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Original Article

Probing associations between interbrain synchronization and interpersonal action coordination during guitar playing

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Playing music in an ensemble is a highly coordinated human action involving musicians' brain-body interactions at different levels of physical and cortical organization in time and space. It has been suggested that interbrain phase synchronization plays an essential role in musical interaction. In this study, we aimed to explore associations between interbrain synchronization and interpersonal action coordination, using electroencephalographic recordings of the brain activity of guitarists playing in a duet as well as the acoustic recordings of their music. By applying phase synchronization algorithms to the musicians' brain activities and the sounds produced during guitar playing, we show that synchronous brain activity is strongly related to instrument sounds and behavioral play-onset synchrony, as indicated by phase alignment in relation to the time differences in play onsets and an angular-linear correlation between phase and time differences across trials and guitarist pairs. Interestingly, this correlation was especially strong in the first part of the music piece, when the guitarists seem to adjust their coordinated play onsets and brain rhythms actively. This suggests that the methods capturing intra- and interbrain synchronization and its relations to coordinated playing provide crucial information about the underlying mechanisms of interpersonal action coordination.

Keywords: intra- and interbrain synchronization; EEG hyperscanning; phase alignment; social interaction; interpersonal action coordination; brain-instrument interaction

Introduction

Twelve years ago, phase synchronization between brains during guitar playing was investigated for the first time, and the term *interbrain synchronization* was coined. Nowadays, interbrain synchronization is an important research topic in neuroscience and behavioral and social sciences that is examined with different methodological and scientific approaches that use hyperscanning or multiperson electroencephalographic, functional magnetic resonance imaging, and near-infrared spectroscopy recordings. There is no doubt today that the brains of several people are able to synchronize when they are involved in interpersonal interaction or common action and that this synchronization can

improve the interaction performance or support it at different time scales with different interbrain synchronization patterns.^{2–8} Nevertheless, the functional meaning of interbrain synchronization and its relation to behavioral entities and underlying real-time neural dynamics of interpersonally coordinated behavior have remained largely unexplored.^{9–12} The present study aims to overcome this limitation, probing the mechanisms of social interaction at behavioral and neural levels of analysis, and exploring the associations between them.

A recently emerging view in music neuroscience with regard to hyperscanning methods holds that playing music in duets or groups requires strong interbrain synchronization and specific hyperbrain

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network activity supporting interpersonal action coordination. 1,2,13-17 This hyperbrain network activity, including both intra- and interbrain synchronization, is enhanced during periods of high demand on musical coordination and exhibits temporal and structural changes in response to the musical situation and rhythm patterns. 13-16 Moreover, it has been shown that musicians' brain activity synchronizes with the instrument sounds produced during guitar playing.13 It has been noted that the instrument's sound is the result of the musician's behavior or action, and at the same time, this sound influences the behavior of musicians through auditory sensory pathways and is, in this sense, an actor. In other words, the functional meaning of the instrument's sound is twofold: (1) it is a result of an action and, therefore, contains within itself the parameters of the action, and (2) it influences the musicians acoustically and thus provides perceptual input. Synchronization between brains and instruments provides information about the action and reaction of musicians in response to the sound they produce during playing.¹³

It is well known that different events or music sounds can induce time- or phase-locked changes in brain electrophysiological activities. In this context, the electroencephalogram (EEG) offers a rich source of information about neural coding dynamics. 18 Besides phase synchronization measures (e.g., PLI, phase-locking index, and PC, phase coherence), power spectral measures, such as evoked and whole power (EP and WP, respectively), can be useful to measure the power or energy costs of involved cell assemblies and considered as local synchronization measures reflecting synchronous cell activity under a given electrode. 19-21 In combination with intra- and interbrain connectivity measures, they should provide a more complete picture regarding the neuronal mechanisms of action and interaction when playing the guitar in a duet or an ensemble.10

Previously, it has been shown that there is phase alignment across trials with regard to the individual EEG phase angles of two guitarists when sorted in relation to the play-onset (a)synchrony.¹ Phase alignment supposes a direct relation or association between neural phase synchrony and behavioral markers of interpersonal action coordination. This relationship can be assessed by using an angular-linear correlation, which is supposed to represent

a better estimate than the traditional linear-linear correlation.^{22,23} In a study on string quartets using motion capture, the performers' rating of the "goodness" of performance was shown to be related to the overall degree of body sway coupling between the string quartet members, indicating that performers align their behavior when playing music together.²⁴ In a study with 13 expert folk dancers for whom the availability of either auditory, visual, or haptic coupling was manipulated, selective inhibition of any one of the three types of sensory coupling significantly reduced group synchrony and influenced joint action performance.²⁵ This demonstrates that synchronization arises at different levels of human behavior and that the relationships between behavioral and neural components must play an important role.

In the current study, we used a trial-based design with EEG recordings taken while guitar duos played a short melody together in unison over about 60 trials. The main aim of the study was to investigate the association between interbrain synchronous activity and behaviorally related actions measured by play-onset time assessed for each note played. This association was explored in terms of the phase alignment computed across all trials and guitarists (separately for guitarists A and B) for each of the notes played and by calculating the angular-linear correlation between phase and time differences related to the play onsets for each of the notes. We also attempted to replicate the results of our previous studies, which were carried out with similar trial-based designs.^{1,16} In addition to phase synchronization measures, we also used power spectral measures (EP and WP) here to acquire more complete information and better understand the basic processes of interbrain synchronization. The same applies to the calculation of guitar-guitar and brain-guitar coupling, which should give us additional information about the interaction constituents. We need to emphasize here that a trialbased design does not allow the study of jazz or free improvisation. We refer readers interested in interbrain synchronization during improvisation to the studies in which single-trail analyses were used. 13,15

Methods

Participants

Twelve pairs of professional guitarists participated in the study. The same person (guitarist A) was the

Fusion One

A. Buck

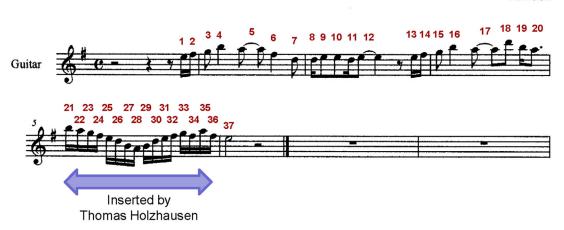


Figure 1. Music sheet of the adapted version of a modern jazz-fusion piece, "Fusion One," composed by Alexander Buck. The melody was changed by the lead guitarist, Thomas Holzhausen, who participated in the study. The inserted additional measure, containing 16 sixteenth notes, is marked by an arrow. The notes played are numbered.

lead guitarist in all pairs. The guitarists in the duos were not known to each other. The participants' mean age was 29.5 years (SD = 10.0). All participants were right-handed and had played the guitar professionally for more than 5 years. The study was approved by the ethics committee of the Max Planck Institute for Human Development (Berlin) and, therefore, performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. All subjects volunteered for this experiment and gave their written informed consent before their inclusion in the study.

