DOI: 10.1111/nyas.15072

ORIGINAL ARTICLE

ANNALS OF THE NEW YORK ACADEMY OF SCIENCES

Dynamics in interbrain synchronization while playing a piano duet

Anja Lender[1,2] | Dionysios Perdikis[1,3] | Walter Gruber[4] | Ulman Lindenberger[1,5,6] | Viktor Müller[1]

[1]Max Planck Institute for Human Development, Center for Lifespan Psychology, Berlin, Germany

[2]Centre for Cognitive Neuroscience, University of Salzburg, Salzburg, Austria

[3]Charité-Universitätsmedizin Berlin, Berlin, Germany

[4]Department of Physiological Psychology, University of Salzburg, Salzburg, Austria

[5]Max Planck UCL Centre for Computational Psychiatry and Ageing Research, London, UK

[6]Max Planck UCL Centre for Computational Psychiatry and Ageing Research, Berlin, Germany

Correspondence
Viktor Müller, Center for Lifespan Psychology, Max Planck Institute for Human Development, Lentzeallee 94, 14195 Berlin, Germany.
Email: vmueller@mpib-berlin.mpg.de

Funding information
Max-Planck-Gesellschaft

Abstract

Humans interact with each other through actions that are implemented by sensory and motor processes. To investigate the role of interbrain synchronization emerging during interpersonal action coordination, electroencephalography data from 13 pairs of pianists were recorded simultaneously while they performed a duet together. The study aimed to investigate whether interbrain phase couplings can be reduced to similar bottom-up driven processes during synchronous play, or rather represent cognitive top-down control required during periods of higher coordination demands. To induce such periods, one of the musicians acted as a confederate who deliberately desynchronized the play. As intended, on the behavioral level, the perturbation caused a breakdown in the synchronization of the musicians' play and in its stability across trials. On the brain level, interbrain synchrony, as measured by the interbrain phase coherence (*IPC*), increased in the delta and theta frequency bands during perturbation as compared to non-perturbed trials. Interestingly, this increase in *IPC* in the delta band was accompanied by the shift of the phase difference angle from in-phase toward anti-phase synchrony. In conclusion, the current study demonstrates that interbrain synchronization is based on the interpersonal temporal alignment of different brain mechanisms and is not simply reducible to similar sensory or motor responses.

KEYWORDS
EEG hyperscanning, interbrain coupling, phase alignment, phase synchronization, piano duos, social interaction

INTRODUCTION

In response to the impact that social interaction processes have on our minds, much research has been conducted on social cognition by taking participatory processes of social interaction into account.[1–4] In cognitive neuroscience, the view that coordination of interpersonal actions or social interaction (e.g., playing music together, dancing, competitive sports, kissing, talking, fighting, etc.) requires strong interbrain synchrony (IBS) and specific hyperbrain activity to support this coordination or interaction has recently gained acceptance.[5,6,7–14,15–20] However, the functional significance of IBS and its relationship to behavioral actions, as well as the underlying real-time neural dynamics of interpersonally coordinated behavior, remain largely unexplored.[13,16,21–24] The present study aims to overcome this limitation by examining the mechanisms of social interaction at the behavioral and neural levels and by exploring the links between them. Furthermore, it is not fully clear which specific factors lead to or elicit IBS. It has been suggested that IBS could be a result of shared perceptual input and/or equal motor output.[12,13] However, there is also evidence that a certain amount of IBS has intrinsic attraction or is influenced by endogenous, cognitive processes (crucial for successful social interaction) and is not necessarily (directly) caused by common systems' input or output.[12,13,16,19,20,25–29] The present study aims to investigate which factors can contribute to the emergence of IBS supporting social interaction when playing music in a duet and how IBS is related to behavioral synchrony when the duet performance is perturbed or non-perturbed. The change in temporal neural dynamics between the participants' brains elicited by altered interaction requirements is of general interest here.

Playing music together is an illustrative example of the interplay between emergent and planned coordination expressed in entrained behavior.[30–32] Temporal entrainment, such as the spatiotemporal synchronization with a rhythmical signal,[33,34] can either be automatic (e.g., unintended foot tapping to music) or volitionally controlled (e.g., complex timing coordination between jazz musicians). When two musicians play together, their entrainment is thought to be caused by automatic bottom-up processes of motor resonance based on neural oscillators that are driven by the musical pulse.[35] When both musicians contribute equally to the music, they mutually adjust their actions by automatic phase correction mechanisms.[36] However, what makes music unique is the creativity and flexibility in temporal adjustment, which requires higher-level ensemble skills.[31,37,38] Musicians have to be aware of both their own sound as well as that of their coperformer. Furthermore, the resulting duet relies on the internal simulation and monitoring of the joint performance.[39] This continuous monitoring process is based on the dynamical allocation of attention resources and can be either more integrative or more selective, depending on the metric structure and requirements of the piece played.[37] When one musician decides to play an expressive tempo change, their partner will attend to the unpredicted change and adjust their own tempo to sustain the behavioral and affective coupling mediated by the music. "Thus, in accordance with enactive approaches to social cognition, performers intentionally and actively participate in making sense of the music so that its 'meaning' is shared among coperformers and communicated to audience members."[37]

Another important feature in joint actions is the observation of unexpected movements or events in relation to the partner.[40,41] It has been shown that hearing and performing different types of musical errors (i.e., wrong notes or unexpected additional notes) when playing with a partner elicits different brain responses, regardless of who made the error.[42] Thanks to the use of virtual reality and continuous recording of electroencephalography (EEG) and motion kinematics data, it is possible to extract the neural activity associated with either the correction of the virtual partner's action or the subsequent behavioral adaptation of both participants.[9,43,44] Just as after the execution of self-induced errors, observing a partner's error leads to a slowing of brain responses.[41,44,45] On a neurophysiological level, the errors of others trigger brain responses similar to those following self-induced errors, which are mainly localized in the posterior part of the medial frontal cortex.[44,46,47]

Much research on social cognition has been conducted by taking participatory processes of social interaction into account. Based on the idea that our minds are embodied and our bodies are embedded in a social environment,[9,21,48–50] people actively regulate their sensory–motor coupling with their surroundings in order to sustain a self-constructed identity as an autonomous agent. When two people sit in rocking chairs next to each other[51] or swing hand-held pendulums together,[52] their behavior is attracted to in-phase or anti-phase modes. Phase attraction is a typical coordination principle in biological systems where the coupling is more relative in terms of its fluctuation around perfect stable states.[53] In interpersonal coordination, fluctuations in stability can be accompanied by changes in cognitive states, such as the focus of attention. Stable interaction modes can deliver higher attention trade-off and, vice versa, focused attention on coordination stabilizes behavioral patterns.[54]

Consequently, besides the bottom-up effects of emergent dynamics, planned top-down processes also play a crucial role in interpersonal coordination.[55] Cognitive scientists commonly explain higher cognitive processes in terms of shared representations of a task, predictions of its outcome, and monitoring processes.[13,22,56,57] A common coding of performed and perceived action, associated with the function of mirror neurons, allows actors to predict the what, when, and where of others' actions.[58] Taking both the dynamic system perspective and cognitive approaches into account, interacting agents intentionally regulate the interpersonal coordination process while emergent dynamics in the interaction have an influence on the cognition of the agents in turn. Thus, everyday social interaction can be considered as a complex interplay of reciprocal bottom-up and top-down regulations using feedback and feedforward loops.[16,22,59–62]

Previous hyperscanning research on IBS showed that interpersonally coordinated actions during guitar playing in a duo or quartet are preceded and accompanied by between-brain oscillatory couplings.[12,14,15,17–20] When using multi-trial designs, this coupling was found to be predominant above fronto-central brain regions in the delta and theta frequency bands during periods of higher interpersonal coordination demands, for example, during preparatory metronome tempo setting and/or during coordinated play onset.[12,15,19] Furthermore, it has been shown that phase alignment in the frequencies, which showed synchronization maxima, strongly followed the time onset differences between the guitarists.[12,15] In addition, significant angular–linear correlations between phase and time differences across all trials and guitarist pairs were found, which were strongest for the first 12 notes of the music piece, indicating higher interpersonal coordination demands, at practically all six harmonics of the metronome frequency.[15] Moreover, the musicians' brain activity was found to synchronize with instrument sounds produced during guitar playing.[14,15] It has also been shown that the relationships between brain and guitar signals are bidirectional.[14] This means that the instrument's sound is considered a result of the musician's behavior, which is based on sensorimotor synchronization and the musician's action, and at the same time, it influences the behavior of the musicians through auditory sensory pathways. Thus, music performance and interaction can be understood only when considering both bidirectional influences (cf. Ref. 14). All this indicates that IBS during music performance has certain relationships to sensory input and motor output, but is not determined by them alone. Rather, a complex interplay of various factors is to be assumed.[12,13] Recently, in a study with piano duos, sensory input and movements were kept comparable across conditions as well as during musical pauses without sensory input or movement, and it could be shown that IBS does not merely depend on shared sensorimotor impact but can also emerge endogenously, from aligned cognitive processes supporting behavioral synchrony and social interaction.[25]

Since the role that IBS may play in social coordination processes has not yet been elucidated,[13,16,25,27,63] the current study aimed to investigate the relations between behavioral and brain responses and to answer the question: Can IBS be associated with the same sensory and motor processes during synchronized behavior or does it represent controlled coordination processes to maintain interaction during challenging coordination periods (e.g., mutual attention during tempo changes)? For this purpose, two pianists played in a duet and one of them perturbed the interpersonal coordination process by a premature entry after a pause. It was assumed that the perturbation would cause a shift from an entrained attractor state of synchronization to a less stable pattern requiring higher cognitive demands (e.g., in the form of selective attention toward the initiator of the tempo change).

