as segments set for inclusion in the data were visually inspected. This process resulted in a minimum number of 0 (0%) and a maximum number of 43 segments (16%) being removed from one data set. In 35 out of 42 data sets, less than 10 segments (< 4%) were removed, and all but one had less than 20 removed segments (< 8%).

In order to remove EOG artefacts from the data, Independent

Component Analysis (ICA) was run for each data set consisting of the remaining segments including data measured with the EEG as well as EOG channels. EEGLAB's IClab 1.3 (Pion-Tonachini et al., 2019) was used to identify these artefacts. Components labeled as ocular artefacts with the probability of 90 percent or higher, according to IClab, were removed from the data. Prior to the removal of each component, the components' spectral map and the effects of the removal of the component on the data set were visually inspected. This IClab criterion was found highly suitable for the removal of EOG artefacts, as all components suggested for rejection based on IClab were found to also reflect ocular artefacts based on visual inspection. Additionally, no components that were not suggested for rejection based on IClab were found likely to reflect ocular artefacts based on visual inspection. The bad channels excluded from the previous steps of preprocessing were then interpolated. After this, the data were re-referenced to the common average in order to preserve data from Cz and ensure a uniform impact on the amplitudes of different channels.

Finally, the data included in the analyses were temporally matched for each pair. Segments rejected from one subject's data were also removed from the data of their partner. Concerning the pair's entire data, including both gaming sessions, this resulted in a minimum of 0 segments (0%), maximum of 45 segments (8%) and an average of 8 segments (2%) removed from a pair's data, leaving an average of 532 segments (98%) per pair. The same temporal matching and segment rejection approach was applied for the false pairs. Concerning the false pair's entire data, including both gaming sessions, this resulted in a minimum of 0 segments (0%), maximum of 45 segments (8%) and an average of 8 segments (2%) removed from a pair's data, leaving an average of 532 segments (98%) per false pair for analysis.

2.7.2. Synchronization and oscillatory analysis

Although the last decade has seen a surge in the amount of research in hyperscanning, there is still a large variety in the methodologies used (Burgess, 2013; Czeszumski et al., 2020). Especially, the range of measures that has been used for quantifying hyperconnectivity from the EEG signal is daunting for the designer of the signal processing pipeline. Spurious hyperconnectivity can arise from external reasons unrelated to interpersonal interaction, such as from the experimental setup, the stimuli used, and the analysis itself (Burgess, 2013). Avoiding it is important to not fall prey of false and overly optimistic results. Burgess (2013) compared different measures in terms of their robustness against spurious connections. The measures for quantifying hyperconnectivity between EEG signals included coherence (COH), partial directed coherence (PDC), phase-locking value (PLV), circular correlation coefficient (CCorr) and Kraskov mutual information (KMI). Another method, which was not included in the comparison, is the covariance of amplitudes in different frequency bands of the EEG signal, described by Burgess as a "weak form of association". CCorr and PLV are measures of phase similarity, or what would generally be considered as synchronization. The comparison with simulated data revealed that the most commonly used methods PDC, PLV, and COH are vulnerable to falsely estimate higher connectivity values when the data is concentrated, i.e., has a low variance. Additionally, real EEG data from non-interacting participants, who were subjected to the same experimental paradigm, showed that PLV was highly susceptible to identifying spurious connections due to similar variations in the EEG signal caused by the paradigm. The methods with lowest bias were CCorr and KMI, and of those CCorr performed best (Burgess, 2013). Several studies have used CCorr since (Goldstein et al., 2018; Davidesco et al., 2019; Pérez et al., 2019).

CCorr measures the circular covariance of differences between the observed phase and the expected, or mean phase. CCorr is given by:

$$CCorr_{\varphi,\psi} = \frac{\sum_{k=1}^N \sin(\varphi_k - \bar{\varphi}) \sin(\psi_k - \bar{\psi})}{\sqrt{\sum_{k=1}^N \sin^2(\varphi_k - \bar{\varphi}) \sin^2(\psi_k - \bar{\psi})}} \quad (1)$$

where φ and ψ represent the phase values for two channels that are being compared, and $\bar{\varphi}$ and $\bar{\psi}$ are the mean phases of the two signals (Burgess, 2013). Essentially, CCorr is the covariance of the phase variance, i.e., it indicates whether the phases of the two oscillators are varying in a similar way. This makes it considerably more robust against coincidental synchronization compared to PLV, which measures in its most common form the instantaneous phase-difference. Because PLV simply measures that there exists a consistent phase relationship between the two signals, it does not guarantee any form of covariance or information exchange between the signals (Burgess, 2013). If the phase distribution of the signal has a small variance, PLV can indicate a strong association, even if the correlation between the signals is small (Burgess, 2013).

The preprocessed data segments saved in the EEGLAB format were loaded into Python and resampled to 128 Hz using functions of the MNE package (Gramfort et al., 2013). CCorr values were calculated using functions of the HyPyP Python package (Ayrolles et al., 2020) for each segment and for each pair of the 40 electrodes that were selected for further analysis, and for each 1 Hz frequency bin from 2 Hz to 45 Hz. This resulted in a connectivity matrix with the dimensions 44xNxN (frequencies, first subject's electrodes, second subject's electrodes) for each time segment and ROI (Fig. 2). The values for each frequency band were calculated as an average of the values in the connectivity matrix corresponding to each electrode pair in the region and each frequency in the frequency band. The same analysis was done for the pairs completing the task, as well as for the false pairs created using the procedure that was described above.

Due to the exploratory nature of the analyses, to avoid Type 2 errors, we could not apply very strict statistical corrections, and therefore also needed to limit the amount of statistical testing in order to decrease the likelihood of Type 1 errors from running too many tests. Because of this, we calculated CCorr values only for connections within the same ROI.

2.8. Statistical analysis

2.8.1. Synchrony arising from interaction

We wanted to know which components of inter-brain synchronization, if any, arose as a result of the interaction between participants, rather than from other factors such as task characteristics and experimental procedure. To control for spurious synchrony arising from the experimental setting, we created false pairs to compare with the actual collaborating pairs. The participants were matched based on their average performance in the task, to create an artificial set of dyads minimizing the total difference in performance across the set, as described in Section 2.6. For each ROI, t-tests were computed between the real and false pairs for each of the analyzed 1-Hz frequency bins and false discovery rate (FDR) correction was applied.

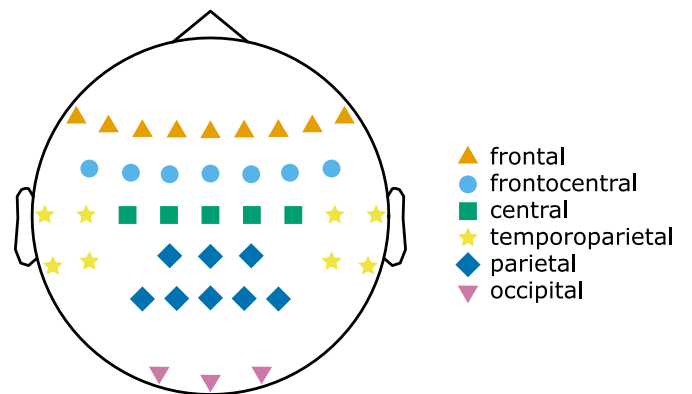


Fig. 2. ROIs used for the analyses: frontal (F1-8, Fz), frontocentral (FC1-6, FCz), central (C1-C4, Cz), temporoparietal (C5-6, CP5-6, T7-8, TP7-8), parietal (CP1-2, CPz, P1-4, Pz), and occipital (O1-2, Oz).

To validate this analysis, we also used a method that accounts for the autocorrelated nature of the datapoints: minimum-width envelopes (MWEs), developed by Korpela et al. (2014). MWEs generalize univariate confidence intervals (CIs) to multivariate time series data. MWE bands tend to be wider than naïve CIs because they account for the non-independent nature of time series data, yet they depict a similar visual interpretation of the data because the true average of the distribution traverses inside the lower and upper bounds with a probability of $1 - \alpha$ (where α is the desired level of control of the Type I error). The MWE model thus represents a statistical test of whether samples from two conditions are drawn from separate distributions: if at any point the mean of one sample is outside the MWE of the other, it shows that the curves as a whole are statistically significantly different. Here, we used $\alpha = 0.05/5$ to provide appropriate control for multiple comparisons ($n_{ROI} - 1 = 5$).