Musical material

The melody the guitarists played during the data acquisition was an adaptation of the first five measures (bars) of a modern jazz-fusion piece, "Fusion One," composed by Alexander Buck (born in 1979). The melody was altered by the lead guitarist, Thomas Holzhausen. He added one additional measure, containing 16 sixteenth (semiquaver) notes, which was inserted between the two last measures, and slightly changed the last of these measures (see Fig. 1). The piece has the time signature of four quarter notes per measure and was played in E minor (cf. Supplementary Audio File, online only). The score of the altered version of the jazz-fusion piece and a MIDI file from it were provided to the

guitarists before the experiment so that they could practice beforehand.

Experimental procedure and data acquisition

The EEG measurements took place in an acoustically and electromagnetically shielded cabin. During the experiment, the guitarists sat facing each other and played in a duet. They were instructed to avoid all unnecessary movement in order to avoid movement artifacts. Data were collected across at least 60 trials, in which the guitarists played a short melody (about 15 s) on their guitars in unison. Each trial was initiated by four metronome beats (100 bpm), after the last of which the leader signaled the beginning by tapping on the guitar board with his right finger (defined hereafter as a start marker). The sounds of the guitars were recorded through two microphones (i.e., one for each guitar) on two channels using an ExG amplifier, simultaneously with the EEG recordings. In addition, video and sound were recorded using the Video Recorder Software (Brain Products, Gilching, Germany) synchronized with the EEG data acquisition. The microphone and video recordings were useful for determining the event triggers that were later set offline in the EEG recordings. The electroencephalogram was simultaneously recorded from both participants using two electrode caps with 64 Ag/AgCl electrodes placed according to the international 10-10 system, with the reference electrode placed at the right mastoid. Separate amplifiers with separate grounds were used for each individual, optically coupled to a computer. The vertical and horizontal electrooculogram was also recorded to control for eye blinks and eye movements. The sampling rate was 5000 Hz, and the antialiasing filter was set to 1000 Hz. EEG recordings were rereferenced offline to an average of the left and right mastoids and then filtered with a bandpass ranging from 1 to 100 Hz. Eye movement correction was accomplished by independent component analysis.²⁶ Thereafter, artifacts from head and body movements were rejected by visual inspection, resulting in the removal of 15% of the trials that were available. Spontaneous EEG activity was resampled at 250 Hz and divided into artifact-free 15-s epochs related to the start marker. For analysis, we used 40 EEG channels for each subject. These channels or electrodes were distributed across the entire cortex so that the information of the remaining electrodes would be rather redundant.

Data analysis

For the analysis, event triggers were placed at the onset of the metronome beats and at the play onset of each of the 37 notes. The triggers were set semiautomatically using a LabVIEW routine searching for audio events and then adjusted manually for each sound or note played. Only correctly played trials were used for further analyses. To explore behavioral play-onset synchrony, we first determined the time difference between the two guitarists within each duo for each of the 37 notes across the 40 artifact-free trials selected for this analysis.

To investigate phase synchronization or coupling within and between the signals, we first analyzed artifact-free epochs using a complex Gabor expansion function, which transformed the EEG time series into a complex time-frequency signal y(f,t) for frequencies up to 20 Hz. In the first step of our analyses aiming at the replication of results of our previous study, we calculated the phase synchronization (*PLI* and *PC*) and power spectral measures (*EP* and *WP*) for 3-s epochs (1000 ms before and 2000 ms after event onset). The frequency resolution of the Gabor transform was given at 0.33 Hz, and the time resolution was fixed at 1 millisecond. For each frequency bin (f) and time point (t), the *PLI* was deter-

mined as a phase synchronization across the k trials at the different electrodes within the brain by the formula:

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

with $\Phi^k(f,t) = arg\{z^k(f,t)\}$ as a phase or argument of the complex number z. The PC was determined as a phase synchronization or coupling between two electrodes both within and between the brains, defined by:

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

where the phase difference $\Delta \Phi^k$ refers to $\Delta \Phi^k_{XY}(f,t) = mod(\Phi^k_X(f,t) - \Phi^k_Y(f,t), 2\pi)$, 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.

For frequency f and time t, EP was calculated from individual ERPs (event-related potentials) according to $EP(f,t) = |Avg(y_i(f,t))|^2$, and WP was calculated as the average (Avg) of the power of a signal in single trials: $WP(f,t) = Avg(|v_i(f,t)|^2)$, with v_i for the raw signal. Evoked and whole power were determined to achieve adequate time-frequency resolution of amplitude estimates reflecting evoked and induced or total spectral activity, respectively. Furthermore, we analyzed the acoustic signals of the guitars obtained from the two microphones. To do so, we first normalized the high-frequency auditory signals and applied an analytic Morlet wavelet transform, and then calculated the amplitude within the four different frequency ranges of interest (frequency components, FC): low (FC1:50-250 Hz), middle (FC2:250-500 Hz), high (FC3:500-2000 Hz), and whole-range (FC4:50-2000 Hz). By averaging the amplitude within these four frequency ranges, we generated a low-frequency time series that varied in a frequency range comparable with the EEG time series. 13 These transformed guitar signals then underwent the synchronization analyses described above.

For the time-frequency representation and corresponding brain maps, grand averages were used, that is, time-frequency transformed data were averaged across individuals or across pairs of guitarists. To identify the topological distribution of the measures, the most representative data were mapped using spherical spline interpolation methods.

For the time-frequency presentation, *PLI*, *EP*, and WP values from six frontocentral electrodes were chosen and averaged in the time-frequency domain. PC values were averaged across the pairs from the Cz electrode to all others within the brain (within- or intrabrain synchronization) or to all electrodes in the other brain (between- or interbrain synchronization). To provide an overview of the observed synchronization and power spectral measures, and to compute the topological distribution of these measures, we determined the average values within a specific time-frequency window (200-ms duration and frequency range of interest) for each of the 40 electrodes across all subjects (separately for guitarists A and B). To compute the topological distribution of PC values, strengths were determined for each electrode as a sum of all connections from this electrode to all other electrodes. For the connectivity maps, grand averages were determined across all connections or electrode pairs within or between the brains as well as between the four guitar nodes in each guitar and the electrodes in the two guitarists' brains.