On the behavioral level, it was expected that the early entry of one player would cause a phase shift between the two voices, and the coperformer would have to accelerate his play to synchronize again.[64] Besides a desynchronization of the play, identified by increased intertap intervals (ITIs) between subjects, the perturbation should also cause a higher variability in the joint behavior due to the implication of more degrees of freedom to react. On the neuronal level, IBS representing synchronized behavior was expected to be eliminated under perturbed compared to unperturbed (control) conditions.

METHODS

Participants

Twenty pianists (12 females and 8 males) were recruited via a mailing list from the choir of the Humboldt University of Berlin and from the Collegium Musicum Berlin (supported and sponsored by the Free University and the Technical University of Berlin). All of them were amateurs and had at least 3 years of relevant experience in playing piano; they were right-handed, and did not have a history of neurological or psychiatric disorders. Four of the participants were trained as confederates who were supposed to induce a standardized temporal perturbation. The musicians were then assembled into 16 pairs, each of which consisted of one regular participant playing with one of the four confederates. Three pairs were excluded from further analysis due to erroneous play or EEG artifacts. Finally, the data of 17 participants (11 females and 6 males) with a mean age of 26.29 years (SD = 4.75) resulting in 13 piano duos were used for further analyses. The Ethics Committee of the Max Planck Institute for Human Development approved the study, and it was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. All participants volunteered for this experiment and gave their written informed consent prior to their inclusion in the study.

Experimental procedure

The experiment took place in an acoustically and electromagnetically shielded cabin in which the participants sat back-to-back at two separate digital pianos. The participants received a standardized introduction about the experimental process and were requested to minimize movements, swallowing, chewing, and eye blinking. To avoid confusion, the regular participants were informed that their partner would make mistakes on purpose, but were kept naive concerning when and how the error would occur. It was emphasized that after the perturbation, both pianists should listen to each other and try to synchronize again as soon as possible. Furthermore, they were told that the tempo had to remain at 120 bpm for the entire duration of the experiment. In order to achieve this, the participants listened to a metronome at the beginning of each experimental block.

After the instructions, the musicians had time to become accustomed to the digital pianos and they were invited to practice the piece with the partner. They received the music to be played several days beforehand and were requested to memorize it. Thus, they could play it by heart, and eye movements during the experiment were minimized. The simple piece was written for two voices, which were judged to be equivalent in terms of complexity and dominance. Each voice was composed of only five different quarter notes (first voice: C4, D4, E4, F4, and G4; second voice: A3, B3, C4, D4, and E4). Thus, the pianists never had to switch fingers and both played with their right hand only. The short piece was written by Sabine Pendl in a 4/4 time signature, starting with a solo part by the confederate followed by a solo by the regular participant. Thereafter, the confederate came into play again and both participants played together. Each of the three parts was four bars in length with a quarter pause at the fourth beat in the second bar of each of the parts (see Figure 1A for details). The analysis was applied only to the duet part, because this was the part in which the musicians were engaged in mutual adjustment of their actions.

To desynchronize playing, the confederates produced a phase shift by shortening the pause, which forced the partner to speed up.[64] The confederates were trained to execute the perturbation in a standardized way so that the advanced entrance was recognizable but without forewarning. Thus, the confederates were taught to reduce the quarter pause to at least 200 ms. Hence, an accurate perturbed interval between taps 7 and 8 was defined as being 500–800 ms long (compared to the 1000 ms under control conditions). Furthermore, the confederates were instructed not to correct themselves by lengthening the next ITI deliberately as this would produce a more primitive form of perturbation called an "event onset shift."[64] To avoid expected anticipatory correction processes of the regular participants,[65] the perturbations

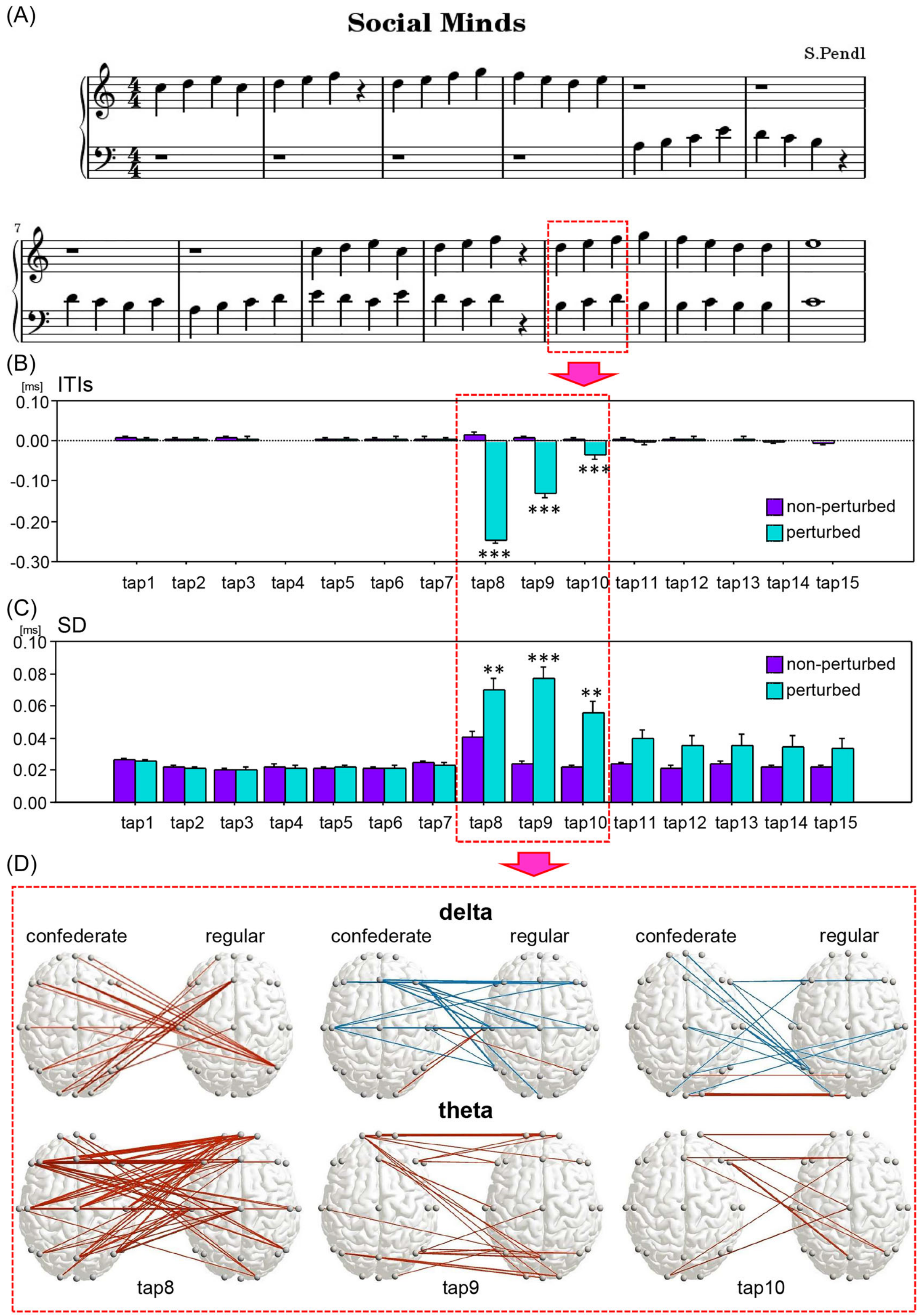

FIGURE 1 Score of the piece of music as well as behavioral and brain data related to the perturbation. (A) Music of a piece written by Sabine Pendl in a 4/4 time signature. The upper voice was played by the confederate with a premature entry after the pause in the duet part in half of the trials; the lower voice was played by the regular participant, who had to adapt to this in perturbed trials. (B) Asynchrony of the playing across the 15 taps, measured by the averaged ITIs (confederate−regular participant) across trials. (C) Constancy of the playing across the 15 taps, measured by the standard deviation of ITIs across trials. (D) Connectivity maps based on the *IPC* values with bootstrap ratios greater than 2.576 for the delta (upper line) and theta (lower line) frequency bands between the electrodes of the confederate (left brain) and regular participant (right brain). The three taps after perturbation (taps 8, 9, and 10) are presented. Red links represent electrode pairs with stronger coupling in the perturbed condition; blue links indicate an inverse contribution to the contrast. $^{**}p < 0.01$; $^{***}p < 0.001$.

occurred randomly in half of the trials. The confederates received an on-screen instruction before each trial, telling them whether or not to make the mistake. One experimental run comprised 80 trials, separated into four blocks of about 15 min each, with breaks in between. After each trial, the participants had to evaluate how harmonious the playing was and how much effort it took to stay in synchrony.