2.8.2. Analysis of performance and synchrony

Based on the results from the false pairs analysis (Section 3.1), we expected that possible cooperative performance effects on synchrony could arise in the alpha (8 – 12 Hz), beta (13 – 30 Hz) and gamma (31 – 45 Hz) frequency bands measured over the frontal, central, parietal and occipital regions. Synchrony in these frequency bands measured over these regions were therefore chosen for further analysis. To explore whether inter-brain synchrony specific to interaction might represent neural activity underlying collaborative success, we investigated the associations between synchrony and the level of task performance while controlling for visuospatial skills. Our goal was to identify possible associations between the overall level of synchrony and performance. We were also interested in the temporal dynamics of synchrony and performance. More specifically, we wanted to investigate whether temporal variation of inter-brain synchrony might reflect processes related to the relative level of performance within dyads. For these reasons we applied a two staged approach in order to 1) examine the associations between the dyad's mean levels of inter-brain synchrony and the dyad's mean level of performance, 2) investigate more specific temporal patterns between synchrony and the relative level of performance of dyads, while controlling for visuospatial skills. These analysis stages were carried out using IBM SPSS version 27.

2.8.3. Synchrony and performance across dyads

For each dyad, the mean synchrony over the entire experiment, including both gaming sessions, was calculated for each frequency band (alpha, beta and gamma) and used as the synchrony index. Similarly, the dyad's mean performance during the entire task was calculated and used as the measure of performance. To explore possible effects of IQ on the investigated associations between task performance and synchrony, we calculated dyadic means for the two WAIS subtest (block design and vocabulary) scores. We examined Pearson correlations between the dyad's mean score in each subtest and the performance in the driving task. No significant correlations were found between either of the WAIS subtest scores and task performance. Similarly the mean score of the block design subtest was not significantly associated with task performance.

Due to the visuospatial nature of the task and the stronger (yet not statistically significant) association between the mean block design score and performance ($r = 0.308$, $p = 0.174$), compared to mean vocabulary score and task performance ($r = 0.190$, $p = 0.409$), the block design test score was included in the following analyses. As the task used in the experiment required substantial visual processing, we wanted to control for not only the mean level of the dyad's visuospatial skills, but also for the level of similarity in visuospatial skills of the collaborating individuals. We expected that inter-brain synchrony in such a highly visual task might partly reflect similarity between the subjects' visuospatial processing, which might be more similar among subjects with similar visuospatial skills.

A linear mixed model with restricted maximum likelihood was used

to predict frequency-specific mean synchrony with dyads' mean performance, mean visuospatial test scores and intra-dyadic differences in the visuospatial test scores (treated as fixed factors). To explore differences in the level of synchrony between regions, synchrony measures from all ROIs were included in the data and ROI was also included as a fixed factor. Dyad was treated as a random factor with an estimated intercept using scaled identity covariance structure (chosen based on the Bayesian Information Criterion). Possible violations of homoscedasticity and multicollinearity were inspected for each model, and assumption of homoscedasticity was met for all three models, and no problems concerning multicollinearity between the predictors were discovered ($VIF < 2.5$ and tolerance > 0.4 for all variables). Difference in estimated marginal means of synchrony in different ROIs was also examined concerning each frequency band. Bonferroni adjustment for multiple comparisons was applied for the analysis of differences in estimated marginal means.

2.8.4. Temporal relationship between synchrony and performance

Next, we investigated the temporal relationship between synchrony and performance. Again, we computed three linear mixed models, each predicting the intra-dyadic synchrony in one of the three frequency bands of interest (alpha, beta and gamma) with restricted maximum likelihood estimation. Here we were interested in the relationship between frequency-specific inter-brain synchrony and momentary performance at each measured time point represented by the beginning time of the 3 s analysis window. A hierarchical model including the ROIs (central, frontal, parietal, and occipital) within dyads and the two blocks (gaming sessions) within each ROI was used to consider the non-independence between measures at the lowest levels (multiple time points within each block) and to minimize risk of false discovery that might arise from an extensive number of separate models constructed for each ROI and frequency band combination. In accordance with the model structure presented above, random intercepts were included for the dyad; dyad and region; dyad and block; as well as for the dyad, region and block interactions. These interactions were specified as the subject variables and the random intercept was included for each level using a scaled identity covariance structure. The repetition of measured synchrony indices and performance scores at each time point within each block was addressed by testing for the fit of a random slope for time at each level. The random slope for time was found fitting at the lowest level of the hierarchy and was therefore included accordingly in each model.

As the relationship between momentary synchrony and performance was our main interest, we included performance as a fixed effect in the model. Each dyad's task performance was calculated as described in Section 2.3. In this analysis, our goal was to explore whether inter-brain synchrony is associated with the varying level of success between two interacting individuals over the course of the task. We were therefore interested in the relative (instead of absolute) task performance of each dyad. Hence the performance value was standardized within each dyad and the z-score value was used as the performance index. Mean visuospatial test score and ROI were also included in the models as fixed factors. Additionally time, within-dyad difference in visuospatial test score and the interaction of ROI and performance were included. ROI-performance interaction was included to consider whether possible associations between synchrony and performance were specific to a certain region. Possible violations of homoscedasticity and multicollinearity were again examined for each model. The inspection of tolerance statistics confirmed no violations of multicollinearity ($VIF < 2.5$ and tolerance > 0.4 for all variables). Assumption of homoscedasticity was also met for each model.

3. Results

3.1. Synchrony arising from interaction

Both the *t*-test and the MWE analyses revealed that interaction within the task produced significant coupling in alpha, beta and low gamma frequencies in frontal, central, parietal and occipital ROIs (Fig. 3). This result was used to select these frequency bands and regions to be used in the performance analyses (see Section 2.8.2 for details).

3.2. Synchrony and performance across dyads

Higher mean alpha synchrony was associated with better performance in the task ($F = 5.52$, $p = 0.031$). The effect of the dyad's mean visuospatial test score on alpha synchrony was also found significant ($F = 11.59$, $p = 0.003$), with higher level of visuospatial skills associated with lower level of synchrony.

The levels of beta and gamma synchrony were found to vary between different ROIs ($F = 22.22$, $p < 0.001$ for beta; $F = 10.26$, $p < 0.001$ for gamma). No other variables were found significant for predicting synchrony in any of the three frequency bands. Details concerning mean performance, visuospatial test score and intra-dyadic difference in

visuospatial test score as predictors of mean alpha, beta and gamma synchrony are presented in Table 1. Further details on the differences in mean alpha, beta and gamma synchrony measured over different regions can be found in the following section.

3.3. Differences in mean synchrony level between different regions

No variation in the level of alpha synchrony measured over different regions was found (mean synchrony was 0.010 in frontal; 0.012 in central; 0.011 in parietal; and 0.011 in occipital region, with all *p* values concerning mean differences > 0.054).

The mean beta synchrony was greatest in the occipital region (mean = 0.039) with significantly higher synchrony in occipital compared to the other three regions. Examination of difference in estimated marginal means also showed a difference in beta synchrony in central compared to frontal region (mean difference 0.011, $p = 0.009$), with higher level of synchrony measured over the central region.

Mean gamma synchrony was greatest in the occipital region (mean = 0.009) with significantly higher synchrony in occipital compared to frontal (mean difference 0.003, $p = 0.002$) and parietal regions (mean difference 0.003, $p = 0.004$). Gamma synchrony in the central region was also higher compared to frontal (mean difference 0.003, $p = 0.012$)