Note that for the presentation of the topological distribution of the measures and the connectivity maps during the metronome condition, grand averages were computed in the time window between -600 and -400 ms (corresponding to the first metronome beat) and in the theta frequency range between 3.33 and 6.67 Hz. For the presentation of the topological distribution of the measures and the connectivity maps after play onset, grand averages were computed in the time window between 0 and 200 ms (corresponding to the first note played) and in the delta frequency range between 0 and 3.33 Hz.

For statistical evaluation of the differences between guitarists A and B in the topological distribution of synchronization measures (i.e., *PLI*, *EP*, *WP*, and *PC*) and also of their changes as compared with the baseline, we determined an average across eight maxima in the topological distribution of each brain. For baseline calculations, time intervals before the first metronome beat (between -800 and -600 ms) and before play onset (between -200 and 0 ms) were used for metronome and play conditions, respectively. The Wilcoxon signed-rank test for paired comparison was used for statistical examination.

In the second step of our analyses aiming at probing associations between interbrain synchro-

nization and interpersonal action coordination during guitar playing, we determined phase angles for six frequencies of interest, which were different harmonics (from the first to the sixth) of the metronome frequency (1.667, 3.333, 5.0, 6.667, 8.333, and 10.0 Hz). The phase angles were computed for each of the 37 notes played in 40 different trials with respect to the 3-s epochs related to the note play onset of guitarists A and B, respectively. Using information about the phase angle, we computed the phase alignment across all 40 trials, and 12 guitarists pairs (480 = 40×12) for each individual note played. The corresponding phase angles were sorted as a function of the behavioral synchrony in play onsets (time difference) between the two guitarists. To quantitatively assess the relationship 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 guitarist pairs. The angular-linear correlation coefficient (r_{al}) is given by^{22}

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

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 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 . The angular–linear correlations were assessed across all trials and guitarist pairs for each of the notes played ($n_1 = 40 \times 12 = 480$) and across all trials and notes for each of the guitarist pairs ($n_2 = 40 \times 37 = 1480$). In the case of $\chi_{0.05,2}^2 = 5.991$, we obtain two significance levels (SL) for r_{al} :²²

$$SL_1 = \sqrt{\frac{\chi_{0.05,2}^2}{n_1}} = \sqrt{\frac{5.991}{480}} = 0.112$$
 and
$$SL_2 = \sqrt{\frac{\chi_{0.05,2}^2}{n_2}} = \sqrt{\frac{5.991}{1480}} = 0.064.$$

All correlation coefficients above the *SL* were considered significant.

Results

Synchronization and spectral brain activity during the preparatory period

In contrast to our previous study describing intertrial synchrony in individual guitarist pairs, we now present grand averages across individuals or pairs. Here, we represent phase synchronization patterns and spectral activity during the preparatory time period or metronome tempo setting. Figure 2 displays time-frequency diagrams and topological distribution of the PLI representing intertrial phase synchrony (Fig. 2A), of the EP representing the phase-locked power of the signal (Fig. 2B), of the WP representing the total power of the signal (Fig. 2C), of the connectivity strengths both within (Fig. 2D) and between (Fig. 2E) the brains, and corresponding connectivity maps also within and between the brains (Fig. 2F). For time-frequency representation, PLI, EP, and WP values were averaged across six frontocentral electrodes (F3, Fz, F4, C3, Cz, and C4), and PC values were averaged across all connections from Cz to all other electrodes within the brains or to all other electrodes in the other brain, respectively. Since all guitarist pairs had the same metronome tempo setting (600 ms interbeat interval), all the measures showed synchronized activity at the occurrence of the four metronome beats at the main oscillation frequency (1.667 Hz) and other harmonics up to 10 Hz. This synchronization, measured at the first metronome beat, was significantly higher as compared with the baseline: PLI_A (Z = -3.06, P = 0.0022), PLI_B (Z = -3.06, P = 0.0022), EP_A (Z = -3.06, P = 0.0022), EP_B $(Z = -2.98, P = 0.0029), WP_A (Z = -3.06,$ P = 0.0022), and WP_B (Z = -2.43, P = 0.015). The differences in intrabrain connectivity strengths as compared with the baseline were significant only in guitarist A: PC_A (Z = -3.06, P = 0.0022) and PC_B (Z = -0.16, P = 0.88), whereas the differences in interbrain connectivity strengths were significant in both guitarists: PC_A (Z = -2.28, P = 0.023) and PC_B (Z = -2.75, P = 0.0060). As to be expected, guitarist A, who was the same person in all guitarist pairs, showed higher phase synchronization and spectral power as compared with guitarist B, who was always different: PLI_{AB} (Z = -2.98, P = 0.0029), EP_{AB} (Z = -2.98, P = 0.0029), and WP_{AB} (Z = -2.12,P = 0.034). The differences in intra- and interbrain connectivity strengths between the two guitarists did not reach the significance level (P > 0.05). These differences in grand averages, at least for local synchronization measures (i.e., PLI, EP, and WP), mirror intra- and interpersonal variability in synchronous brain activity. Most importantly, in line with our previous results, this activity both within and between the brains has a pronounced frontocentral distribution and thus represents an important replication of previous findings (cf. Refs. 1 and 16).

Synchronization and spectral brain activity after play onset

In Figure 3, the corresponding phase synchronization patterns and spectral activity, as well as connectivity maps, are displayed in relation to play onset. The highest phase synchronization measured by PLI is represented in the frequency range between 0 and 7 Hz with a topological maximum at centrofrontal and left-temporal sites (Fig. 3A). Similarly, *EP* is pronounced in the same frequency range (0-7 Hz) with a symmetric frontocentral distribution (Fig. 3B). By contrast, WP is not only present in low delta-theta frequency ranges but also in the alpha frequency range (Fig. 3C). This indicates that only the power in the frequency range between 0 and 7 Hz is phase-locked, whereas the alpha frequency is exclusively, or to the greatest extent, represented by induced or total power. The topological distribution of WP is also frontocentral and mostly concentrated at midline electrodes. Interestingly, within-brain connectivity is also pronounced in delta and alpha frequency ranges (Fig. 3D), whereas between-brain connectivity is mainly restricted to the delta frequency under 5 Hz (Fig. 3E). Figure 3F illustrates the within- and betweenbrain connectivity at play onset. Between-brain connectivity is predominantly frontocentrally distributed with marked left-temporal connections in guitarist B.

