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Interpersonal synchrony and network dynamics in social interaction

Edited by
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Interpersonal synchrony and network dynamics in social interaction

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Editorial: Interpersonal synchrony and network dynamics in social interaction

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Editorial on the Research Topic
Interpersonal synchrony and network dynamics in social interaction

This Research Topic was launched with the aim of highlighting and exploring the mechanisms and functions of interpersonal interaction, and thereby deepening our understanding of these highly interesting and complex phenomena and their downstream effects on real-life social interaction. The collection of contributions includes a Hypothesis and Theory article, a Review, two Brief Research Reports, and 11 Original Research articles written by leading researchers in the field. They showcase the breadth of research studies, going from hyper-brain cell assembly hypothesis and theory of mind hyperscanning to ensemble singing and soccer playing to healthcare teams, music therapy and psychotherapy concepts based on the inter-brain plasticity model. This range exemplifies the promise of this field in being able to span multiple facets of life. Figure 1 illustrates the diversity yet thematic relatedness of the contributions. It displays the joint forward model for interpersonal action coordination with three representation levels (i.e., representation of individual, other's, and joint forward models with corresponding sensorimotor feedbacks) and the impact of a joint goal as well as external influences (cf. Müller et al., 2021). This model is a construct integrating and reflecting a variety of influences and interactions of human social behavior. Figure 1 also highlights different interaction situations described in the Research Topic.