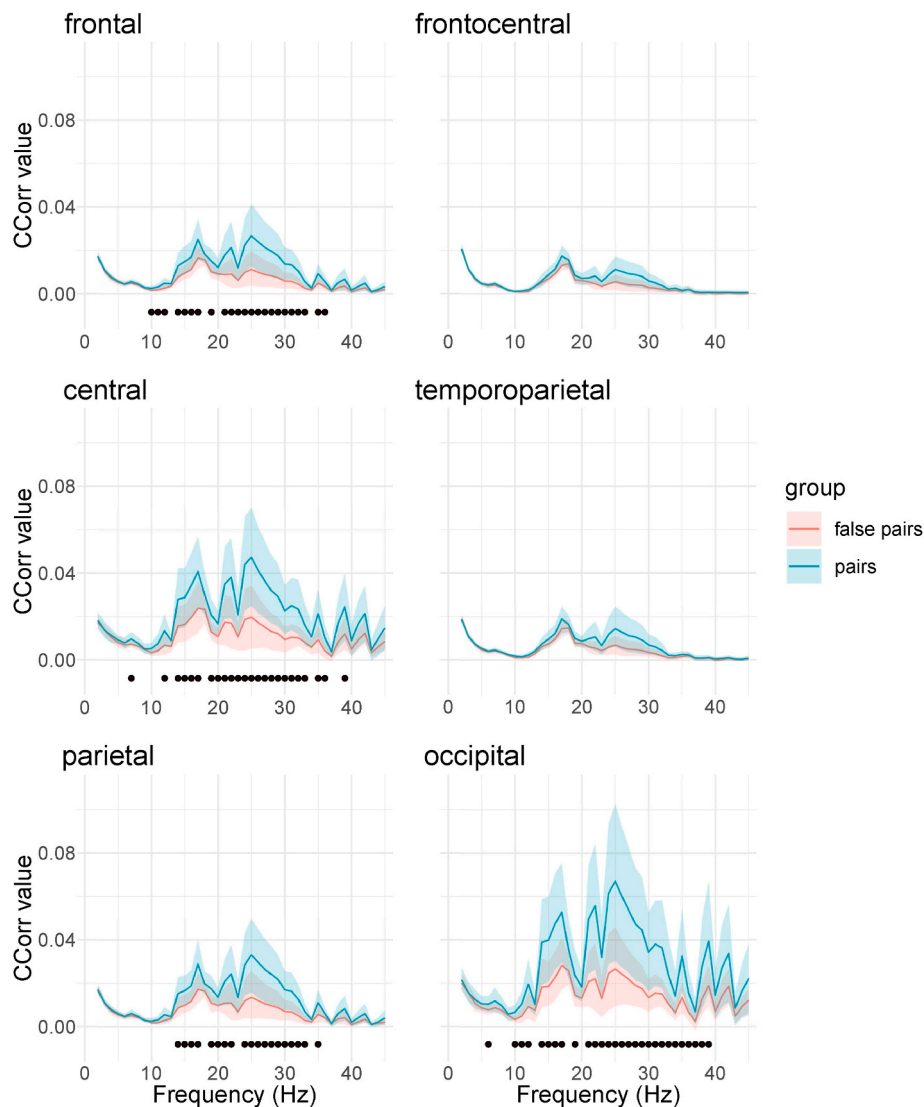


Fig. 3. CCorr over the analyzed frequencies for pairs and unpairs for the different ROIs. Solid lines are the means, MWE-based confidence band is shown by the filled area. Black dots on the x-axis mark significant ($p < 0.05$) differences for FDR corrected *t*-test results between real and false pairs for each frequency.

Table 1

Continuous predictors in the three linear mixed models predicting the mean levels of alpha, beta and gamma synchrony. Significance values of $p < 0.05$ are marked in bold.

Predictor	β	SE (β)	F	p	CI (95%)
Alpha frequency band					
Performance	0.00244	0.00104	5.52	0.031	0.00025, 0.00463
WAIS	-0.00041	0.00120	11.59	0.003	-0.00066, -0.00016
WAIS difference	-0.00012	0.00087	2.05	0.170	-0.00031, 0.00005
Beta frequency band					
Performance	0.01022	0.01040	0.97	0.340	-0.01172, 0.03216
WAIS	-0.00047	0.00120	0.15	0.702	-0.00301, 0.00207
WAIS difference	0.00055	0.00087	0.41	0.532	-0.00128, 0.00238
Gamma frequency band					
Performance	0.00073	0.00144	0.25	0.621	-0.00232, 0.00377
WAIS	-0.00026	0.00017	2.40	0.140	-0.00061, 0.00009
WAIS difference	0.00006	0.00012	0.27	0.608	-0.00019, 0.00032

and parietal (mean difference 0.003, $p = 0.017$) regions. No significant difference was found between mean gamma synchrony measured over occipital compared to central region or frontal compared to parietal region. All reported p -values concerning comparisons of mean synchrony between different regions in each frequency band were Bonferroni corrected.

3.4. Temporal relationship between synchrony and performance

Alpha synchrony was found to decrease over time ($F = 8.42$, $p = 0.004$). Alpha synchrony was also positively associated with dyads' mean visuospatial test scores ($F = 5.57$, $p = 0.030$). No association was found between alpha synchrony and performance or within-dyad difference in visuospatial test score.

A significant main effect of time on beta synchrony ($F = 133.11$, $p < 0.001$) was found, with synchrony decreasing over time. The level of beta synchrony was found to be dependent on region ($F = 47.97$, $p < 0.001$). No significant effects of the other measures were found on beta synchrony.

Higher gamma synchrony was found to be correlated with better momentary performance in the task ($F = 4.06$, $p = 0.044$). Significant effects of time ($F = 34.85$, $p < 0.001$) and region ($F = 7.57$, $p < 0.001$) were also found for gamma synchrony. The association between synchrony and time was negative, meaning that gamma synchrony decreased over time. Details concerning predictors of momentary alpha, beta and gamma synchrony can be found in Table 2.

As synchrony was found to be related to time in all frequency bands, we decided to visualize the average synchrony over time for both blocks (Fig. 4). The means of each dyad's blockwise synchrony were compared using dependent t -tests for paired samples. Alpha synchrony in block 1 ($M = 0.0101$, $SD = 0.0023$) was found to be lower than in block 2 ($M = 0.0113$, $SD = 0.0026$), $t(20) = -2.57$, $p = 0.018$. Beta synchrony in block 1 ($M = 0.0178$, $SD = 0.0199$) was also found to be lower than in block 2 ($M = 0.0274$, $SD = 0.0202$), $t(20) = -3.29$, $p = 0.0036$. Likewise, gamma synchrony in block 1 ($M = 0.0057$, $SD = 0.0028$) was found to be lower than in block 2 ($M = 0.0083$, $SD = 0.0035$), $t(20) = -3.37$, $p = 0.0031$.

Table 2

Continuous predictors in the three linear mixed models predicting momentary level of alpha, beta and gamma synchrony. Significance values of $p < 0.05$ are marked in bold.

Predictor	β	SE (β)	F	p	CI (95%)
Alpha frequency band					
Time	-0.000003	0.000001	8.42	0.004	-0.000005, 0.00000
Performance	0.00030	0.00049	1.53	0.217	-0.00065, 0.00125
WAIS	-0.00030	0.00013	5.57	0.030	-0.00058, -0.00003
WAIS difference	-0.00005	0.00008	0.53	0.476	-0.00021, 0.00010
Beta frequency band					
Time	-0.00005	0.000004	133.11	0.001	-0.00006, -0.00004
Performance	-0.0010	0.00077	0.11	0.746	-0.00255, 0.00050
WAIS	-0.00047	0.00108	0.19	0.670	-0.00272, 0.00179
WAIS difference	0.00099	0.00062	2.50	0.132	-0.00326, 0.00230
Gamma frequency band					
Time	-0.000008	0.000001	34.84	0.001	-0.00001, -0.000005
Performance	0.00186	0.000632	4.06	0.044	0.00619, 0.00310
WAIS	-0.00021	0.000152	1.98	0.177	-0.00054, 0.00012
WAIS difference	0.00009	0.00009	1.19	0.290	-0.00009, 0.00266

4. Discussion

Previous experiments have predominantly investigated connections between inter-brain synchrony and positive social outcomes without regard for the temporal dynamics of interaction and collaborative performance. These studies have also for the most part been conducted with participants located in the same room, and often in situations where communication verbally, using bodily and facial expressions, or a combination of these has been possible or even necessary. The extent to which colocation is required for inter-brain phase synchronization of electrical activity to occur has remained largely unexplored. To answer these questions, we investigated the connections between EEG synchrony and momentary performance during a collaborative task with physically isolated participants. We expected the cues from actions taken by the participants in the game to provide weak, but still sufficient signals for activating the mechanisms underlying inter-brain synchronization. We thereby also expected to be able to investigate temporally changing connections between inter-brain synchrony and collaborative performance during the task. These hypotheses were confirmed.

Collaboration in the task was associated with higher synchrony in the alpha, beta, and gamma bands, when comparing the synchrony between real pairs and performance-matched false pairs. This result supports previous findings of synchronization in these frequency bands during interaction (Levy et al., 2017; Barraza et al., 2020; Richard et al., 2021; Kawasaki et al., 2018; Hu et al., 2017; Pérez et al., 2017, 2019; Kinreich et al., 2017; Liu et al., 2021; Davidesco et al., 2019; Goldstein et al., 2018). There are several possible explanations for what concurrent activity in these different frequency bands signifies.