Statistical evaluation of the time interval after play onset (0-200 ms) in the delta frequency range (0-3.33 Hz) as compared with the baseline (between -200 and 0 ms) revealed significant differences for all local synchronization measures: PLI_A (Z=-2.98, P=0.0029), PLI_B (Z=-3.06, P=0.0022), EP_A (Z=-3.06, P=0.0022), EP_B (Z=-2.98, P=0.0029), WP_A (Z=-3.06, P=0.0022), WP_B (Z=-2.12, P=0.034) as well

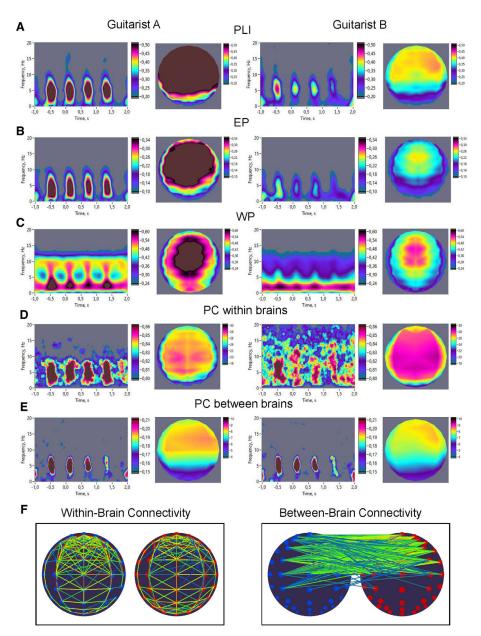


Figure 2. Grand averages of spectral power and phase synchronization within and between brains during the preparatory period of metronome tempo setting. (A) Time-frequency diagrams and topological distribution of average *PLI* for guitarists A and B separately. (B) Time-frequency diagrams and topological distribution of average *EP* for guitarists A and B separately. (C) Time-frequency diagrams and topological distribution of average *WP* for guitarists A and B separately. (D) Time-frequency diagrams of *PC* and topological distribution of strengths within the brains of guitarists A and B. (E) Time-frequency diagrams of *PC* and topological distribution of strengths of the between-brain connectivity for guitarists A and B separately. (F) Within- and between-brain connectivity maps. For time-frequency representation, *PLI*, *EP*, and *WP* values were averaged across six frontocentral electrodes (F3, Fz, F4, C3, Cz, and C4), and *PC* values were averaged across all connections from Cz to all other electrodes within the brains or to all other electrodes in the other brain, respectively. For topological distribution, the measures were averaged within the time window between -600 and -400 ms and the frequency range between 3.33 and 6.67 Hz. All four metronome beats induced high spectral power and phase synchronization within and between the brains.

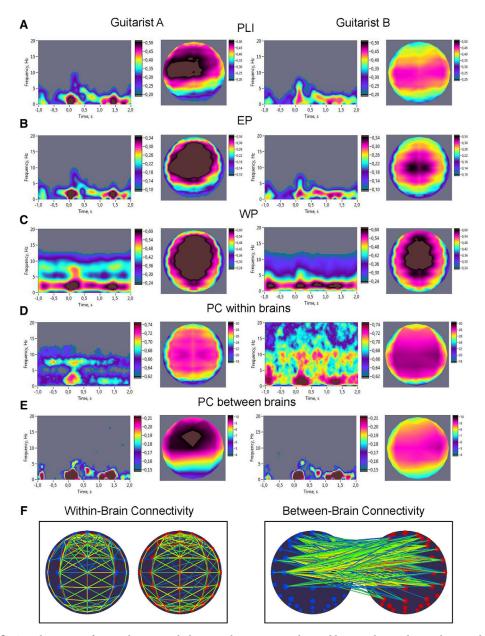


Figure 3. Grand averages of spectral power and phase synchronization within and between brains during the period of guitar playing. (A) Time-frequency diagrams and topological distribution of average *PLI* for guitarists A and B separately. (B) Time-frequency diagrams and topological distribution of average *EP* for guitarists A and B separately. (C) Time-frequency diagrams and topological distribution of average *WP* for guitarists A and B separately. (D) Time-frequency diagrams of *PC* and topological distribution of strengths within the brains of guitarists A and B. (E) Time-frequency diagrams of *PC* and topological distribution of strengths of the between-brain connectivity for guitarists A and B separately. (F) Within- and between-brain connectivity maps. For time-frequency representation, *PLI*, *EP*, and *WP* values were averaged across six frontocentral electrodes (F3, Fz, F4, C3, Cz, and C4), and *PC* values were averaged across all connections from Cz to all other electrodes within the brains or to all other electrodes in the other brain, respectively. For topological distribution, the measures were averaged within the time window between 0 and 200 ms and the frequency range between and 0 and 3.33 Hz. High spectral power and phase synchronization within and between the brains in both guitarists not only occurred at play onset but also at the time point of the finger gesture serving as the starting signal, and at individual guitar strokes.

as for intrabrain: PC_A (Z = -2.59, P = 0.0096), PC_B (Z = -2.98, P = 0.0029), and interbrain: PC_A (Z = -2.90, P = 0.037), PC_B (Z = -2.98, P = 0.0029) connectivity strengths. Unlike the metronome condition, there were no significant differences in the topological distribution between guitarists A and B in the play condition.

Synchronization of guitars and brains during playing

As described in the Methods section, acoustic guitar signals obtained through microphones were transformed into low-frequency signals by averaging the signal amplitude within the four frequency ranges of interest. Figure 4A displays the phase synchronization within and between the guitars. For this timefrequency representation, all connections between the four FCs were averaged within and between the guitars, respectively. As to be expected, synchronization within the guitars was strongly enhanced at the start marker (the lead guitarist's tapping on the guitar board) and at the notes played, spread out across the entire frequency range. This synchronization spreading across the frequencies is presumably due to the acoustic resonances of the guitars. Synchronization between the guitars is also strong but restricted to the frequencies below 10 Hz, with the exception of synchronization at the start marker keeping spread across the frequencies. This damping of acoustic resonances during playing is presumably caused by play-onset asynchronies in two guitarists. Synchronization between guitars and brains occurs at the low delta-theta frequencies below 7 Hz (Fig. 4B and C) and is strongly related to the notes played. Most interestingly, the topological distribution of synchronization between the guitarist's brain and his/her own instrument showed the maxima at left central sites of both guitarists, apparently indicating the activity of the cortex representing the right hand, which is dominant during guitar playing. The topological distribution of synchronization between the guitarist's brain and the instrument of the other guitarist showed rather centroparietal and temporal maxima without visible cortical asymmetry, apparently indicating an influence of hearing and motor actions of both left and right hands. This can be seen more precisely in the guitar-brain connectivity maps (Fig. 4D). Statistical testing did not reveal any significant differences in the topological distribution of synchronization measures between

the guitarists A and B in relation to their guitars (P>0.05), but as to be expected, the changes compared with the baseline were highly significant in both guitarists: guitar A to brain A (Z=-2.98, P=0.0029), guitar B to brain B (Z=-2.98, P=0.0029), guitar A to brain B (Z=-2.59, P=0.0096), and guitar B to brain A (Z=-2.59, P=0.0096).