Data acquisition

Behavioral data

The pianists performed on two Yamaha NP-11 weighted-key digital pianos (Yamaha Cooperation). As a standardized timbre, "Grand Piano" was chosen and presented through two integrated speakers. The volume was adjusted so that the participants would be able to hear both each other and themselves well. MIDI output was used for behavioral data acquisition. MIDI stands for Musical Instrument Digital Interface and is a technical standard that conveys event messages such as notation, pitch time, and velocity of digital instruments. Several studies have previously taken advantage of the compact MIDI protocol for behavioral data analysis in musical experiments.[36,66,67] The MIDI data were sent from the digital pianos to the computer via a UM-2G MIDI-USB interface (Roland Corporation) and recorded with the MIDI-sequencer and digital audio workstation Cubase 7 Artist (Steinberg Media Technologies). To analyze the behavioral data, the standard MIDI files were read into MATLAB (MathWorks) using the MIDI toolbox.[68]

To avoid jitter in the timelines, the EEG and MIDI data were recorded on separate computers. For the post-hoc synchronization of MIDI and EEG timelines, two supplementary channels for audio signals were added to the EEG recording. For this, the digital pianos were manipulated to allow simultaneous use of the headphone audio output and the speakers. The audio signal from the headphone output was sent to an amplifier for bipolar and sensor data acquisition (BrainAmp ExG, Brain Products) via an internally developed audio bipolar converter. The audio channels in the EEG recording permitted offline marker setting in the EEG timeline for each piano key tap, corresponding to the MIDI data. Unintentionally erroneous trials and trials in which the intended perturbation did not match the standards defined above were excluded from further analysis. In total, two pairs were excluded because they produced fewer than 30 precise trials per condition.

EEG data

EEGs from both pianists were simultaneously and continuously recorded using two electrode caps (actiCAP, Brain Products) with 64 active Ag/AgCl electrodes each, arranged according to the international 10–10 system. By monitoring vertical and horizontal electrooculograms, eye blinks and eye movements were controlled for. The reference electrode was placed on the right mastoid at the position of TP10, and the ground electrode was placed at the position of AFz. Electrode impedances were maintained below 25 kΩ, which was adequate for preamplified active electrodes. Two separate EEG amplifiers (BrainAmp DC, Brain Products) for each participant were optically coupled to the recording computer via a PCI adapter card in order to guarantee synchrony between the two EEG recordings. All channels were recorded at a sampling rate of 5000 Hz with an antialiasing bandpass filter, ranging from 0.016 to 1000 Hz.

The EEG raw data were preprocessed using commercial software for neurophysiological data analyses (Brain Vision Analyzer 2, Brain Products). The data were re-referenced offline to an average of the left and right mastoid separately for each participant. Thereafter, the EEG was downsampled to 250 Hz and filtered with a bandpass ranging from 0.5 to 70 Hz. Blinks and eye movements were corrected using an automatic FastICA (independent component analysis) algorithm.[69] The average number of removed ICA components was 8.8 (1.1) across participants. The remaining artifacts were rejected by visual inspection and the corrected EEG was segmented into epochs related to the confederate's first tap of the duet part. The epochs ranged from 1000 ms before to 15,000 ms after time-lock and included the whole duet part. Only artifact-free duet parts were analyzed. Artifact-free epochs of 21 selected electrodes were exported as a binary file into MATLAB. By selecting only 21 electrodes (Fp1, Fpz, Fp2, F7, F3, Fz, F4, F8, T7, C3, Cz, C4, T8, P7, P3, Pz, P4, P8, O1, Oz, and O2), based on the 10–20 system, redundant data and volume conduction effects between electrodes were reduced.

Phenomenological data

After each trial, both participants were asked to indicate perceived harmony and coordination demands on a 5-point rating scale. For the question, "How harmonious was this run?", 1 represented "very harmonious" and 5 represented "not harmonious at all." Accordingly, for the question "How strenuous was it to stay in synchrony?", 1 represented "not at all strenuous" and 5 represented "very strenuous." The ranking was performed using the five highest keys of the digital piano. Like the behavioral data, the ranking data were sent to the computer running Cubase via MIDI-out and extracted from the MIDI protocol afterward using the MIDI toolbox.[68]

Data analysis

Behavioral data

To check whether the intended perturbation had the expected influence on interpersonal coordination, two measures were compared between the perturbed and control conditions. Both measures were based on the ITIs, which indicate the difference between the onset time of the participant's key tap and that of the confederate. First, the behavioral asynchrony between the two taps of participant and confederate was calculated by averaging the length of ITIs across trials. Second, the variability of asynchrony was determined by the standard deviation (SD) of ITIs across trials. The differences in asynchrony and variability between conditions (non-perturbed vs. perturbed) were evaluated for the three taps after the perturbation (taps 8, 9, and 10) using separate *t*-tests for paired comparisons (Bonferroni corrected).

EEG data

Artifact-free EEG time series from 1000 ms before to 1000 ms after the confederate's taps were transformed into a complex time-frequency signal ($\gamma = f,t$) of up to 20 Hz using a complex Gabor expansion function. This kind of time-frequency analysis (based on the short-time Fourier transform) uses a basic function with a Gaussian shape around its central frequency *f*. The SD of the Gaussian envelope determines the width of the function in a way that the Heisenberg uncertainty time-bandwidth product is minimized.[70] Hence, the complex Gabor function has an optimal time and frequency resolution that remains unchanged for all frequencies. Here, the frequency resolution of the Gabor transform was given at 0.5 Hz, and the time resolution was fixed at 4 ms. For each frequency bin (*f*) and time point (*t*), the interbrain phase coherence (*IPC*) was determined as a phase synchronization across *k* trials between two electrodes located on the two different brains[12]:

$$IPC(f,t) = \left| \left\langle e^{j \cdot \Delta\Phi^{k}(f,t)} \right\rangle \right|, \; j = \sqrt{-1},$$

where the phase difference $\Delta\Phi^k$ refers to $\Delta\Phi^k_{XY}(f,t) = \mathrm{mod}(\Phi^k_X(f,t) - \Phi^k_Y(f,t), 2\pi)$, with instantaneous phases of the two signals (X and Y) across *k* trials: $\Phi^k_X(f,t) = \arg\{z^k_X(f,t)\}$ and $\Phi^k_Y(f,t) = \arg\{z^k_Y(f,t)\}$, respectively. Thus, the *IPC* represents the degree of constancy of the instantaneous phase differences between the brains across *k* trials. It is a measure of synchronization in terms of phase locking, quantifying the temporal relationship between oscillators independent of their amplitude. As a multi-trial measure, it allows the detection of instantaneous phase differences of constant latencies to the time-lock or play onset (tap). The *IPC* is close to one if the phase differences vary little across trials, and is otherwise close to zero. In addition to the *IPC*, we also calculated the phase locking index (*PLI*), defined by:

$$PLI(f,t) = \left| \left\langle e^{j \cdot \Phi^{k}(f,t)} \right\rangle \right|, \quad j = \sqrt{-1},$$

as a phase synchronization measure across the trials above the different electrodes within brains.

After the inspection of the time-frequency diagrams averaged across the participant pairs, two time-frequency windows from 100 to 300 ms after a tap for the delta (0.5–4 Hz) and theta (4.5–8 Hz) frequency bands were chosen to determine the average of *IPC* values within these windows across couples for further evaluation (see Figure S1 for details). To evaluate whether *IPC* values significantly differed between perturbed and controlled conditions and to identify those *IPC* values that reliably explain the difference, partial least squares (PLS) analysis was performed.[71] PLS is a data reduction technique particularly suited to extract latent variables from large data sets with high collinearity among the dependent measures. Using mean-centered task PLS, the associations between *IPC* values and experimental design were analyzed by operating on the entire connectivity data set at once. For additional details regarding PLS analysis, the reader is referred to the Supplementary Material and to Refs. 71 and 72. Results on within-brain synchronization as measured by *PLI* can also be found in the Supplementary Material.

During the calculation of the *IPC*, we not only determined the mean direction or the length of the vector of phase differences but also its angle (θ) in the complex space. In contrast to *IPC*, the angle was first determined within the two time-frequency windows from 100 to 300 ms after a tap, for the delta (0.5–4 Hz) and theta (4.5–8 Hz) frequency bands, respectively, and then averaged across *k* trials:

$$\theta(f_i) = \arctan\left(\frac{\left\langle j \sin \Delta\Phi^k_{f,t} \right\rangle}{\left\langle \cos \Delta\Phi^k_{f,t} \right\rangle} \right).$$

The Watson–William test was then used to compare the mean angles of phase differences between the two task conditions separately for each tap. The Benjamini–Hochberg procedure, a popular method for controlling for the false discovery rate, was used for multiple comparison correction.