In studies with individuals, oscillatory activity in the alpha band has been linked to attention (Hanslmayr et al., 2011) and inhibitory control (Jensen and Mazaheri, 2010), beta oscillations with execution of motor tasks and sensorimotor interaction (Kilavik et al., 2013), and cortical gamma oscillations with generic neural control operations (Merker, 2013) (for a review, see Herrmann et al. (2016)). Synchrony between

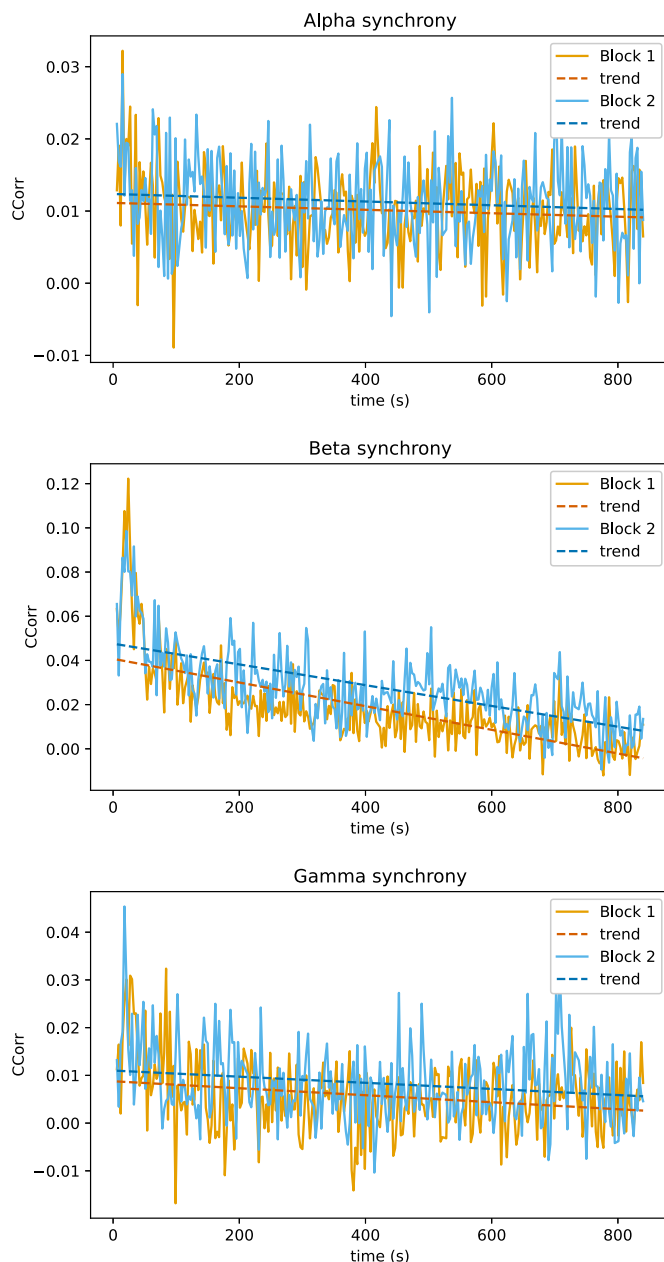


Fig. 4. Alpha, beta, and gamma frequency band synchrony over time averaged across subjects and across the frontal, central, parietal, and occipital electrode sites for the two blocks. Linear trends are shown with dashed lines.

individuals in these frequency bands may therefore reflect concurrent attentional and inhibitory processes during a task that requires continuous attentional monitoring, inhibitory control over behavior, and execution of motor tasks. However, links between oscillatory activity in the alpha, beta, and gamma bands, and processes specific to social cognition have also been found. For instance, joint attention in comparison to individual attention has been connected with a decrease in alpha power in individuals (Lachat et al., 2012). Beta oscillations in right temporal areas have been found to be connected with correctly assessing others' preferences (Park et al., 2018), to increase prior to joint attention, and to correlate with mentalizing abilities in children (Soto-Icaza et al., 2019). Recently, stronger desynchronization in the alpha and beta frequency bands over precentral and parietal areas was associated with higher arousal while viewing emotion-inducing video clips, and taken to reflect functioning of the mirror neuron system (Kim et al., 2021). Increased synchrony measured by coherence in gamma

band activity over frontal and temporal areas has been uniquely associated with collaboration (Barraza et al., 2020) and interpreted as reflecting shared intentionality and not merely joint coordination. Gamma band activity recorded from the superior temporal sulcus has also been connected with mentalizing (Cohen et al., 2009). It is possible that synchronization over these frequency bands observed in the current study reflects the activation of mechanisms supporting joint attention, mentalizing and joint intentionality during the collaborative task.

Our models also revealed a tendency for synchronization to decrease over time during a playing session, with the effect especially strong in the beta frequency band but also present in the alpha and gamma frequency bands. Additional analyses revealed that inter-brain synchrony in all three frequency bands was elevated in the second playing session, compared to the first one. This effect could be related to a finding that action video games seem to induce high workload states, including increased theta and beta activation, and a characteristic de-assimilation of beta waves occurring as an increase in frontal and a decrease in occipital activity (Gong et al., 2019). The decrease in beta synchronization over the duration of the playing session could be related to attention given to the task. It is interesting however, that this effect was replicated in the second playing session, and the overall synchrony level was also higher, which does not seem to suggest that the effect was due to the unfamiliarity of the task requiring higher attentional demands in the beginning, but instead it may be related to fatigue or other type of habituation. Prior practice, on the other hand, led to higher synchrony in all frequency bands during the second playing session.

Our study also showed that inter-individual synchronization of oscillatory brain activity over several frequency bands can occur without physical presence or direct visual or auditory information of the counterpart of interaction. Previously, inter-brain synchrony of the brain's hemodynamic activity has been observed in interacting individuals located in separate rooms (Stolk et al., 2014), but prior fNIRS and EEG studies have placed individuals in the same room, at most separated with partitions (e.g. in the fNIRS study by Cheng et al. (2019)). Our results therefore extend the findings of Stolk et al. (2014); Cheng et al. (2019) to phase synchrony of EEG oscillatory activity.

After removing the cues that colocation offers, what could be the mediator causing the inter-brain synchronization observed in this experiment? Face-to-face interaction as a medium offers vast amounts of different information, and engages the processes of primary intersubjectivity, which are the intuitive and nearly instant processes that allow reading gaze, facial expressions, and other basic interpersonal signals (Gallagher, 2008). In our study, we attempted to remove those "natural" signals: the only mediator was the game that the subjects played – the cooperative movement of the car. This required predicting and observing the partner's actions, and responding to them with the participant's own actions, either by controlling the direction or the speed of the car. Although the interaction in the car racing game is much more limited than face-to-face interaction, the continuous nature of the task requires similar quick reactions, negotiation, and building rapport. It also invites mental simulation of the other's intent. It seems that individuals readily perform these actions even with such restricted information. After all, already Heider and Simmel (1944) found out that even the movement of primitive shapes tends to be interpreted to reflect personhood and intentionality.

Our investigation of temporally changing connections between inter-brain synchrony and collaborative performance showed positive links between task performance and alpha synchrony across dyads, and momentary task performance and gamma synchrony within dyads. This finding confirms earlier results about a connection between synchronization and better team performance (Reinero et al., 2020; Szymanski et al., 2017), and expands this phenomenon to the online gaming environment. It may also further elucidate the meaning of the inter-brain synchronization observed in our study.

In individuals, activity in the alpha frequency band has been connected to attention (Hanslmayr et al., 2011) and the mirror neuron

system (Kim et al., 2021), and activity in the gamma frequency band with mentalizing (Cohen et al., 2009). Increased alpha synchrony could therefore signify concurrent attentional processes which could be expected to have an effect on task performance in a joint coordination task – stronger shared attention on the object being coordinated would likely enable faster reaction times to the actions of the other player, and thereby lead to better results. Gamma synchronization, if taken to reflect concurrent mentalizing, could facilitate pair performance in the task, as very little information of the other was available. Synchronous mentalizing could increase information of the other, which, even if imagined, could facilitate better prediction of the other's actions in the game, leading to faster responses to the other's actions and quicker joint decision-making. Similarly, concurrent activation of the mirror neuron system, potentially reflected by alpha synchrony, could lead to improved speed and accuracy in predicting the movements of the partner. Better joint intentionality as reflected by gamma synchrony (Barraza et al., 2020) could support pair performance, because success in the game required continuous shared decision-making. Pairs with more shared intention could potentially focus more resources on the available information of the other, helping to predict each other's actions better, leading to faster decisions.