Relationship between synchronization and behavioral measures

To test whether the synchronization patterns were related to the behavioral play-onset synchronies, we determined phase angles in single trials at the six frequencies of interest representing the metronome frequency (1.667 Hz) and the first five harmonics of that frequency and then sorted them according to the time difference between the play onsets of the guitarists (play-onset synchrony) across all trials and guitarist pairs. We computed this relationship for each of the 37 notes played. In Figure 5, we present this relationship for phase angles at the metronome frequency of three selected notes for each of the two guitarists (the relationship for the other notes can be found in Figs. S1-S4, online only). The results indicate a strong phase alignment that closely follows the behavioral onset synchrony across all trials and guitarists in pairs. This phase alignment was only present for notes 1-20. As can be seen in Figure 1, from note 21 onward, the guitarists played the fast 16 notes, which are presumably too fast to be aligned to the fundamental frequency of 1.667 Hz. Interestingly, the first notes in the music piece showed phase alignment across several brain wave cycles indicating temporal phase synchrony, especially at play onset. At the beginning of the fast part (at note 21), there seems to be a phase alignment, but it is rather an aftereffect of note 20 (cf. Figs. S1–S4, online only). As shown for note 25, the phase alignment could not be continued for the following sixteenth notes, at least not at the fundamental metronome frequency (see Figs. S1-S4 for details, online only).

To quantitatively assess the relationship between behavioral and brain synchrony, we calculated angular–linear correlations (r_{al}) between phase (angular) and time (linear) differences across all trials and guitarist pairs (n=480, SL=0.112) for each of the notes played. As can be seen in Figure 5B, the correlation is strongest for the first

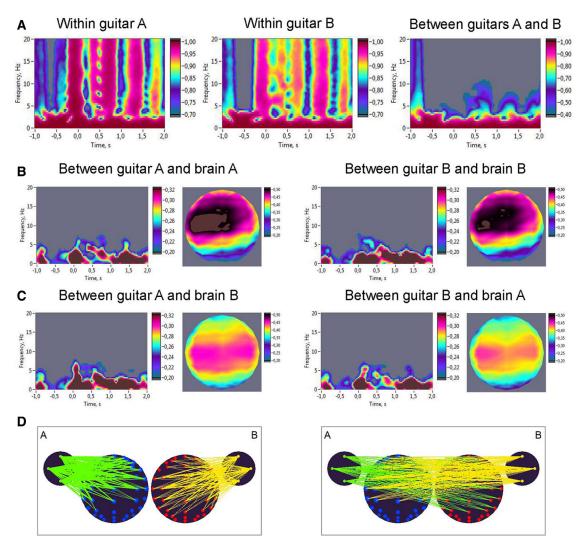


Figure 4. Phase synchronization within and between the guitars, and between the guitars and brains. (A) Time-frequency diagrams of the phase synchronization within and between the guitars as measured by *PC* between the four frequency components. For this representation, all connections were averaged in the time-frequency domain. Note synchronization spreading across the frequencies, which is presumably due to the acoustic resonances of the guitars. (B) Time-frequency diagrams and topological distribution of average *PC* between the guitarists' brains and their own instruments depicted for guitarists A and B separately. (C) Time-frequency diagrams and topological distribution of average *PC* between the guitarists' brains and the other guitarists' instruments depicted for guitarists A and B separately. (D) Connectivity maps between the guitarists' brains and their own instruments, and between the guitarists' brains and the instruments of the other guitarists. The topological distribution of synchronization between the guitarists' brains and their own instruments showed the maxima at left central sites of both guitarists, apparently indicating the influence of cortical activity related to the right hand, which is dominant during guitar playing. The topological distribution of synchronization between the guitarists' brains and the instruments of the other guitarists showed rather centroparietal and temporal maxima without visible cortical asymmetry, apparently indicating influence of hearing and motor actions of both left and right hands.

12 notes of the music piece (especially for notes 4, 7, and 9) at practically all six harmonics of the metronome frequency. We also calculated the angular–linear correlation across all trials and notes

(n = 1480, SL = 0.064) for each of the guitarist pairs. Figure 5C shows that this correlation is mostly significant (except for pair 4) and that the brain responses of the two guitarists (phase differences)

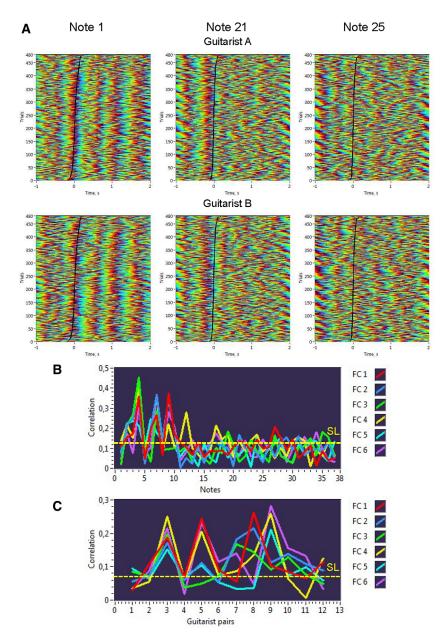


Figure 5. Phase alignment of phase angles related to behavioral play-onset synchrony and angular-linear correlation between the time and phase differences. (A) Phase alignment of phase angles related to the behavioral play-onset synchrony across all trials and guitarist pairs for three selected notes (1, 21, and 25) for guitarists A and B separately. Trials were sorted by behavioral onset synchrony between the players (guitarist A's play onset time minus guitarist B's play onset time in the case of the guitarist A, and the inverse for guitarist B). Behavioral synchrony is depicted by the black curve. Note that phase alignment was calculated here for the mid-central electrode Cz. (B) Angular-linear correlation between phase and time differences across all trials and guitarist pairs for each of the notes played. The correlation is strongest for the first 12 notes of the music piece (especially for notes 4, 7, and 9) at practically all six harmonics of the metronome frequency. (C) Angular-linear correlation across all trials and notes for each of the guitarist pairs. The correlation is mostly significant (with exception of pair 4). The brain responses of the two guitarists were maximally related to their behavioral play-onset synchrony at different frequencies in each pair. Note that correlation values for this representation were calculated between the Cz electrodes in guitarist A's and B's brains.