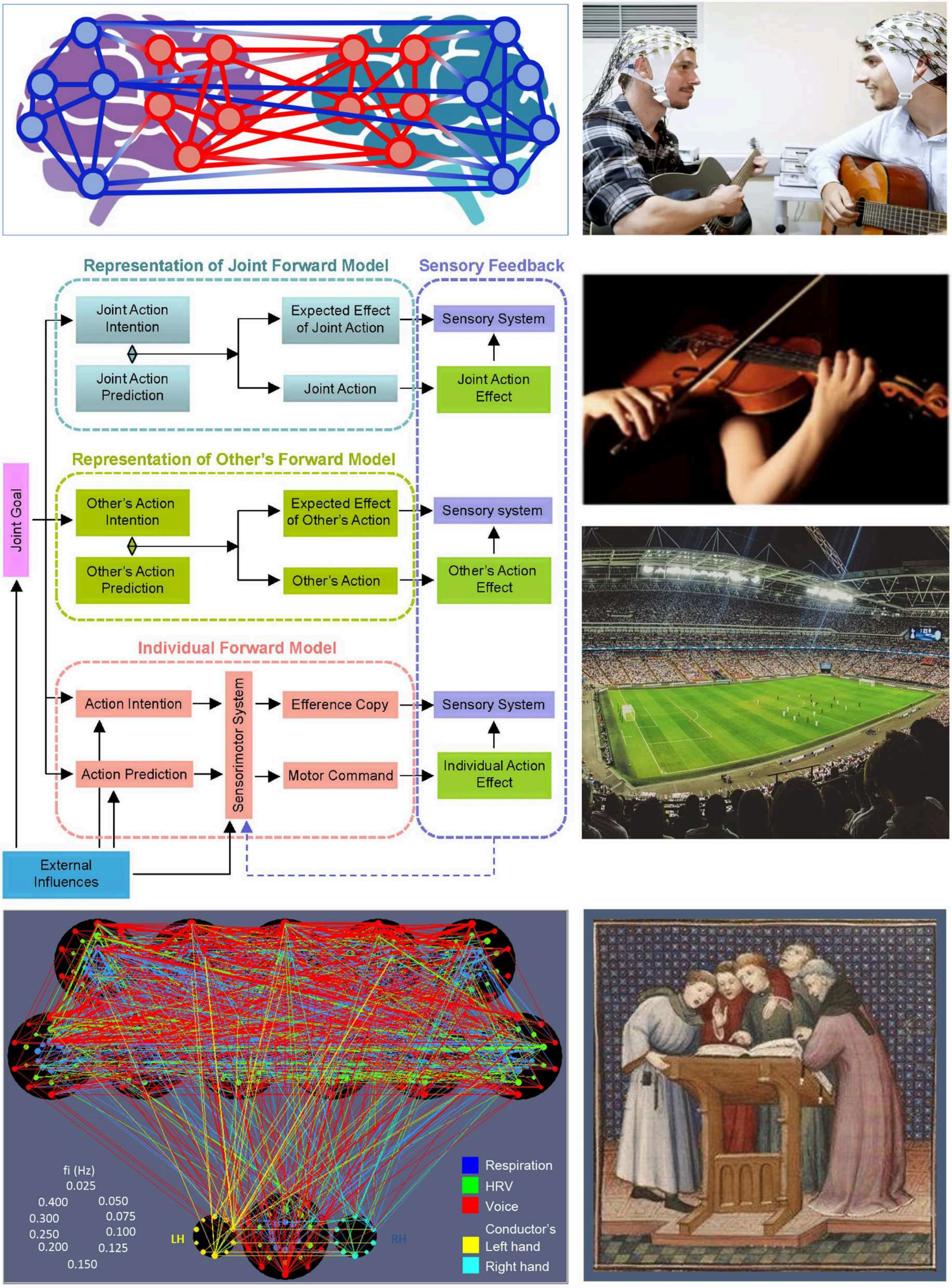

FIGURE 1

Joint forward model for interpersonal action coordination and various social interaction situations described in the Research Topic. The joint forward model for interpersonal action coordination with three representation levels (i.e., representation of individual, other's, and joint forward models with corresponding sensorimotor feedbacks) is represented in the middle left (adapted from Müller et al., 2021). This model reflects

(Continued)

FIGURE 1 (Continued)
a variety of the interactions described in the Research Topic. On the bottom left, a hyper-frequency connectivity structure of a choir singing a canon with different voices is displayed (adapted from Müller et al., 2018a). A hyper-brain network with intra- and inter-brain connectivity emerging during an interaction of two people is schematically represented on the top left. The structure represents two hyper-brain modules or communities (coded in blue and red) comprising nodes from two different brains, as described in Müller. On the right, different interaction situations described in the Research Topic are presented (adapted from Klein et al. and Lange et al.; cf. also Müller et al. for the soccer game; the guitarist duo on the top right, Copyright © Arne Sattler).

Neural synchrony and network dynamics in social interaction and communication behavior

A recently emerging view in social and cognitive neuroscience with regard to hyperscanning methods holds that interpersonal action coordination or communicative behavior require inter-brain synchronization and specific hyper-brain network activity (cf. Müller et al., 2021). This collection begins with a Hypothesis and Theory article by Müller proposing a *hyper-brain cell assembly* hypothesis, which states that cell assemblies can emerge not only within, but also between the interacting brains, following roughly the same rules as within brains. More precisely, the *hyper-brain cell assembly* encompasses and integrates oscillatory activity within and between brains, and represents a common hyper-brain unit that has a certain relation to social behavior and interaction. The suggested hyper-brain cell assembly assumes simultaneous firing of neural cells in two or more brains supported by intra- and inter-brain synchronization patterns and their continual adjustment to each other. Hyper-brain modules or communities, comprising nodes across several brains, are considered as possible representations of the hypothesized hyper-brain cell assemblies that can also have a multidimensional or multilayer structure and operate at different frequencies in their complex interplay. Müller concludes that the neuronal dynamics during interpersonal interaction and communication behavior is brain-wide, i.e., it is based on common neuronal activity of several brains or, more generally, of the coupled physiological and sensorimotor systems including brains.