Another explanation for connections between specifically alpha synchrony and performance stem from the concept of flow. Video games are generally an effective tool for inducing flow, but the complexity of this mental state makes it hard to pinpoint exact neural correlates for it, instead calling for the investigation of distinct aspects (Khoshnoud et al., 2020). Previous studies have identified individual alpha activity as a predictor for the performance dimension of the flow experience during a car racing game (Kramer, 2007), and peak performance in another individually played car racing game was related to intra-brain beta band synchronization (De Kock, 2014). Alpha, low beta, and mid beta band activity have also been indicated as the most reliable predictors for the flow state in comparison to boredom and anxiety in a plane battle game (Berta et al., 2013). It is conceivable that a state of team flow (Shehata et al., 2021) could explain our results, which indicate that dyads with higher alpha synchrony performed better in the collaborative car racing game. Inducing team flow could be a very desirable outcome of multiplayer gaming, and influence performance in the game, as well as social relationships and collaboration outside of gaming.

Lastly, another possible explanation for why momentary synchronization would be connected to better performance is simultaneous activation of the reward system when succeeding in the task. Indeed, oscillatory activity in the beta and gamma ranges has been connected with processing of surprising rewards during tasks that require learning (HajiHosseini et al., 2012) (for a review, see Marco-Pallarés et al. (2015)). Additionally, the emotions felt by the pair when succeeding and failing in the task could be a source of synchronization, as suggested by Nummenmaa et al. (2012), although it is not entirely clear how this would lead to positive links between synchrony and task performance, as concurrent negative emotions could be expected to lead to synchronization as well as positive ones.

4.1. Future work

The need for collaborative problem solving is increasing and there is a current need to develop better tools and metrics for it (Fiore et al., 2018). At the same time, using technical tools for cooperative work is becoming widespread, with the COVID-19 pandemic leading many to work from home for extended periods of time. We might see a permanent change in the balance between time spent working remotely and at the office, as well as between physical and virtual meetings, as the circumstances have forced companies and individuals to adopt new strategies rapidly and some are likely to see cost, productivity and quality-of-life benefits of working remotely (Brynjolfsson et al., 2020).

Our results, along with previous face-to-face studies (Szymanski et al., 2017; Reinerio et al., 2020) indicate that increased inter-brain

synchrony is related to improved collaborative task performance. Since inter-brain synchrony can occur even without physical presence, its role in online interaction and remote work becomes an interesting question. Apart from professional performance, inter-brain synchronization could be expected to have positive effects also on social relationships online, as previous studies have often demonstrated links between both interpersonal and inter-brain synchronization and affiliation, cooperation and prosocial tendency in face-to-face interaction (Kinreich et al., 2017; Cui et al., 2012; Toppi et al., 2016; Hu et al., 2017). Future work needs to investigate whether computer-mediated synchronizing activities will show similar prosocial effects. Different types of tasks, which rely more on socioemotional processes, would be ideal to investigate group differences between socially close and socially distant dyads in online interaction.

We expect that the importance of inter-brain synchrony in online interaction could be two-fold: to optimize virtual multi-user environments for supporting the occurrence of synchronization, and to develop virtual activities that specifically induce it. Inter-brain synchronization has already been demonstrated in same-room virtual reality, in which the participants' bodies are accurately tracked (Gumilar et al., 2021), and our results suggest that specialized equipment is not necessary for inducing it: Activities similar to our task, such as cooperative multiplayer computer games, could be a potential way to induce synchronization over distance. However, our results also show that inter-brain synchrony in all analyzed frequency bands decreased over time during a playing session, while being elevated in another playing session after a short break compared to the first session. These are effects that should be taken into account if designing a game meant for inducing inter-brain synchronization.

The results obtained with the novel paradigm also suggest that inter-brain synchrony can be measured continuously during interaction, finding a positive link between gamma synchrony and momentary task performance as well as revealing a decrease in synchrony during a playing session. Continuous measurement makes it possible to build experiments, in which the progression of inter-brain synchrony is tracked over time, and also as a response to either pre-coded or afterwards observed events in the interaction. As social interaction studies often involve an a posteriori action coding process, combining those results with continuous inter-brain synchrony analysis can reveal more about which situations and patterns of interaction are linked to synchrony. With improved methods for measurement and analysis of synchrony in the future, there exists potential to observe collaborative capability in real time, e.g. for monitoring and for adaptive interactive systems.

Future work also needs to explore the possibly detrimental effects of network latency on inter-brain synchronization, as in our study the two shielded rooms being located in the same laboratory allowed us to use the same computer for presenting the game and registering actions from both participants, essentially eliminating latency altogether.

Whether a connection exists between inter-brain synchrony and the flow state (Csikszentmihalyi, 1991) during multiplayer online video games is an interesting question for future work, as achieving a team flow state (Shehata et al., 2021) could be expected to affect performance positively, and in itself be a desirable outcome of gaming.

4.2. Strengths and limitations

To avoid spurious synchronization, we created an experiment in which participants had distinct roles, not requiring synchronized motor activity or similar and simultaneous action. Such activity would likely be a potential way to induce neural synchronization, but motor artefacts would confound the EEG analysis. Visually, the task had continuous movement, avoiding sudden onset visual stimuli, which could also be a source of spurious synchronization. The false pair analysis was done by preserving the temporal progression of the experiment to further minimize causes of spurious synchrony arising from the experimental setting.

A limitation of this experiment was that both participants in a dyad viewed the same image on the screen at the same time, and while the false pairs were also viewing a similar image, with the same track being pictured with a moving car, the movements of the car on the track would not have been the same between the participants in a false pair. Similar visual stimulation has indeed been shown to cause widespread cortical synchronization (Hasson et al., 2004). We found that synchronization in the beta and gamma bands was strongest over occipital electrode sites, which may reflect similarities in visual processing during the task. However, due to the effects observed on other variables, especially both momentary and average task performance, the similarity of the visual stimulus is not enough to explain all of the observed inter-brain synchrony, and it seems that mediated interaction, attention, and prediction of the partner's intentions also played a role.

We took notable measures in the design of the statistical models to avoid running an extensive number of tests, hence diminishing the risk of type 1 errors. Due to this, we wanted to prevent further increasing the risk of type 2 errors that would have been likely to occur in case of applying additional statistical corrections to the exploratory analyses. However, as even more conservative methods were not carried out in order to prevent false discoveries, we encourage use of the current findings related to task performance in relation to synchrony in different frequency bands and regions of interest in guiding future research, but request caution in interpreting the results.

More studies are needed to explore the effects of adding more cues about the counterpart of interaction. Additionally, the effects of other activities, both collaborative, competitive, and without a clear goal should be investigated. The joint coordination task used in this experiment represents a specific type of cooperative activity, and the results related to real-time task performance are not directly applicable to other activities, although task performance effects on inter-brain synchrony have been observed also in other types of tasks (Szymanski et al., 2017; Reinerio et al., 2020).

As our study did not focus on investigating the effects of familiarity or closeness, we invited only socially close individuals, and cannot therefore make any conclusions about whether social affiliation has a similar effect on inter-brain synchrony in on-screen interaction as has been previously observed face-to-face.

5. Conclusion

We have conducted an experiment in which physically isolated dyads performed a joint coordination task in the form of a multiplayer online car racing game. In this game, one participant steers and the other controls the speed of the car. The results show synchronization during task execution in the alpha, beta, and gamma frequency bands. Looking further at synchrony in these frequency bands reveals a connection between mean alpha synchrony and task performance across dyads, with

better performance in the task linked with increased synchrony. Additionally, temporal within-dyad analysis reveals that momentary performance in the task is connected with increased gamma synchrony. This confirms earlier reports of inter-brain synchronization being linked to team performance and extends those results to the online gaming environment. Analysis of temporal progression of synchrony in each frequency band shows a decrease within a playing session, but an increase in the second session compared to the first. The analysis of momentary performance also shows that inter-brain synchrony can be observed in real time. These results suggest that synchrony can have a role in online interaction, which should be further examined. For example, targeting inter-brain synchrony in the design of computer-mediated interaction is an interesting possibility.