To quantitatively assess the relation between behavioral and brain synchrony, we calculated the angular–linear correlations between phase (angular) and time (linear) differences ($\Delta\Phi$ and Δt, respectively) across all trials and pianist pairs. The angular–linear correlation coefficient (r_{al}) is given by the following equation[73]:

$$r_{al} = \sqrt{\frac{r^2_{XC} + r^2_{XS} - 2r_{XC}r_{XS}r_{CS}}{1 - r^2_{CS}}},$$

where r_{XC} is the Pearson product-moment correlation between Δt and the cosine of $\Delta\Phi$, r_{XS} is the correlation between Δt and the sine of $\Delta\Phi$, and r_{CS} is the correlation between the cosine and the sine of $\Delta\Phi$. For the angular–linear correlation, the correlation coefficient (r_{al}) ranges between 0 and 1 (i.e., there is no negative correlation). The significance of the correlation may be assessed by comparing nr^2 to χ^2_2.[73] The angular–linear correlations were calculated across all trials and pianist pairs for each of the notes played in non-perturbed ($n_1 = 480$) and perturbed ($n_2 = 456$) conditions. Given $\chi^2_{0.0033,2} = 10.65$ (Bonferroni adjusted), we obtain a significance level (*SL*) of 0.16 for r_{al} in both cases.[73] All correlation coefficients above the *SL* were considered significant (cf. Ref. 15).

In the next step of our analyses aiming at probing associations between behavioral and phase synchronization data, we determined phase angles for two frequencies of interest (2 and 6 Hz), representing the first and the third harmonics of the metronome frequency. The phase angles were computed for each of the 15 taps played in different trials with respect to the 2-s epochs related to the tap onset of the confederate. Using information about the phase angle, we computed the phase alignment across all trials and pianist pairs for each tap and frequency of interest. The corresponding phase angles were sorted as a function of the behavioral asynchrony in play onsets (ITIs) between the two piano players. For simplicity, we only present the results related to the three taps that have a close relationship to the perturbation (i.e., taps 8, 9, and 10) and compare them with the respective control condition by visual inspection.

Phenomenological data

Based on the operational theory of measurement, which questions the interval scale level of rating data, a nonparametric statistical analysis was chosen to compare the participant's rating data between conditions. The values of the perceived harmony and the effort to stay in synchrony were averaged across trials within each participant and were compared between conditions using two separate Wilcoxon signed rank tests for each scale. Since these two scales were different in polarity, we reversed the harmony scale so that 1 indicated low harmony and 5 indicated high harmony. We used the survey only from the regular subject who was naive to the manipulation.

RESULTS

Behavioral results

On the behavioral level, asynchrony (mean of ITIs across trials) and variability of asynchrony (SD of ITIs across trials) presented in Figure 1 were analyzed. As expected, asynchrony in perturbed trials was more significantly negative (the confederate was faster) than in non-perturbed trials: tap 8, ITI diff. = 260 ms, $t(12) = 28.11$, $p < 0.001$; tap 9, ITI diff. = 137 ms, $t(12) = 11.17$, $p < 0.001$; tap 10, ITI diff. = 40 ms, $t(12) = 5.70$, $p < 0.001$ (see Figure 1B for details). The variability of asynchrony measured by SD was significantly higher in perturbed than in non-perturbed trials as expected: tap 8, SD diff. = 0.029, $t(12) = 4.86$, $p < 0.01$; tap 9, SD diff. = 0.053, $t(12) = 6.75$, $p < 0.001$; tap 10, SD diff. = 0.034, $t(12) = 4.89$, $p < 0.01$ (see Figure 1C for details). All p values are Bonferroni corrected.

EEG results

IPC analysis

In line with the behavioral data, the *IPC* analyses were restricted to the three taps of interest (i.e., taps 8, 9, and 10), which showed the strongest effect of perturbation or mistake. The mean-centered task PLS analysis identified one latent variable that represented the impact of the experimental manipulation on the three taps of interest. Only 91 out of 10,000 new permutation samples had greater singular values than the original sample. Thus, the identified data-driven contrast can be declared as significant ($p < 0.01$). *IPC* saliences, which made a reliable contribution to the contrast identified by the bootstrap test, are shown in Figure 1D. Red lines indicate those electrode pairs with stronger coupling under the perturbed condition, whereas blue lines indicate those electrode pairs that contributed to the contrast inversely. In the delta band, after the tap of perturbation (tap 8), all reliable *IPC* values indicated a greater coupling under the perturbed condition. While the interbrain network on the confederate's side showed a wide distribution, the majority of the couplings were bundled at the electrodes P8 and Fz for the regular participant. While P8 showed strong couplings with the frontal electrodes of the confederate, Fz was more coupled to the confederate's parieto-occipital area. A different effect was observed at the second and third tap after perturbation (taps 9 and 10, respectively). Here, a vast amount of coupling was lower under the perturbed than under the control conditions (except for a few couplings between parieto-occipital areas). After tap 9, most of the couplings that contributed to the contrast were found between the left parietal area of the regular participant and the right frontal area of the confederate, whereas at tap 10, no topographical asymmetry was appreciable; the coupling at this tap was distributed across fronto-central sites of both participants. In the theta band, the perturbation caused an increase in *IPC* in a widely distributed interbrain network. All reliable *IPC* values across all three taps indicated a greater coupling under the perturbed condition. After the perturbation (tap 8), there was a tendency for higher couplings between the regular participant's fronto-central electrodes and the confederate's centro-parietal as well as frontal electrodes. After tap 9 (and also tap 10), most of the couplings were found between the frontal and parieto-occipital areas of both participants.

In the Supplementary Material, we provide additional analyses conducted on *PLI* and *IPC* values averaged across all electrodes (in the case of *PLI*) or electrode pairs (in the case of *IPC*). The *PLI* analyses showed that the perturbation effect described above (higher synchronization in perturbed than in non-perturbed trials) concerns the regular participant above all. In addition, we calculated *PLI* and *IPC* values for two electrodes (Fz and Cz) and two electrode pairs (Fz–Fz and Cz–Cz) across all 15 taps. This representation confirmed the observed perturbation effect. Additionally, the confederate showed higher within-brain local synchrony (*PLI*) in taps before perturbation, at least above the Fz electrode.

Phase difference angles, angular–linear correlation, and phase alignment

Phase difference angles were calculated between two homologous electrodes in the confederate's and regular participant's brains (i.e., Fz–Fz and Cz–Cz). These results in the two frequency bands across the 15 taps and two task conditions are presented in Figure 2A for the Fz–Fz and Cz–Cz electrode pairs, respectively. It can be seen that the phase difference angles in the delta band for both electrode pairs mostly oscillate around zero and only deviate from zero at taps 8 and 9 for Fz–Fz and at tap 8 for Cz–Cz electrode pairs, both in the error condition. The Watson–William test revealed significant differences in the phase difference angles between the two conditions (Fz–Fz: tap 8, $F_{1,24} = 8.49$, $p < 0.05$, and tap 9, $F_{1,24} = 37.46$, $p < 0.001$; Cz–Cz: tap 8, $F_{1,24} = 34.46$, $p < 0.001$). This indicates that delta-band