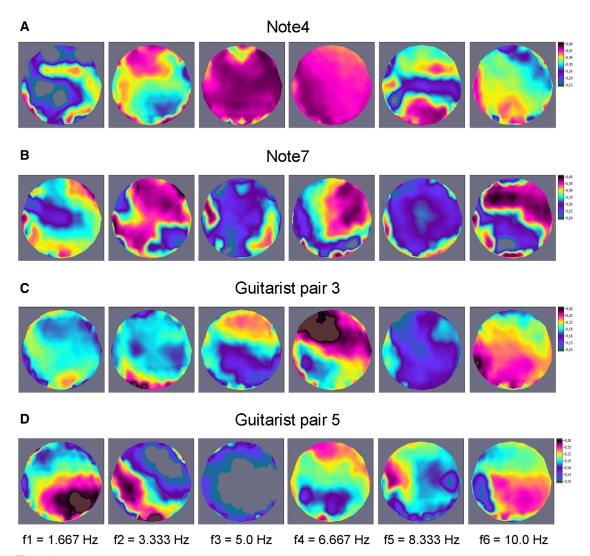


Figure 6. Topological distribution of angular-linear correlation between the time and phase differences for the six frequencies of interest. (A) Topological distribution of the angular-linear correlation between phase and time differences across all trials and guitarist pairs for note 4. (B) Topological distribution of the angular-linear correlation between phase and time differences across all trials and guitarist pairs for note 7. (C) Topological distribution of the angular-linear correlation across all trials and notes for guitarist pair 3. (D) Topological distribution of the angular-linear correlation across all trials and notes for guitarist pair 5. The correlation is mostly significant (with exception of pair 4). Note that correlation values for this representation were calculated between the same electrodes in guitarist A's and B's brains.

were maximally related to their behavioral playonset synchrony at different frequencies in each pair. Note that correlation values for this representation were calculated between the Cz electrodes in guitarist A's and B's brains. The topological distribution of correlation values, determined for other electrode pairs (the same electrodes in guitarist A's and B's brains) for two notes (notes 4 and 7) and two guitarist pairs (guitarist pairs 3 and 5) across

the six frequencies of interest (different harmonics of the metronome frequency), is displayed in Figure 6, which shows that the topological distribution of the correlation values differs in these six frequencies.

Discussion

The primary objective of our study was to investigate the association between behavioral entities

of guitar playing and its neuronal implementation. The main findings are that when playing guitar in a duet, (1) a synchronization between guitars and brains can be observed at the low delta-theta frequencies below 7 Hz, which is strongly related to the notes played; (2) the phase angles of both guitarists in the pair were strongly aligned with regard to the behavioral onset synchrony when computed across all trials and guitarists in pairs; (3) the angularlinear correlation between interbrain phase differences and time-onset synchronies in pairs was strongest for the first 12 notes of the music piece at practically all six harmonics of the metronome frequency; and (4) this correlation, when calculated within pairs, was mostly significant, whereby each guitarist pair seems to have preferred different frequencies at which the brain responses of the two guitarists (phase differences) were maximally related to their behavioral play-onset synchrony. Furthermore, it should be noted that, to a great extent, the results of this study replicated the results of our previous studies (cf. Refs. 1 and 16) and showed similar intra- and interbrain synchronization patterns with frontocentral maxima in the topological distribution of these measures. As these synchronization patterns were represented by grand averages across guitarists and pairs, the findings seem to confirm stable and common features of a musical interaction when playing guitar in a duet.

Thus, synchronized delta and theta oscillations both within and between the brains found during metronome tempo setting and during duet playing (especially after play onset) as well as the frontocentral topological distribution of synchronization indices can be regarded as indicating a stable and indisputable result in this experimental setting. As previously suggested,1 enhanced synchronization at frontal and central electrode sites may indicate coordinated firing of neuronal assemblies located in the motor and somatosensory cortices that control and coordinate motor activity and can also be involved in regulatory activity to coordinate interactive behavior between oneself and others.^{27,28} With respect to connectivity patterns within the brains, which exhibited a broader topological distribution, additionally including temporal, parietal, and occipital sites, it can be supposed that the within-brain network activity strongly binds different sensory inputs coming from the visual and auditory cortices and also integrates these with

motor activation in central brain regions. Together with the between-brain connections, these withinbrain connections build a common hyperbrain network space regulating the entire activity in the guitarist pairs and thereby support coordinated guitar playing. 15,16 Additionally, we computed EP and WP, which can be considered as indicators of local synchrony that describe (together with PLI) local neural information processing at individual electrode sites. It has been suggested²⁹ that spectral power measures (e.g., EP and WP) are indicative of the "rate code," 30 whereas PLI is rather indicative of the "temporal code." These different types of neural processing and coding are complementary to each other and form the basis for different neural mechanisms supporting perception, action, and interpersonal interaction. Moreover, as shown in Figures 2 and 3, spectral power in the alpha frequency range (8–12 Hz), which can be seen in the WP but not in the EP time-frequency diagrams, is not phase-locked; nevertheless, large-scale withinbrain PC showed synchronization patterns at this frequency, at least during playing (see Fig. 3D). This indicates that although local brain activity is not synchronized at this frequency, global or large-scale brain activity remains synchronized, that is, different brain sites change their phases in similar ways. This large-scale within-brain alpha synchrony has a predominantly parietooccipital distribution and could be observed within the brains but not between the brains. As alpha-band oscillations have a timing besides an inhibitory function and play an active (above all regulatory) role in information processing,³² we propose that the observed local activity (WP) and corresponding within-brain synchrony play a crucial role in the temporal organization of coordinated action.