Data/code availability statement

Code for the cooperative car racing game is available as a git repository at <https://github.com/vatte/autopeli> (accessed Nov 10, 2021). The raw data are not openly available since the participants have not given their explicit consent. The preprocessed anonymous data are available upon a reasonable request addressed to the corresponding author.

Funding

This work was supported by the University of Helsinki (Helsinki Challenge/NEMO) and Business Finland (HUMEX and CRELU projects).

CRediT author statement

Valtteri Wikström: Writing - original draft, Writing - review & editing, Software, Formal analysis, Investigation, Methodology, Data curation, Conceptualization, Visualization, Funding acquisition. **Katri Saarikivi:** Writing - original draft, Writing - review & editing, Investigation, Conceptualization, Funding acquisition. **Mari Falcon:** Writing - original draft, Writing - review & editing, Formal analysis, Investigation, Methodology, Data curation, Funding acquisition. **Tommi Makkonen:** Writing - review & editing, Methodology, Conceptualization, Funding acquisition. **Silja Martikainen:** Writing - review & editing, Methodology, Funding acquisition. **Vesa Putkinen:** Writing - review & editing, Methodology, Conceptualization. **Benjamin Cowley:** Writing - review & editing, Methodology, Visualization. **Mari Tervaniemi:** Writing - review & editing, Methodology, Funding acquisition.

Declaration of competing interest

The authors declare no competing financial interests.

Appendix A. Game tracks

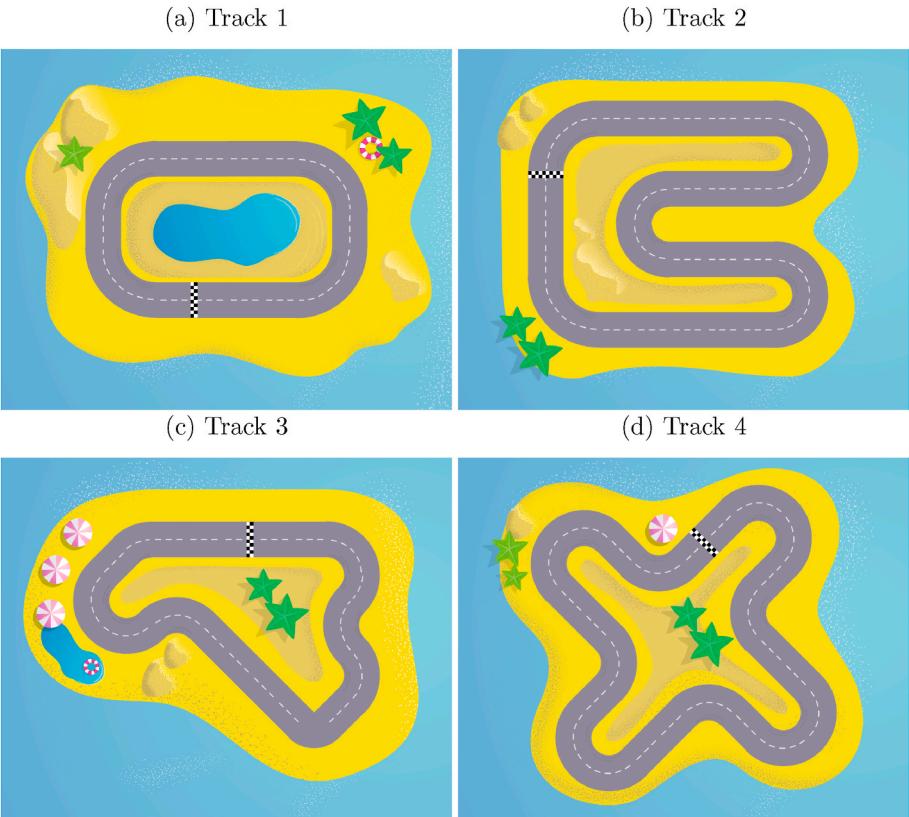


Fig. A.5. The four tracks included in the car racing game.

Appendix B. Button presses

Table B.3
Statistics about the amount of button presses in each role.

Measure	Steerer	Accelerator
Mean amount of presses	1197.9 (<i>SD</i> = 169.6)	908.9 (<i>SD</i> = 288.2)
Mean length of presses	0.227 s (<i>SD</i> = 0.174 s)	0.491 s (<i>SD</i> = 0.808 s)

Table B.3 shows the mean amount of presses and the mean length of presses for the roles of accelerator and steerer during the experiment. The mean time difference between an accelerators press and the closest press of the steerer was 0.236 s (*SD* = 0.351 s).

References

Ayrolles, A., Brun, F., Chen, P., Djalovski, A., Beauxis, Y., Delorme, R., Bourgeron, T., Dikker, S., Dumas, G., 2020. HyPyP: a Hyperscanning Python Pipeline for inter-brain connectivity analysis. *Soc. Cognit. Affect Neurosci.* 16, 72–83. <https://doi.org/10.1093/scan/nsaa141>.

Barraza, P., Pérez, A., Rodríguez, E., 2020. Brain-to-brain coupling in the gamma-band as a marker of shared intentionality. *Front. Hum. Neurosci.* 14, 295. <https://doi.org/10.3389/fnhum.2020.00295>.

Berta, R., Bellotti, F., De Gloria, A., Pranantha, D., Schatten, C., 2013. Electroencephalogram and physiological signal analysis for assessing flow in games. *IEEE Trans. Comput. Intell. AI Games* 5, 164–175. <https://doi.org/10.1109/TCIAIG.2013.2260340>.

Brynjolfsson, E., Horton, J.J., Ozimek, A., Rock, D., Sharma, G., TuYe, H.Y., 2020. COVID-19 and Remote Work: an Early Look at US Data. National Bureau of Economic Research. <https://doi.org/10.3386/w27344>. Working Paper 27344.

Burgess, A., 2013. On the interpretation of synchronization in EEG hyperscanning studies: a cautionary note. *Front. Hum. Neurosci.* 7, 881. <https://doi.org/10.3389/fnhum.2013.00881>.

Cheng, X., Pan, Y., Hu, Y., Hu, Y., 2019. Coordination elicits synchronous brain activity between co-actors: frequency ratio matters. *Front. Neurosci.* 13 <https://doi.org/10.3389/fnins.2019.01071>.

Churchward, P., Doyle, P., 2008. Top Gear – Showdown: the British (Top Gear) vs. The Germans (D Motor). British Broadcasting Corporation (BBC) [TV series episode]. Season 11, Episode 6.

Cohen, M.X., David, N., Vogeley, K., Elger, C.E., 2009. Gamma-band activity in the human superior temporal sulcus during mentalizing from nonverbal social cues. *Psychophysiology* 46, 43–51. <https://doi.org/10.1111/j.1469-8986.2008.00724.x>.

Csikszentmihalyi, M., 1991. *Flow: the Psychology of Optimal Experience*. Harper Perennial, New York, NY.

Cui, X., Bryant, D.M., Reiss, A.L., 2012. NIRS-based hyperscanning reveals increased interpersonal coherence in superior frontal cortex during cooperation. *Neuroimage* 59, 2430–2437. <https://doi.org/10.1016/j.neuroimage.2011.09.003>.

Czeczumski, A., Eustergerling, S., Lang, A., Menrath, D., Gerstenberger, M., Schuberth, S., Schreiber, F., Rendon, Z.Z., König, P., 2020. Hyperscanning: a valid method to study neural inter-brain underpinnings of social interaction. *Front. Hum. Neurosci.* 14, 39. <https://doi.org/10.3389/fnhum.2020.00039>.

Davidesco, I., Laurent, E., Valk, H., West, T., Dikker, S., Milne, C., Poeppel, D., 2019. Brain-to-brain synchrony between students and teachers predicts learning outcomes. *bioRxiv*. <https://doi.org/10.1101/644047>.

De Kock, F.G., 2014. *The Neuropsychological Measure (eeg) of Flow under Conditions of Peak Performance*.

Delorme, A., Makeig, S., 2004. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J. Neurosci. Methods* 134, 9–21. <https://doi.org/10.1016/j.jneumeth.2003.10.009>.

Dikker, S., Wan, L., Davidesco, I., Kaggen, L., Oostrik, M., McClintock, J., Rowland, J., Michalareas, G., Van Bavel, J.J., Ding, M., Poeppel, D., 2017. Brain-to-brain synchrony tracks real-world dynamic group interactions in the classroom. *Curr. Biol.* 27, 1375–1380. <https://doi.org/10.1016/j.cub.2017.04.002>.