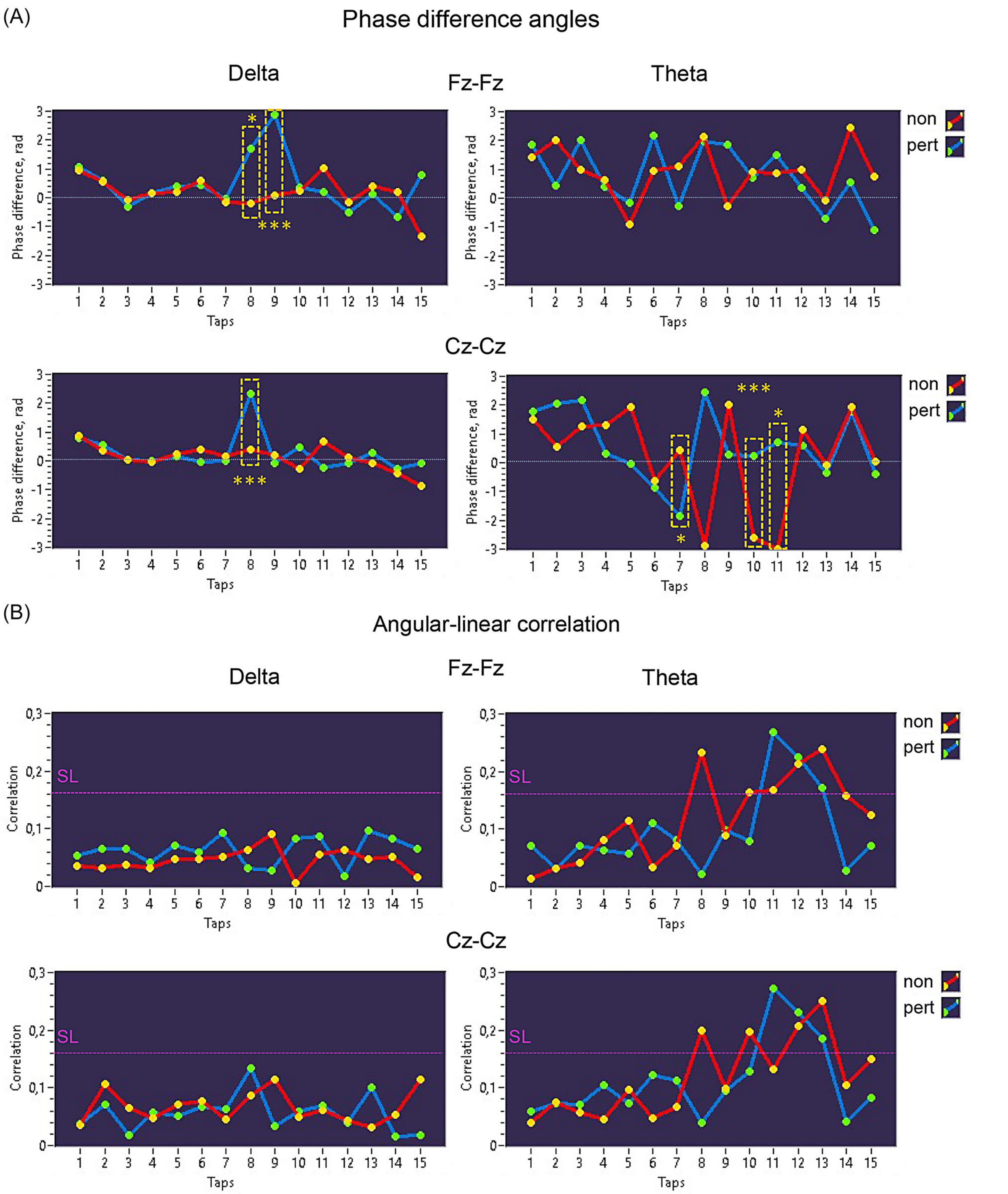

FIGURE 2 Phase differences and angular–linear correlation for two electrode pairs in the delta and theta frequency bands. (A) Phase differences (confederate—regular participant) for the Fz–Fz (upper diagrams) and Cz–Cz (lower diagrams) electrode pairs in the delta (left) and theta (right) frequency bands across the 15 taps for non-perturbed (red line) and perturbed (blue line) trials. Phase difference angles were averaged across trials for each participant across the 15 taps and then the Watson–William test was applied to compare the mean angles of phase differences between the two task conditions. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$. (B) Angular–linear correlation between phase and time differences across all trials and pianist pairs for the Fz–Fz (upper diagrams) and Cz–Cz (lower diagrams) electrode pairs in the delta (left) and theta (right) frequency bands across the 15 taps for non-perturbed (red) and perturbed (blue line) trials. non, non-perturbed; pert, perturbed; SL, significance level.

synchronization is mostly in-phase, whereas it tends to be in anti-phase under perturbation (e.g., taps 8 and 9). In the theta frequency band, the phase difference angles were mostly unstable across the taps, oscillating between $-\pi$ and $+\pi$ with no clear tendency, even with respect to some significant differences between the two conditions at the Cz–Cz electrode pair (see Figure 2A for details). This indicates that theta-band synchronization is not obviously in-phase and may vary depending on different circumstances, or even randomly.

Next, we calculated the angular–linear correlations between phase (angular) and time (linear) differences across all trials and pianist pairs to quantitatively assess the relation between behavioral and interbrain synchrony patterns. Results of this analysis are presented in Figure 2B for the Fz–Fz and Cz–Cz connections, respectively. Interestingly, significant angular–linear correlation was mostly found with phase differences in the theta band. In the non-perturbed trials, this correlation was significant at tap 8 and taps 10–13, while in the perturbed trials, it was significant at taps 11–13. This indicates that time and phase differences are related to each other at the faster theta (as compared to delta) frequency of EEG oscillations. This adjustment of behavioral and neural components of joint piano playing occurs in the second part of the music piece after perturbation or during the respective period of correct playing.

Finally, we computed phase alignment across all trials and pianist pairs for each tap and frequency of interest (2 and 6 Hz) by sorting the corresponding phase angles of the two participants as a function of the behavioral asynchrony in play onsets (ITIs) of the two piano players. In Figure 3, we present this relationship for phase angles at the two frequencies of interest and two selected electrodes (Fz and Cz) for each of the two pianists at tap 8 for non-perturbed and perturbed conditions (the relationship for taps 9 and 10 can be found in Figures S4 and S5, respectively). The results for tap 8 indicate a strong phase alignment that closely follows the behavioral onset synchrony across all trials and pianists in the pairs. For taps 9 and 10, phase alignment was strong at the low delta frequency of 2 Hz, but became less pronounced or absent at the faster theta frequency of 6 Hz. Thus, phase alignment was most prominent at tap 8, and mainly in perturbed trials in the regular participant.

Phenomenological results

Comparing the conditions under consideration of the individual rankings (see Figure 4), Wilcoxon signed rank tests revealed a significant loss of perceived harmony under the perturbed condition ($p < 0.05$). Furthermore, the perturbation subjectively required significantly more effort to stay in synchrony ($p < 0.01$).

DISCUSSION

The primary objective of this study was to investigate the association between behavioral entities of piano playing in a duo and its neuronal implementation under perturbed and non-perturbed (control) conditions and to clarify whether IBS—measured by *IPC*—merely reflects the same sensory input and/or motor output during synchronous play or represents cognitive processes required during periods of demanding interpersonal coordination, or a combination of these or other factors. Our main findings are that (1) on the behavioral level, asynchrony and variability of ITIs in perturbed trials were significantly higher than in non-perturbed trials; (2) on the neural level, *IPC* in the delta and especially in the theta band was higher in perturbed as compared to non-perturbed trials; (3) the phase angles of both pianists in the pair were strongly aligned with regard to the behavioral onset asynchrony when computed across all trials and pianists in the pairs, especially in perturbed as compared to non-perturbed trials; (4) delta-band synchronization as indicated by the phase difference angles was mostly in-phase and tended to be anti-phase under perturbation; and (5) the angular–linear correlation between interbrain phase differences and time-onset asynchronies across trials and pianist pairs was significant in both perturbed and non-perturbed trials only in the theta band during and after perturbation.

As hypothesized, musicians played less synchronously and the intervals between their taps were less constant or more variable across trials after the perturbation, compared with those in the non-perturbed control condition. This behavioral effect lasted for three taps after the perturbation. Thereafter, the musicians synchronized again. Regarding IBS, the PLS analysis revealed a notable contrast between the experimental conditions. This contrast manifested differently in two distinct frequency bands. In the case of theta *IPC*, the differences closely mirrored changes in ITIs and exhibited a decline over the three taps after perturbation. Conversely, delta *IPC* displayed higher differences during perturbed trials compared to non-perturbed trials, particularly at the first tap after perturbation (tap 8). Subsequently (taps 9 and 10), delta *IPC* exhibited an opposing pattern, with mostly higher *IPC* during non-perturbed trials. Similar results were recently found in an EEG hyperscanning study with pianist duos showing higher IBS in delta and theta frequency bands at the beginning of trials with incongruent as compared to congruent tempo instructions.[25] The authors attributed the observed delta/theta IBS increase "to the compensatory increase of attention to the partner and mutual adaptive behavior upon detection of the subtle temporal mismatches between self- and other-produced sounds."[25]

Neurophysiological evidence indicates that delta/theta activity represents attention to external salient stimuli and internal concentration processes as well as the generation and inhibition of motor output.[74–77] Delta power and spectral coherence increases during externally driven processes of orientation after distractions.[78,79] Furthermore, enhanced P3 amplitude and delta power were found during endogenously driven top-down control after task-switch cues. A general increase in delta/theta phase synchronization was also found during Go as well as NoGo trials, which are associated with response production and inhibition, respectively.[80,81] There is also evidence associating frontal theta activity to attentional demands and working memory load.[74,75,77] It can be argued that these cognitive processes are particularly involved during the tap of perturbation in our paradigm and may explain the identified increase in delta–theta *IPC*. The change