We have shown that interbrain synchrony mostly occurs in the low delta and theta frequency ranges and is mostly related to notes during playing. Moreover, we found phase coupling between guitars (transformed acoustic microphone signals) and brains at these frequencies. We recently described this phenomenon in our previous study. We have now shown that the topological distribution of synchronization between the guitarist's brain and his/her own instrument is maximal at the left central sites of both guitarists. We assume that this synchrony pattern indicates the activity of the cortex representing the right hand, which is dominant

during guitar playing. This fact is especially interesting with regard to the finding that the topological distribution of synchronization between the guitarist's brain and the other guitarist's instrument showed rather centroparietal and temporal maxima without recognizable cortical asymmetry, apparently indicating the influence of hearing and motor actions of both left and right hands. Given the relatively low spatial resolution of electroencephalography, we can only speculate about the neuronal circuitry contributing to this interesting finding: The differences in the topological distribution of these two synchrony cases cannot be arbitrary and, therefore, requires logical explanation. In our view, different sensorimotor loops influencing this coupling are at work. Recently, we reported that the vocalizing patterns of singers are coupled to their respiratory and cardiac oscillations during choir singing.^{33,34} Furthermore, there is evidence for the coupling between an instrument (piano assessed by MIDI tone onsets) and the brains of pianists performing a musical duet.³⁵ Further studies are required to better understand this interesting relationship between the instruments and brains.

In the present study, we also found a strong phase alignment determined in the two guitarists, which closely followed behavioral onset synchrony. In point of fact, this finding is a further replication of our previous results.1 As all guitarist pairs played the same music piece with the same metronome tempo in the current study, we were able to accumulate and sort the phase angles across all guitarist pairs (separately for guitarists A and B) and trials. In sum, phase alignment was then computed across 480 trials and was strongly recognizable for the first 20 notes. From the 21st note, the guitarists played the sixteenth notes, which are presumably too fast to be aligned to the fundamental frequency of 1.667 Hz. Note 21 seems to induce phase alignment, but as mentioned in the Results section, it is rather an aftereffect of note 20. As shown for all the following sixteenth notes, the phase alignment diminished or was absent, at least for the fundamental metronome frequency. The phase alignment related to playonset synchrony indicates that brain responses in each of the guitarists' brains have an intrinsic relation not only to the individual notes played in the duo but also to the synchronicity at which they were played. The absence or decrease of alignment when playing the fast sixteenth notes presumably indicates that brain responses can hardly follow these fast actions. Interestingly, the first notes in the music piece showed phase alignment across several brain wave cycles indicating temporal phase synchrony or emergence of specific temporal structures, both of which facilitate or support synchronous playing.

Most importantly, we found an angular-linear correlation between phase and time differences across all trials and guitarist pairs that were strongest for the first 12 notes of the piece at practically all six harmonics of the metronome frequency. Furthermore, the angular-linear correlation calculated across all trials and notes for each of the guitarist pairs was mostly significant, with a preference for different frequencies in pairs, at which the two guitarists' brain responses (phase differences) were maximally related to their behavioral outcomes (play-onset differences). As the topological distributions of the correlation values in these six frequencies of interest change both across notes and guitarist pairs, it can be concluded that different brain regions are of importance at different time points of playing (notes) and can also vary in different guitarist pairs. In sum, phase alignment related to the play-onset synchrony together with an angular-linear correlation between brain responses and behavioral outcomes provides important evidence for an association between interbrain synchrony and behaviorally related actions.

In conclusion, this study shows that interbrain synchrony is a complex construct that is intertwined with several brain components reflected in applied measures that may control and influence behavioral and instrument-related outcomes. The results indicate that the behavior-brain association occurring when two individuals play guitar in a duet is not straightforward but rather depends on different factors and the emergence of specific temporal structures, facilitating brain-brain and braininstrument interactions. As the brain is not only a perceptive and controlling system but is also able to predict the occurrence of events and prepare corresponding or necessary actions to be in line with the environment and also with other actors,36-39 the neural processes and involved cell assemblies must be able to mirror and handle all these factors in a common multidimensional space. Therefore, different approaches or measures reflecting different aspects of interpersonal action coordination and social interaction are necessary to cover the different facets of this space. ^{10,39,40} In a number of studies, it has been shown that hyperscanning as a neuroimaging technique investigating dynamic social interaction is an indispensable tool for understanding the role of these factors in interpersonal action coordination and collective behavior. ^{2,4,13–15,33,34,39,41–43}

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, the grand averages presented in the study provide stable and distinctive synchronization patterns, which are in line with previous research. Second, although the angular-linear correlation showed a significant relationship between phase and time differences, other techniques should be tested to better understand interbrain synchronous 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 study jazz or free improvisation. Synchronization across time may provide more detailed information about direct relations between synchronization and performance indexes reflecting interpersonal action coordination, especially if the interesting case of musical improvisation needs to be explored.

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Author contributions

V.M. and U.L. designed the study. V.M. acquired and analyzed the data. V.M. and U.L. discussed the results, wrote the article, and read and approved the final version of the manuscript.

Supporting information

Additional supporting information may be found in the online version of this article.

Figure S1. Phase alignment of phase angles related to behavioral play-onset asynchrony for the notes from 1 to 20 played by guitarist A.

Figure S2. Phase alignment of phase angles related to behavioral play-onset asynchrony for the notes from 21 to 37 played by guitarist A.

Figure S3. Phase alignment of phase angles related to behavioral play-onset asynchrony for the notes from 1 to 20 played by guitarist B.

Figure S4. Phase alignment of phase angles related to behavioral play-onset asynchrony for the notes from 21 to 37 played by guitarist B.

Supplement Material

Competing interests

The authors declare no competing interests.

References

- Lindenberger, U., S.-C. Li, W. Gruber, et al. 2009. Brains swinging in concert: cortical phase synchronization while playing guitar. BMC Neurosci. 10: 22.
- Acquadro, M.A.S., M. Congedo & D. De Riddeer. 2016. Music performance as an experimental approach to hyper-scanning studies. Front. Hum. Neurosci. 10: 242.
- 3. D'Ausilio, A., G. Novembre, L. Fadiga, *et al.* 2015. What can music tell us about social interaction? *Trends Cogn. Sci.* 19:
- Dikker, S., L. Wan, I. Davidesco, et al. 2017. Brain-to-brain synchrony tracks real-world dynamic group interactions in the classroom. Curr. Biol. 27: 1375–1380.
- Hu, Y., Y. Hu, X. Li, et al. 2017. Brain-to-brain synchronization across two persons predicts mutual prosociality. Soc. Cogn. Affect. Neurosci. 12: 1835–1844.
- Müller, V. & U. Lindenberger. 2014. Hyperbrain networks support romantic kissing in humans. PLoS One 9: e112080.
- Nozawa, T., K. Sakaki, S. Ikeda, et al. 2019. Prior physical synchrony enhances rapport and inter-brain synchronization during subsequent educational communication. Sci. Rep. 9: 12747.
- Pérez, A., M. Carreiras & J.A. Duñabeitia. 2017. Brain-tobrain entrainment: EEG interbrain synchronization while speaking and listening. Sci. Rep. 7: 4190.
- Hari, R. & M.V. Kujala. 2009. Brain basis of human social interaction: from concepts to brain imaging. *Physiol. Rev.* 89: 453–479.
- Müller, V., K.-R.P. Ohström & U. Lindenberger. 2021. Interactive brains, social minds: neural and physiological mechanisms of interpersonal action coordination. *Neurosci. Biobehav. Rev.* 128: 661–677.
- Sänger, J., U. Lindenberger & V. Müller. 2011. Interactive brains, social minds. Commun. Integr. Biol. 4: 655–663.
- Schilbach, L., B. Timmermans, V. Reddy, et al. 2013. Toward a second-person neuroscience. Behav. Brain Sci. 36: 393– 414.