Dikker, S., Michalareas, G., Oostrik, M., Serafimaki, A., Kahraman, H.M., Struiksma, M. E., Poeppel, D., 2021. Crowdsourcing neuroscience: inter-brain coupling during face-

- to-face interactions outside the laboratory. *Neuroimage* 227, 117436. <https://doi.org/10.1016/j.neuroimage.2020.117436>.
- Dunbar, R.I.M., Baron, R., Frangou, A., Pearce, E., van Leeuwen, E.J.C., Stow, J., Partridge, G., MacDonald, I., Barra, V., van Vugt, M., 2012. Social laughter is correlated with an elevated pain threshold. *Proc. R. Soc. B Biol. Sci.* 279, 1161–1167. <https://doi.org/10.1098/rspb.2011.1373>.
- Entertainment Software Association, 2021. 2021 Essential Facts About the Video Game Industry. URL: <https://www.theesa.com/resource/2021-essential-facts-about-the-video-game-industry/>.
- Fiore, S.M., Graesser, A., Greiff, S., 2018. Collaborative problem-solving education for the twenty-first-century workforce. *Nat. Human Behav.* 2, 367–369. <https://doi.org/10.1038/s41562-018-0363-y>.
- Gallagher, S., 2008. Inference or interaction: social cognition without precursors. *Phil. Explor.* 11, 163–174. <https://doi.org/10.1080/13869790802239227>.
- Goldstein, P., Weissman-Fogel, I., Dumas, G., Shamay-Tsoory, S.G., 2018. Brain-to-brain coupling during handholding is associated with pain reduction. *Proc. Natl. Acad. Sci.* 115, E2528–E2537. <https://doi.org/10.1073/pnas.1703643115>.
- Gong, D., Li, Y., Yan, Y., Yao, Y., Gao, Y., Liu, T., Ma, W., Yao, D., 2019. The high-working load states induced by action real-time strategy gaming: an eeg power spectrum and network study. *Neuropsychologia* 131, 42–52. <https://doi.org/10.1016/j.neuropsychologia.2019.05.002>. URL: <https://doi.org/10.1016/j.neuropsychologia.2019.05.002>.
- Good, A., Russo, F.A., 2016. Singing promotes cooperation in a diverse group of children. *Soc. Psychol.* 47, 340–344. <https://doi.org/10.1027/1864-9335/a000282>.
- Gramfort, A., Luessi, M., Larson, E., Engemann, D., Strohmeier, D., Brodbeck, C., Goj, R., Jas, M., Brooks, T., Parkkonen, L., Hämäläinen, M., 2013. MEG and EEG data analysis with MNE-Python. *Front. Neurosci.* 7, 267. <https://doi.org/10.3389/fnins.2013.00267>.
- Gumilar, I., Sareen, E., Bell, R., Stone, A., Hayati, A., Mao, J., Barde, A., Gupta, A., Dey, A., Lee, G., Billingham, M., 2021. A comparative study on inter-brain synchrony in real and virtual environments using hyperscanning. *Comput. Graph.* 94, 62–75. <https://doi.org/10.1016/j.cag.2020.10.003>.
- HajjHosseini, A., Rodríguez-Fornells, A., Marco-Pallarés, J., 2012. The role of beta-gamma oscillations in unexpected rewards processing. *Neuroimage* 60, 1678–1685. <https://doi.org/10.1016/j.neuroimage.2012.01.125>.
- Hanslmayr, S., Gross, J., Klimesch, W., Shapiro, K.L., 2011. The role of alpha oscillations in temporal attention. *Brain Res. Rev.* 67, 331–343. <https://doi.org/10.1016/j.brainresrev.2011.04.002>.
- Hasson, U., Nir, Y., Levy, I., Fuhrmann, G., Malach, R., 2004. Intersubject synchronization of cortical activity during natural vision. *Science* 303, 1634–1640. <https://doi.org/10.1126/science.1089506>.
- Heider, F., Simmel, M., 1944. An experimental study of apparent behavior. *Am. J. Psychol.* 57, 243–259. <https://doi.org/10.2307/1416950>.
- Herrmann, C.S., Strüder, D., Helfrich, R.F., Engel, A.K., 2016. EEG oscillations: from correlation to causality. *Int. J. Psychophysiol.* 103, 12–21. <https://doi.org/10.1016/j.ijpsycho.2015.02.003>.
- Hu, Y., Hu, Y., Li, X., Pan, Y., Cheng, X., 2017. Brain-to-brain synchronization across two persons predicts mutual prosociality. *Soc. Cognit. Affect Neurosci.* 12, 1835–1844. <https://doi.org/10.1093/scan/nsx118>.
- 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/10.1016/j.neuroimage.2017.06.024>.
- Jensen, O., Mazaheri, A., 2010. Shaping functional architecture by oscillatory alpha activity: gating by inhibition. *Front. Hum. Neurosci.* 4, 186. <https://doi.org/10.3389/fnhum.2010.00186>.
- Kastrenakes, J., Heath, A., 2021. Facebook is Spending at Least \$10 Billion this Year on its Metaverse Division. The Verge. URL: <https://www.theverge.com/2021/10/25/22745381/facebook-reality-labs-10-billion-metaverse/>.
- Kawasaki, M., Kitajo, K., Yamaguchi, Y., 2018. Sensory-motor synchronization in the brain corresponds to behavioral synchronization between individuals. *Neuropsychologia* 119, 59–67. <https://doi.org/10.1016/j.neuropsychologia.2018.07.026>.
- Khosnoud, S., Igarzábal, F.A., Wittmann, M., 2020. Peripheral-physiological and neural correlates of the flow experience while playing video games: a comprehensive review. *PeerJ* 8, e10520. <https://doi.org/10.7717/peerj.10520>.
- Kilavik, B.E., Zaepffel, M., Brovelli, A., MacKay, W.A., Riehle, A., 2013. The ups and downs of beta oscillations in sensorimotor cortex. *Exp. Neurol.* 245, 15–26. <https://doi.org/10.1016/j.expneurol.2012.09.014>.
- Kim, H., Seo, P., Choi, J.W., Kim, K.H., 2021. Emotional arousal due to video stimuli reduces local and inter-regional synchronization of oscillatory cortical activities in alpha- and beta-bands. *PLoS One* 16, 1–13. <https://doi.org/10.1371/journal.pone.0255032>.
- Kinreich, S., Djalovski, A., Kraus, L., Louzoun, Y., Feldman, R., 2017. Brain-to-brain synchrony during naturalistic social interactions. *Sci. Rep.* 7, 17060. <https://doi.org/10.1038/s41598-017-17339-5>.
- Korpela, J., Puolamäki, K., Gionis, A., 2014. Confidence bands for time series data. *Data Min. Knowl. Discov.* 28, 1530–1553. <https://doi.org/10.1007/s10618-014-0371-0>.
- Kramer, D., 2007. Predictions of performance by eeg and skin conductance. *Indiana Undergrad. J. Cognit. Sci.* 2, 3–13.
- Lachat, F., Huguette, L., Lemarechal, J.D., Conty, L., George, N., 2012. Oscillatory brain correlates of live joint attention: a dual-EEG study. *Front. Hum. Neurosci.* 6, 156. <https://doi.org/10.3389/fnhum.2012.00156>.
- Levy, J., Goldstein, A., Feldman, R., 2017. Perception of social synchrony induces mother-child gamma coupling in the social brain. *Soc. Cognit. Affect Neurosci.* 12, 1036–1046. <https://doi.org/10.1093/scan/nsx032>.
- Li, R., Maysseless, N., Balters, S., Reiss, A.L., 2021. Dynamic inter-brain synchrony in real-life inter-personal cooperation: a functional near-infrared spectroscopy hyperscanning study. *Neuroimage* 238, 118263. <https://doi.org/10.1016/j.neuroimage.2021.118263>.
- Liu, H., Zhao, C., Wang, F., Zhang, D., 2021. Inter-brain amplitude correlation differentiates cooperation from competition in a motion-sensing sports game. *Soc. Cognit. Affect Neurosci.* 16, 552–564. <https://doi.org/10.1093/scan/nsab031>.
- Marco-Pallarés, J., Münte, T.F., Rodríguez-Fornells, A., 2015. The role of high-frequency oscillatory activity in reward processing and learning. *Neurosci. Biobehav. Rev.* 49, 1–7. <https://doi.org/10.1016/j.neubiorev.2014.11.014>.