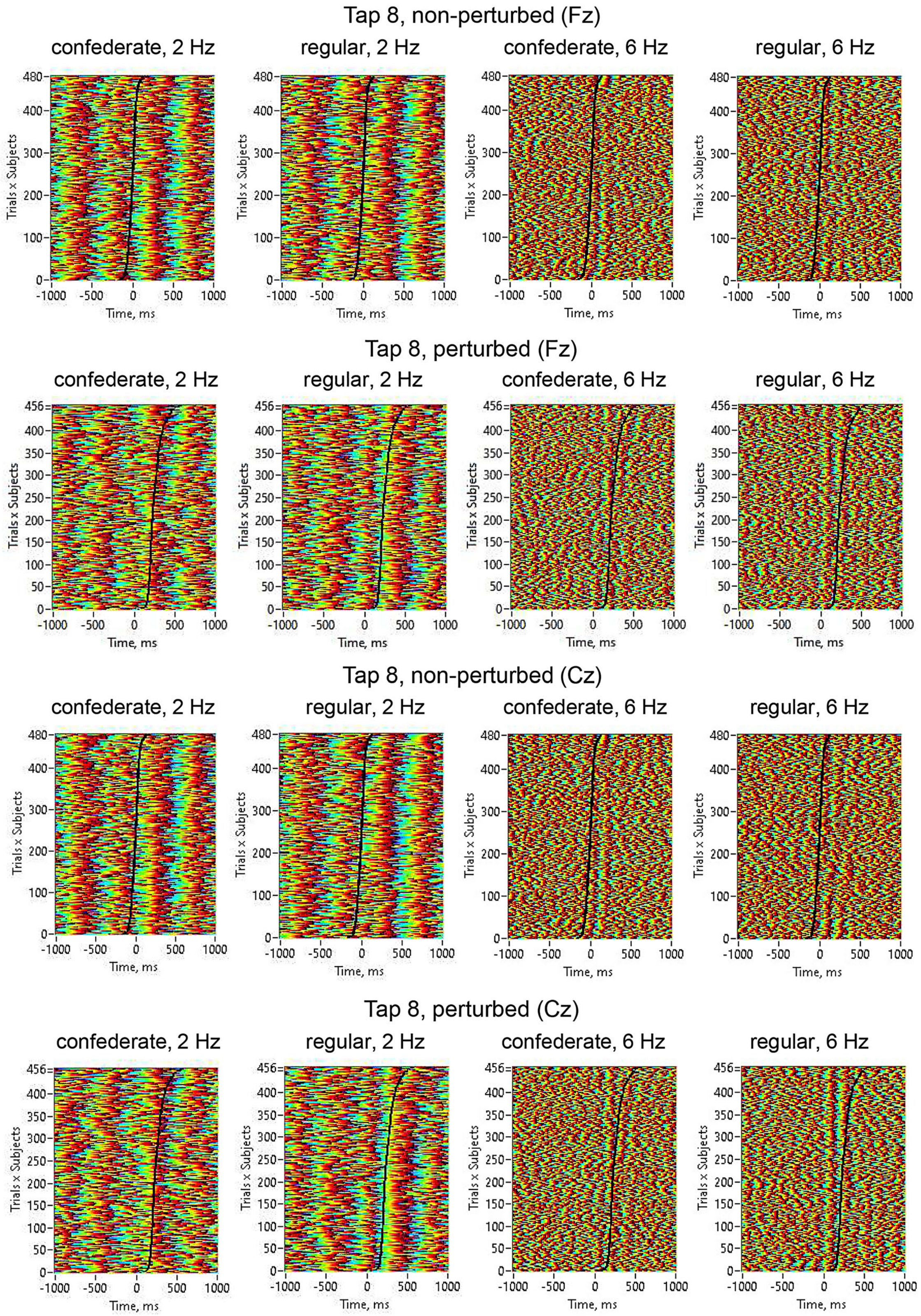

FIGURE 3 Phase alignment of phase angles related to behavioral play-onset asynchrony. Phase alignment of phase angles at the delta (2 Hz) and theta (6 Hz) frequencies related to the behavioral play-onset asynchrony across all trials and pianist pairs at tap 8, separately for confederate and regular participant. Phase angles were sorted as a function of the behavioral asynchrony in play onsets between the two piano players (regular participant's onset time minus confederate's play-onset time). Behavioral asynchrony is depicted by the black curve. Note that phase alignment was calculated here for the mid-frontal (Fz) and mid-central (Cz) electrodes under non-perturbed and perturbed conditions.

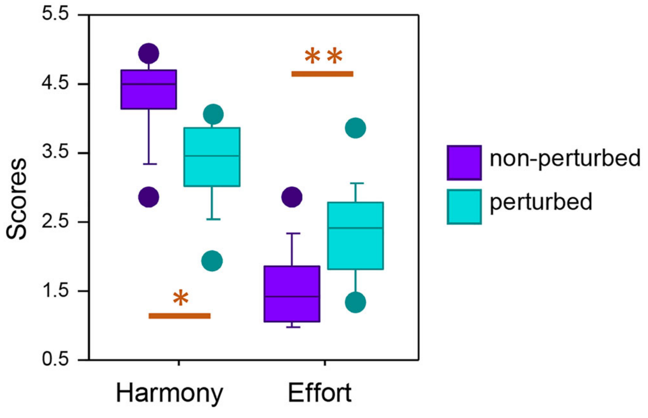

FIGURE 4 Harmony and effort rating scores. The harmony and effort scores are presented as box plots for the non-perturbed and perturbed conditions. Both phenomenological rating scales showed significant differences between the two conditions. $^{*}p < 0.05$; $^{**}p < 0.01$.

in IBS at the second and third tap after perturbation can be regarded as reflecting a change in cognitive demands. After the intentional perturbation, the confederate no longer inhibited entrained motor responses and concentrated on her own playing. More likely, the resynchronization of playing was based on automatic phase correction mechanisms between the musicians.[36] Previous research has shown that IBS increases during periods of high demands on musical coordination.[12,14,15,17–20] As shown by the phenomenological scaling, the perceived effort in the perturbed condition was higher than in the control condition, indicating higher cognitive/attentional demands in this case, which was accompanied by high IBS in both frequency ranges (at least at the tap of perturbation).

Interestingly, in the delta band, the phase difference angle mostly oscillated around zero, indicating in-phase synchrony, with the exception of the taps of perturbation, where this angle tended toward π, indicating anti-phase synchrony. This means that at the time of the perturbation, there is a constant (positive) phase lag between the two brain responses, with the phase of the confederate preceding that of the regular participant, who must adjust their brain response to that of the confederate. Nevertheless, this phase lag between the two participants remains constant across trials, leading to high *IPC* values in the perturbed condition. Unfortunately, the phase angle is rarely considered in studies of phase synchronization, especially of IBS. Nevertheless, we consider this information to be very useful and important. In- and anti-phase synchronization are seen as two different regimes in brain modeling that may be related to time delay and/or oscillation frequency of brain signals.[82,83] It has also been shown that anti-phase synchronization is limited to small networks and that the anti-phase synchronized state rapidly becomes unstable as the number of oscillators increases.[84] In our case, these two regimes (i.e., in- and anti-phase) occur in the delta band during two different conditions (non-perturbed and perturbed, respectively), whereby the anti-phase regime is characterized by higher IBS. However, this higher delta IBS affects only a few frontal and parietal brain regions, possibly indicating the recruitment of smaller networks. In the theta band, the angle of phase differences was unstable across taps without the specific pattern seen in the delta band.

The relationship between the behavioral and brain data was assessed using the angular–linear correlation between phase and time differences across trials and pianist pairs as well as using phase alignment representation with respect to ITI asynchrony. The correlation analyses showed that the relationship between behavioral and neural data was significant only for the phase difference in the theta band and proved to be relevant only at tap 8 and thereafter (taps 10–13) in non-perturbed trials and only after perturbation (taps 11–13) in perturbed trials. To date, only the study by Müller and Lindenberger[15] has used this type of analysis on guitarist duets. The authors found the highest correlation for the first 12 notes of a piece that appeared most important for coordinated play. In the present study, the part after the pause (tap 8 and thereafter) seems to be the most important, both in perturbed and non-perturbed trials. This is probably the reason for the significant correlations in non-perturbed trials up to tap 8 and up to tap 11 in perturbed trials. The perturbation presumably prevents the correlation between the time and phase asynchronies, at least at the first three taps after perturbation. Inspection of the phase alignment in the two pianists revealed strong phase alignment at the tap of perturbation (tap 8) in both frequencies of interest (i.e., 2 and 6 Hz), which was especially strong in perturbed trials, and above all in the regular participant. This is in line with the result on *PLI*, which showed stronger within-brain synchronization in the regular participant during perturbation, and with previous studies on guitarist duets.[12,15] The finding indicates that brain responses in each of the pianists' brains have an intrinsic relation not only to the individual notes played in the duo but also to the synchronicity (or asynchronicity) in which they were played. In the aforementioned studies, it has also been shown that phase alignment is particularly strong during periods of high demands on musical coordination,[12,15] which in our case corresponds to the period after the pause or that of the perturbation. Strong phase alignment during perturbation with respect to ITI asynchronies as well as high *IPC* probably indicate that the brain responses of the two pianists (especially those of the regular participant) were actively adjusting to each other. Moreover, these adaptation processes need strong within-brain synchrony in the regular participant, which appears to be associated with enhanced brain resource allocation during the perturbation.

Limitations and future research

The present experiment has limitations and leaves room for questions to be addressed in future research. First, the sample size of the study was small. However, stable result patterns that are in line with previous research were obtained. Second, although some relations between behavioral and neural components were found, other techniques and/or approaches should be tested to better understand IBS activity and its relation to behavioral outcomes. Third, the synchronization measures used in this study referred to synchronization across trials, which does not allow one to capture free improvisation or more natural interactions free of experimental constraints. In this regard, synchronization across time may provide more detailed information about direct relations with performance patterns reflecting interpersonal action coordination.

CONCLUSION

This study shows that IBS is a complex construct that is intertwined with several brain components, reflected in the applied measures, that may control and influence behavioral outcomes. The results indicate that the behavior–brain association occurring in a piano duo is not straightforward but rather depends on different factors that are determined by play circumstances. Using a standardized musical interaction paradigm, the experiment revealed changes in IBS elicited by a perturbation intentionally performed by a confederate. Even though the perturbation caused a breakdown in behavioral synchronization, phase synchronization between the brains increased. This finding demonstrates that IBS is not reducible to the reflection of the same movements and sensory input during synchronous play. More likely, the results can be explained by the temporal alignment of higher cognitive processes involved in the execution and perception of the perturbation, like focused attention and performance monitoring. Different approaches or measures reflecting different aspects of interpersonal interaction are necessary to cover the different facets of this interaction and underlying neural mechanisms.