- Müller, V. & U. Lindenberger. 2019. Dynamic orchestration of brains and instruments during free guitar improvisation. Front. Integr. Neurosci. 13: 50.
- Müller, V., J. Sänger & U. Lindenberger. 2018. Hyperbrain network properties of guitarists playing in quartet. *Ann. N.Y. Acad. Sci.* 1423: 198–210.
- Müller, V., J. Sänger & U. Lindenberger. 2013. Intra- and inter-brain synchronization during musical improvisation on the guitar. PLoS One 8: e73852.
- Sänger, J., V. Müller & U. Lindenberger. 2012. Intra- and interbrain synchronization and network properties when playing guitar in duets. Front. Hum. Neurosci. 6: 312.
- Sänger, J., V. Müller & U. Lindenberger. 2013. Directionality in hyperbrain networks discriminates between leaders and followers in guitar duets. Front. Hum. Neurosci. 7: 234.
- Nunez, P.L. 1995. Neocortical Dynamics and Human EEG Rhythms. Oxford, England: Oxford University Press.
- Buzsáki, G. 2006. Rhythms of the Brain. Oxford; New York: Oxford University Press.
- Pfurtscheller, G. & F.H. Lopes da Silva. 1999. Event-related EEG/MEG synchronization and desynchronization: basic principles. Clin. Neurophysiol. 110: 1842–1857.
- Varela, F.J., J.-P. Lachaux, E. Rodriguez, et al. 2001. The brainweb: phase large-scale integration. Nat. Rev. Neurosci. 2: 229–239
- Zar, J.H. 2010. Biostatistical Analysis. 5th ed. Hoboken, NJ: Pearson Prentice Hall.
- Kempter, R., C. Leibold, G. Buzsáki, et al. 2012. Quantifying circular–linear associations: hippocampal phase precession. J. Neurosci. Methods 207: 113–124.
- Chang, A., S.R. Livingstone, D.J. Bosnyak, et al. 2017. Body sway reflects leadership in joint music performance. Proc. Natl. Acad. Sci. USA 114: E4134–E4141.
- Chauvigné, L.A.S., A. Walton, M.J. Richardson, et al. 2019.
 Multi-person and multisensory synchronization during group dancing. Hum. Mov. Sci. 63: 199–208.
- Vigário, R.N. 1997. Extraction of ocular artefacts from EEG using independent component analysis. *Electroencephalogr. Clin. Neurophysiol.* 103: 395–404.
- Frith, C.D. & D.M. Wolpert. 2003. Decoding, imitating, and influencing the actions of others: the mechanisms of social interaction. *Philos. Trans. R. Soc. B Biol. Sci.* 358: 431–434.
- Gallese, V. 2003. The manifold nature of interpersonal relations: the quest for a common mechanism. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 358: 517–528.
- Müller, V., W. Gruber, W. Klimesch, et al. 2009. Lifespan differences in cortical dynamics of auditory perception. Dev. Sci. 12: 839–853.

- Stein, R.B., E.R. Gossen & K.E. Jones. 2005. Neuronal variability: noise or part of the signal? *Nat. Rev. Neurosci.* 6: 389–397.
- Hestrin, S. & M. Galarreta. 2005. Synchronous versus asynchronous transmitter release: a tale of two types of inhibitory neurons. *Nat. Neurosci.* 8: 1283–1284.
- Klimesch, W. 2012. Alpha-band oscillations, attention, and controlled access to stored information. *Trends Cogn. Sci.* 16: 606–617.
- Müller, V., J.A.M. Delius & U. Lindenberger. 2019. Hyperfrequency network topology changes during choral singing. Front. Physiol. 10: 207.
- 34. Müller, V., J.A.M. Delius & U. Lindenberger. 2018. Complex networks emerging during choir singing. *Ann. N.Y. Acad. Sci.* **1431:** 85–101.
- Zamm, A., S. Debener, A.R. Bauer, et al. 2018. Amplitude envelope correlations measure synchronous cortical oscillations in performing musicians. Ann. N.Y. Acad. Sci. 1423: 251–263
- Wolpert, D.M. & Z. Ghahramani. 2000. Computational principles of movement neuroscience. *Nat. Neurosci.* 3: 1212–1217.
- Wolpert, D.M., K. Doya & M. Kawato. 2003. A unifying computational framework for motor control and social interaction. *Philos. Trans. R. Soc. B Biol. Sci.* 358: 593–602.
- Vesper, C., E. Abramova, J. Bütepage, et al. 2017. Joint action: mental representations, shared information and general mechanisms for coordinating with others. Front. Psychol. 7: 2039.
- Keller, P.E., G. Novembre & M.J. Hove. 2014. Rhythm in joint action: psychological and neurophysiological mechanisms for real-time interpersonal coordination. *Philos. Trans. R. Soc. B Biol. Sci.* 369: 20130394.
- Ayrolles, A., F. Brun, P. Chen, et al. 2021. HyPyP: a hyperscanning Python Pipeline for inter-brain connectivity analysis. Soc. Cogn. Affect. Neurosci. 16: 72–83.
- Müller, V., D. Perdikis, M.A. Mende, et al. 2021. Interacting brains coming in sync through their minds: an interbrain neurofeedback study. Ann. N.Y. Acad. Sci. https://doi.org/10. 1111/nyas.14605.
- 42. Dumas, G., F. Lachat, J. Martinerie, *et al.* 2011. From social behaviour to brain synchronization: review and perspectives in hyperscanning. *IRBM* **32**: 48–53.
- Dumas, G., G.C. de Guzman, E. Tognoli, et al. 2014. The human dynamic clamp as a paradigm for social interaction. Proc. Natl. Acad. Sci. USA 111: E3726–3734.