- Merker, B., 2013. Cortical gamma oscillations: the functional key is activation, not cognition. *Neurosci. Biobehav. Rev.* 37, 401–417. <https://doi.org/10.1016/j.neubiorev.2013.01.013>.
- Mogan, R., Fischer, R., Bulbulia, J.A., 2017. To be in synchrony or not? a meta-analysis of synchrony's effects on behavior, perception, cognition and affect. *J. Exp. Soc. Psychol.* 72, 13–20. <https://doi.org/10.1016/j.jesp.2017.03.009>.
- Novembre, G., Knoblich, G., Dunne, L., Keller, P.E., 2017. Interpersonal synchrony enhanced through 20 hz phase-coupled dual brain stimulation. *Soc. Cognit. Affect Neurosci.* 12, 662–670. <https://doi.org/10.1093/scan/nsw172>.
- Noy, L., Dekel, E., Alon, U., 2011. The mirror game as a paradigm for studying the dynamics of two people improvising motion together. *Proc. Natl. Acad. Sci.* 108, 20947–20952. <https://doi.org/10.1073/pnas.1108155108>.
- Nozawa, T., Sakaki, K., Ikeda, S., Jeong, H., Yamazaki, S., dos Santos Kawata, K.H., dos Santos Kawata, N.Y., Sasaki, Y., Kulason, K., Hirano, K., et al., 2019. Prior physical synchrony enhances rapport and inter-brain synchronization during subsequent educational communication. *Sci. Rep.* 9, 1–13. <https://doi.org/10.1038/s41598-019-49257-z>.
- Nozawa, T., Kondo, M., Yamamoto, R., Jeong, H., Ikeda, S., Sakaki, K., Miyake, Y., Ishikawa, Y., Kawashima, R., 2021. Prefrontal inter-brain synchronization reflects convergence and divergence of flow dynamics in collaborative learning: a pilot study. *Front. Neuroergonomics* 2, 19. <https://doi.org/10.3389/fnrgo.2021.686596>.
- Nummenmaa, L., Glerean, E., Viinikainen, M., Jääskeläinen, I.P., Hari, R., Sams, M., 2012. Emotions promote social interaction by synchronizing brain activity across individuals. *Proc. Natl. Acad. Sci.* 109, 9599–9604. <https://doi.org/10.1073/pnas.1206095109>.
- Palumbo, R.V., Marraccini, M.E., Weyandt, L.L., Wilder-Smith, O., McGee, H.A., Liu, S., Goodwin, M.S., 2017. Interpersonal autonomic physiology: a systematic review of the literature. *Pers. Soc. Psychol. Rev.* 21, 99–141. <https://doi.org/10.1177/108868316628405>.
- Pan, Y., Dikker, S., Goldstein, P., Zhu, Y., Yang, C., Hu, Y., 2020a. Instructor-learner brain coupling discriminates between instructional approaches and predicts learning. *Neuroimage* 211, 116657. <https://doi.org/10.1016/j.neuroimage.2020.116657>.
- Pan, Y., Novembre, G., Song, B., Zhu, Y., Hu, Y., 2020b. Dual brain stimulation enhances interpersonal learning through spontaneous movement synchrony. *Soc. Cognit. Affect Neurosci.* 16, 210–221. <https://doi.org/10.1093/scan/nsaa080>.
- Park, J., Kim, H., Sohn, J.W., Choi, J.R., Kim, S.P., 2018. EEG beta oscillations in the temporoparietal area related to the accuracy in estimating others' preference. *Front. Hum. Neurosci.* 12, 43. <https://doi.org/10.3389/fnhum.2018.00043>.
- Pearce, E., Launay, J., Dunbar, R.I.M., 2015. The ice-breaker effect: singing mediates fast social bonding. *R. Soc. Open Sci.* 2, 150221. <https://doi.org/10.1098/rsos.150221>.
- Peirce, J., Gray, J.R., Simpson, S., MacAskill, M., Höchenberger, R., Sogo, H., Kastman, E., Lindeløv, J.K., 2019. PsychoPy2: experiments in behavior made easy. *Behav. Res. Methods* 51, 195–203. <https://doi.org/10.3758/s13428-018-01193-y>.
- Pérez, A., Carreiras, M., Duñabeitia, J.A., 2017. Brain-to-brain entrainment: EEG interbrain synchronization while speaking and listening. *Sci. Rep.* 7, 1–12. <https://doi.org/10.1038/s41598-017-04464-4>.
- Pérez, A., Dumas, G., Karadag, M., Duñabeitia, J.A., 2019. Differential brain-to-brain entrainment while speaking and listening in native and foreign languages. *Cortex* 111, 303–315. <https://doi.org/10.1016/j.cortex.2018.11.026>.
- Pion-Tonachini, L., Kreutz-Delgado, K., Makeig, S., 2019. ICLABEL: an automated electroencephalographic independent component classifier, dataset, and website. *Neuroimage* 198, 181–197. <https://doi.org/10.1016/j.neuroimage.2019.05.026>.
- Reinero, D.A., Dikker, S., Van Bavel, J.J., 2020. Inter-brain synchrony in teams predicts collective performance. *Soc. Cognit. Affect Neurosci.* <https://doi.org/10.1093/scan/nsaa135>.
- Richard, C., Karić, M.S., McConnell, M., Poole, J., Rupp, G., Fink, A., Meghdadi, A., Berka, C., 2021. Elevated inter-brain coherence between subjects with concordant stances during discussion of social issues. *Front. Hum. Neurosci.* 15, 241. <https://doi.org/10.3389/fnhum.2021.611886>.
- Shehata, M., Cheng, M., Leung, A., Tsuchiya, N., Wu, D.A., Tseng, C.h., Nakauchi, S., Shimono, S., 2021. Team flow is a unique brain state associated with enhanced information integration and interbrain synchrony. *eNeuro* 8. <https://doi.org/10.1523/ENEURO.0133-21.2021>.
- Shiraishi, M., Shimada, S., 2021. Inter-brain synchronization during a cooperative task reflects the sense of joint agency. *Neuropsychologia* 154, 107770. <https://doi.org/10.1016/j.neuropsychologia.2021.107770>.
- Soto-Icaza, P., Vargas, L., Aboitiz, F., Billeke, P., 2019. Beta oscillations precede joint attention and correlate with mentalization in typical development and autism. *Cortex* 113, 210–228. <https://doi.org/10.1016/j.cortex.2018.12.018>.
- Stolk, A., Noordzij, M.L., Verhagen, L., Volman, I., Schoffelen, J.M., Oostenveld, R., Hagoort, P., Toni, I., 2014. Cerebral coherence between communicators marks the emergence of meaning. *Proc. Natl. Acad. Sci.* 111, 18183–18188. <https://doi.org/10.1073/pnas.1414886111>.
- Szymanski, C., Pesquita, A., Brennan, A.A., Perdakis, D., Enns, J.T., Brick, T.R., Müller, V., 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. <https://doi.org/10.1016/j.neuroimage.2017.03.013>.
- Tarr, B., Launay, J., Dunbar, R.I., 2016. Silent disco: dancing in synchrony leads to elevated pain thresholds and social closeness. *Evol. Hum. Behav.* 37, 343–349. <https://doi.org/10.1016/j.evolhumbehav.2016.02.004>.
- Tonna, M., Marchesi, C., Parmigiani, S., 2019. The biological origins of rituals: an interdisciplinary perspective. *Neurosci. Biobehav. Rev.* 98, 95–106. <https://doi.org/10.1016/j.neubiorev.2018.12.031>.
- Toppi, J., Borghini, G., Petti, M., He, E.J., De Giusti, V., He, B., Astolfi, L., Babiloni, F., 2016. Investigating cooperative behavior in ecological settings: an EEG hyperscanning study. *PLoS One* 11, 1–26. <https://doi.org/10.1371/journal.pone.0154236>.
- Valdesolo, P., DeSteno, D., 2011. Synchrony and the social tuning of compassion. *Emotion* 11, 262. <https://doi.org/10.1037/a0021302>.
- Wechsler, D., 2012. WAIS-IV Käsikirja [Wechsler Adult Intelligence Scale–, fourth ed. Psykologien Kustannus Oy, Helsinki. Finland.
- Wiltermuth, S.S., Heath, C., 2009. Synchrony and cooperation. *Psychol. Sci.* 20, 1–5. <https://doi.org/10.1111/j.1467-9280.2008.02253.x>.