AUTHOR CONTRIBUTIONS

A.L., D.P., U.L., and V.M. designed the study. W.G. designed the analyses of phase synchronization. A.L. and V.M. acquired, prepared, and analyzed the data. A.L., D.P., W.G., U.L., and V.M. discussed the results. A.L. and V.M. wrote the article. All authors read and approved the final version of the manuscript.

ACKNOWLEDGMENTS

This research was supported by the Max Planck Society. Special thanks go to Daphna Raz and Sabine Pendl for composing the piece and their musical support in general. Technical assistance by Anna Würtz, Anne Baero, Christine Wolter, Karl Hosang, Lissa Mapouyat, and Jakob Volhard during data acquisition is greatly appreciated. The authors are grateful to Tim Brick for helpful discussions. We also thank Dorothée Grevers and Julia Delius for language assistance.

Open access funding enabled and organized by Projekt DEAL.

COMPETING INTERESTS

The authors declare no competing interests.

PEER REVIEW

The peer review history for this article is available at: https://publons.com/publon/10.1111/nyas.15072

REFERENCES

1. Froese, T., & Di Paolo, E. A. (2011). The enactive approach: Theoretical sketches from cell to society. *Pragmatics & Cognition*, *19*, 1–36.
2. Fuchs, T., & De Jaegher, H. (2009). Enactive intersubjectivity: Participatory sense-making and mutual incorporation. *Phenomenology and the Cognitive Sciences*, *8*, 465–486.
3. Himberg, T., Laroche, J., Bigé, R., Buchkowski, M., & Bachrach, A. (2018). Coordinated interpersonal behaviour in collective dance improvisation: The aesthetics of kinaesthetic togetherness. *Behavioral Sciences*, *8*, 23.
4. Schiavio, A., Gesbert, V., Reybrouck, M., Hauw, D., & Parncutt, R. (2019). Optimizing performative skills in social interaction: Insights from embodied cognition, music education, and sport psychology. *Frontiers in Psychology*, *10*, 1542.
5. Acquadro, M. A. S., Congedo, M., & De Riddeer, D. (2016). Music performance as an experimental approach to hyperscanning studies. *Frontiers in Human Neuroscience*, *10*, 242.
6. Astolfi, L., Toppi, J., Ciaramidaro, A., Vogel, P., Freitag, C. M., & Siniatchkin, M. (2020). Raising the bar: Can dual scanning improve our understanding of joint action? *Neuroimage*, *216*, 116813.
7. Astolfi, L., Toppi, J., De Vico Fallani, F., Vecchiato, G., Salinari, S., Mattia, D., Cincotti, F., & Babiloni, F. (2010). Neuroelectrical hyperscanning measures simultaneous brain activity in humans. *Brain Topography*, *23*, 243–256.
8. Czeszumski, 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. *Frontiers in Human Neuroscience*, *14*, 39.
9. Dumas, G., Moreau, Q., Tognoli, E., & Kelso, J. A. S. (2020). The human dynamic clamp reveals the fronto-parietal network linking real-time social coordination and cognition. *Cerebral Cortex*, *30*, 3271–3285.
10. Dumas, G., Chavez, M., Nadel, J., & Martinerie, J. (2012). Anatomical connectivity influences both intra- and inter-brain synchronizations. *PLoS ONE*, *7*, e36414.
11. Dumas, G., Nadel, J., Soussignan, R., Martinerie, J., & Garnero, L. (2010). Inter-brain synchronization during social interaction. *PLoS ONE*, *5*, e12166..
12. Lindenberger, U., Li, S.-C., Gruber, W., & Müller, V. (2009). Brains swinging in concert: Cortical phase synchronization while playing guitar. *BMC Neuroscience*, *10*, 22.
13. Müller, V. (2022). Neural synchrony and network dynamics in social interaction: A hyper-brain cell assembly hypothesis. *Frontiers in Human Neuroscience*, *16*, 848026.
14. Müller, V., & Lindenberger, U. (2019). Dynamic orchestration of brains and instruments during free guitar improvisation. *Frontiers in Integrative Neuroscience*, *13*, 50.
15. Müller, V., & Lindenberger, U. (2022). Probing associations between interbrain synchronization and interpersonal action coordination during guitar playing. *Annals of the New York Academy of Sciences*, *1507*, 146–161.
16. Müller, V., Ohström, K.-R. P., & Lindenberger, U. (2021). Interactive brains, social minds: Neural and physiological mechanisms of interpersonal action coordination. *Neuroscience and Biobehavioral Reviews*, *128*, 661–677.
17. Müller, V., Sänger, J., & Lindenberger, U. (2013). Intra- and inter-brain synchronization during musical improvisation on the guitar. *PLoS ONE*, *8*, e73852.
18. Müller, V., Sänger, J., & Lindenberger, U. (2018). Hyperbrain network properties of guitarists playing in quartet. *Annals of the New York Academy of Sciences*, *1423*, 198–210.
19. Sänger, J., Müller, V., & Lindenberger, U. (2012). Intra- and interbrain synchronization and network properties when playing guitar in duets. *Frontiers in Human Neuroscience*, *6*, 312.
20. Sänger, J., Müller, V., & Lindenberger, U. (2013). Directionality in hyperbrain networks discriminates between leaders and followers in guitar duets. *Frontiers in Human Neuroscience*, *7*, 234.

21. Schilbach, L., Timmermans, B., Reddy, V., Costall, A., Bente, G., Schlicht, T., & Vogeley, K. (2013). Toward a second-person neuroscience. *Behavioral and Brain Sciences*, *36*, 393–414.
22. Sänger, J., Lindenberger, U., & Müller, V. (2011). Interactive brains, social minds. *Communicative & Integrative Biology*, *4*, 655–663.
23. Hari, R., & Kujala, M. V. (2009). Brain basis of human social interaction: From concepts to brain imaging. *Physiological Reviews*, *89*, 453–479.
24. Moreau, Q., & Dumas, G. (2021). Beyond correlation versus causation: Multi-brain neuroscience needs explanation. *Trends in Cognitive Sciences*, *25*, 542–543.
25. Gugnowska, K., Novembre, G., Kohler, N., Villringer, A., Keller, P. E., & Sammler, D. (2022). Endogenous sources of interbrain synchrony in duetting pianists. *Cerebral Cortex*, *32*, 4110–4127.
26. Gvirts, H. Z., & Perlmutter, R. (2020). What guides us to neurally and behaviorally align with anyone specific? A neurobiological model based on fNIRS hyperscanning studies. *Neuroscientist*, *26*, 108–116.
27. Novembre, G., & Iannetti, G. D. (2021). Hyperscanning alone cannot prove causality. Multibrain stimulation can. *Trends in Cognitive Sciences*, *25*, 96–99.
28. Reinero, D. A., Dikker, S., & Van Bavel, J. J. (2021). Inter-brain synchrony in teams predicts collective performance. *Social Cognitive and Affective Neuroscience*, *16*, 43–57.
29. Szymanski, C., Pesquita, A., Brennan, A. A., Perdikis, 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.
30. D'ausilio, A., Novembre, G., Fadiga, L., & Keller, P. E. (2015). What can music tell us about social interaction? *Trends in Cognitive Sciences*, *19*, 111–114.
31. Keller, P. E., Novembre, G., & Hove, M. J. (2014). Rhythm in joint action: Psychological and neurophysiological mechanisms for real-time interpersonal coordination. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*, 20130394.
32. Phillips-Silver, J., & Keller, P. E. (2012). Searching for roots of entrainment and joint action in early musical interactions. *Frontiers in Human Neuroscience*, *6*, 26.
33. Clayton, M. R. L. (2007). Observing entrainment in music performance: Video-based observational analysis of Indian musicians' tanpura playing and beat marking. *Music & Science*, *11*, 27–59.
34. Clayton, M. R. L., Sager, R., & Will, U. (2005). In time with the music: The concept of entrainment and its significance for ethnomusicology. *Ethnomusicology*, *11*, 1–82.
35. Large, E. W. (2008). Resonating to musical rhythm: Theory and experiment. In S. Grondin (Ed.), *Psychology of time* (pp. 189–231). Emerald Group Publishing Limited.
36. Konvalinka, I., Vuust, P., Roepstorff, A., & Frith, C. D. (2010). Follow you, follow me: Continuous mutual prediction and adaptation in joint tapping. *Quarterly Journal of Experimental Psychology*, *63*, 2220–2230.
37. Keller, P. E. (2008). Joint action in music performance. In F. Morganti, A. Carassa, & G. Riva (Eds.), *Enacting intersubjectivity: A cognitive and social perspective on the study of interactions* (pp. 205–221). IOS Press.
38. Keller, P. E., Novembre, G., & Loehr, J. (2016). Musical ensemble performance: Representing self, other and joint action outcomes. In S. S. Obhi & E. S. Cross (Eds.), *Shared representations: Sensorimotor foundations of social life* (pp. 280–310). Cambridge University Press.
39. Loehr, J. D., & Palmer, C. (2011). Temporal coordination between performing musicians. *Quarterly Journal of Experimental Psychology*, *64*, 2153–2167.
40. Musco, M. A., Zazzera, E., Paulesu, E., & Sacheli, L. M. (2023). Error observation as a window on performance monitoring in social contexts? A systematic review. *Neuroscience and Biobehavioral Reviews*, *147*, 105077.
41. Sacheli, L. M., Musco, M. A., Zazzera, E., Banfi, G., & Paulesu, E. (2022). How shared goals shape action monitoring. *Cerebral Cortex*, *32*, 4934–4951.
42. Paas, A., Novembre, G., Lappe, C., & Keller, P. E. (2021). Not all errors are alike: Modulation of error-related neural responses in musical joint action. *Social Cognitive and Affective Neuroscience*, *16*, 512–524.
43. Moreau, Q., Candidi, M., Era, V., Tieri, G., & Aglioti, S. M. (2020). Midline frontal and occipito-temporal activity during error monitoring in dyadic motor interactions. *Cortex*, *127*, 131–149.
44. Moreau, Q., Tieri, G., Era, V., Aglioti, S. M., & Candidi, M. (2023). The performance monitoring system is attuned to others' actions during dyadic motor interactions. *Cerebral Cortex*, *33*, 222–234.
45. Sacheli, L. M., Musco, M. A., Zazzera, E., & Paulesu, E. (2021). Mechanisms for mutual support in motor interactions. *Scientific Reports*, *11*, 3060.
46. Cracco, E., Desmet, C., & Brass, M. (2016). When your error becomes my error: Anterior insula activation in response to observed errors is modulated by agency. *Social Cognitive and Affective Neuroscience*, *11*, 357–366.
47. Desmet, C., Deschrijver, E., & Brass, M. (2014). How social is error observation? The neural mechanisms underlying the observation of human and machine errors. *Social Cognitive and Affective Neuroscience*, *9*, 427–435.
48. Varela, F. J., Thompson, E., & Rosch, E. (1991). *The embodied mind cognitive science and human experience*. MIT Press.
49. Clark, A. (1996). *Being there: Putting brain, body, and world together again*. MIT Press.
50. Friston, K., & Frith, C. (2015). A duet for one. *Consciousness and Cognition*, *36*, 390–405.
51. Richardson, M. J., Marsh, K. L., Isenhower, R. W., Goodman, J. R. L., & Schmidt, R. C. (2007). Rocking together: Dynamics of intentional and unintentional interpersonal coordination. *Human Movement Science*, *26*, 867–891.
52. Schmidt, R. C., & O'brien, B. (1997). Evaluating the dynamics of unintended interpersonal coordination. *Ecological Psychology*, *9*, 189–206.
53. Kelso, J. A. S. (1995). *Dynamic patterns: The self-organization of brain and behavior*. MIT Press.
54. Temprado, J.-J., & Laurent, M. (2004). Attentional load associated with performing and stabilizing a between-persons coordination of rhythmic limb movements. *Acta Psychologica*, *115*, 1–16.
55. Knoblich, G., Butterfill, S., & Sebanz, N. (2011). Psychological research on joint action. In B. Ross (Ed.), *The psychology of learning and motivation* (pp. 59–101). Academic Press.
56. Sebanz, N., Bekkering, H., & Knoblich, G. (2006). Joint action: Bodies and minds moving together. *Trends in Cognitive Sciences*, *10*, 70–76.
57. Vesper, C., Butterfill, S., Knoblich, G., & Sebanz, N. (2010). A minimal architecture for joint action. *Neural Networks*, *23*, 998–1003.
58. Sebanz, N., & Knoblich, G. (2009). Prediction in joint action: What, when, and where. *Trends in Cognitive Sciences*, *1*, 353–367.
59. Wolpert, D. M., & Ghahramani, Z. (2000). Computational principles of movement neuroscience. *Nature Neuroscience*, *3*, 1212–1217.
60. Wolpert, D. M., Doya, K., & Kawato, M. (2003). A unifying computational framework for motor control and social interaction. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *358*, 593–602.
61. Wolpert, D. M., Ghahramani, Z., & Jordan, M. I. (1995). An internal model for sensorimotor integration. *Science*, *269*, 1880–1882.
62. Kelso, J. A. S., Dumas, G., & Tognoli, E. (2013). Outline of a general theory of behavior and brain coordination. *Neural Networks*, *37*, 120–131.
63. Konvalinka, I., & Roepstorff, A. (2012). The two-brain approach: How can mutually interacting brains teach us something about social interaction? *Frontiers in Human Neuroscience*, *6*, 215.
64. Repp, B. H. (2005). Sensorimotor synchronization: A review of the tapping literature. *Psychonomic Bulletin & Review*, *12*, 969–992.
65. Repp, B. H., & Moseley, G. P. (2012). Anticipatory phase correction in sensorimotor synchronization. *Human Movement Science*, *31*, 1118–1136.

66. Pecenka, N., & Keller, P. E. (2011). The role of temporal prediction abilities in interpersonal sensorimotor synchronization. *Experimental Brain Research*, *211*, 505–515.
67. Repp, B. H., & Keller, P. E. (2008). Sensorimotor synchronization with adaptively timed sequences. *Human Movement Science*, *27*, 423–456.
68. Eerola, T., & Toiviainen, P. (2004). *MIDI toolbox: MATLAB tools for music research*.
69. Hyvärinen, A., & Oja, E. (2000). Independent component analysis: Algorithms and applications. *Neural Networks*, *13*, 411–430.
70. Wacker, M., & Witte, H. (2013). Time-frequency techniques in biomedical signal analysis: A tutorial review of similarities and differences. *Methods of Information in Medicine*, *52*, 279–296.
71. Mcintosh, A. R., & Lobaugh, N. J. (2004). Partial least squares analysis of neuroimaging data: Applications and advances. *Neuroimage*, *23*(1), S250–S263.
72. Krishnan, A., Williams, L. J., Mcintosh, A. R., & Abdi, H. (2011). Partial least squares (PLS) methods for neuroimaging: A tutorial and review. *Neuroimage*, *56*, 455–475.
73. Zar, J. H. (2010). *Biostatistical analysis* (5th ed.). Pearson Prentice Hall.
74. Deiber, M.-P., Missonnier, P., Bertrand, O., Gold, G., Fazio-Costa, L., Ibañez, V., & Giannakopoulos, P. (2007). Distinction between perceptual and attentional processing in working memory tasks: A study of phase-locked and induced oscillatory brain dynamics. *Journal of Cognitive Neuroscience*, *19*, 158–172.
75. Gevins, A. (1997). High-resolution EEG mapping of cortical activation related to working memory: Effects of task difficulty, type of processing, and practice. *Cerebral Cortex*, *7*, 374–385.
76. Knyazev, G. G. (2012). EEG delta oscillations as a correlate of basic homeostatic and motivational processes. *Neuroscience and Biobehavioral Reviews*, *36*, 677–695.
77. Sauseng, P., Hoppe, J., Klimesch, W., Gerloff, C., & Hummel, F. C. (2007). Dissociation of sustained attention from central executive functions: Local activity and interregional connectivity in the theta range. *European Journal of Neuroscience*, *25*, 587–593.
78. Isler, J. R., Grieve, P. G., Czernochowski, D., Stark, R. I., & Friedman, D. (2008). Cross-frequency phase coupling of brain rhythms during the orienting response. *Brain Research*, *1232*, 163–172.
79. Prada, L., Barceló, F., Herrmann, C. S., & Escera, C. (2014). EEG delta oscillations index inhibitory control of contextual novelty to both irrelevant distracters and relevant task-switch cues. *Psychophysiology*, *51*, 658–672.
80. Harmony, T., Alba, A., Marroquín, J. L., & González-Frankenberger, B. (2009). Time-frequency-topographic analysis of induced power and synchrony of EEG signals during a Go/No-Go task. *International Journal of Psychophysiology*, *71*, 9–16.
81. Müller, V., & Anokhin, A. P. (2012). Neural synchrony during response production and inhibition. *PLoS ONE*, *7*, e38931.
82. Petkoski, S., & Jirsa, V. K. (2019). Transmission time delays organize the brain network synchronization. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, *377*, 20180132.
83. Petkoski, S., Palva, J. M., & Jirsa, V. K. (2018). Phase-lags in large scale brain synchronization: Methodological considerations and in-silico analysis. *PloS Computational Biology*, *14*, e1006160.
84. Vathakkattil Joseph, G., & Pakrashi, V. (2020). Limits on anti-phase synchronization in oscillator networks. *Scientific Reports*, *10*, 10178.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Lender, A., Perdikis, D., Gruber, W., Lindenberger, U., & Müller, V. (2023). Dynamics in interbrain synchronization while playing a piano duet. *Ann NY Acad Sci.*, *1530*, 124–137. https://doi.org/10.1111/nyas.15072