Social interaction in general, and communication in particular, are dynamic processes with constant updating and adaptation of interaction/communication information and behavioral strategies, where the interacting agents are dynamically coupled rather than simply aligned (Hasson and Frith, 2016; Tognoli et al., 2020; Dumas and Fairhurst, 2021; Müller et al., 2021). As shown in a number of hyperscanning studies, such dynamic interaction is supported by brain-to-brain coupling and network dynamics (Müller et al., 2018b; Müller and Lindenberger, 2019, 2022). In a fNIRS hyperscanning study, Wang et al. used sliding window approach and k-mean clustering to investigate the temporal occurrence of the inter-brain states and network dynamics during two different group communication tasks (creative vs. non-creative). The authors found that states that occurred less frequently than others had higher network global efficiency and a shorter characteristic path length. These were termed efficient interbrain states, compared to inefficient ones, which in turn occurred very frequently. At the same time, the occurrence of efficient interbrain states and state transitions during creative communication was significantly more frequent than during non-creative communication, indicating a more active and integrated neural network during a creative task. Moreover, efficient interbrain states correlated positively with collaborative behavior and group performance. The authors conclude that there is a close correspondence between inter-brain network states and cooperative social behavior, both of which are more flexible during creative than non-creative communication.

Theory of Mind (ToM) is a construct in cognitive and developmental psychology introduced by Premack and Woodruff (1978) that indicates the ability of an individual to represent other people's mental states and drives the capacity for social interaction. ToM is not a singular skill and relies on multiple subprocesses, including, but not limited to, distinguishing self from other. Mossad et al. used fMRI (functional magnetic resonance imaging) and MEG (magnetoencephalography) neuroimaging techniques to explore the neural mechanisms of ToM abilities. In the study, where the participants had to describe videos containing three moving shapes designed to depict either social interactions or random motion (control condition), they observed increased fMRI activation in frontal-parietal regions in the social compared to the control condition, and the recruitment of ToM networks in the social condition in theta, beta, and gamma bands of MEG signals. More precisely, the right supramarginal, and angular gyri (right temporal parietal junction), right inferior parietal lobe, and right temporal pole were recruited in the first 5 s of the MEG experiment. Brain regions such as the superior frontal gyrus and the bilateral amygdalae were recruited in the second time window (5–10 s). While the earlier processes or networks were detectable in all three frequency bands, the later ones only occurred during the oscillatory activity in the beta band. Combining the strengths of the spatial resolution of fMRI and temporal resolution of MEG allowed the authors to delineate the mechanism by which ToM processing unfolds over time in a frequency-specific manner.

The ability to perceive, notice and pay attention to one's internal body state, including visceral feelings, has been defined as Interoceptive Attentiveness (IA), which represents one of the dimensions of interoception (Schulz, 2016). In a functional near-infrared spectroscopy (fNIRS) hyperscanning study, Angioletti and Balconi explored the effect of explicit IA manipulation on hemodynamic brain responses during a motor synchronization task involving interpersonal coordination framed with a social goal. An increased oxygenated hemoglobin fNIRS response in the prefrontal cortex (PFC) was found when inducing an explicit focus (IA) on the breath during the socially framed motor task requiring synchronization. Overall, the authors showed that hemodynamic activity is significantly enhanced in brain regions that support sustained attention, reorientation of attention, and social responsiveness when a joint task is performed and participants focus on their physiological body reactions.

Group cohesion can also be influenced by emotions shared in a group of people, indicating that cohesion is a multi-faceted process comprising different components or relations (Casey-Campbell and Martens, 2009). Chabin et al. investigated interbrain coupling in a group of people attending a concert and focus on the emotional dynamics of the group as a whole. The authors identified specific moments in the concert that evoked strong or weak emotions, as well as strong or weak group emotional cohesion. They found that synchrony between listeners' brains in the theta frequency band is mainly associated with the experience of high music pleasure and that emotional cohesion in the group can enhance interbrain synchrony. However, the emotional cohesion of the group is not solely responsible for inter-brain synchrony in this context. Sharing a high level of pleasure related to music presumably elicits similar brain activity in several group members, thus enhancing interbrain synchrony in the group.

Sensorimotor synchronization and intrapersonal coordination in music ensembles and other groups

Team sport implies teamwork with a precise interpersonal coordination in a common timeframe. Such a teamwork or social group interaction can best be described in terms of dynamical system theory or generalized synchronization (Rulkov et al., 1995). On the one hand, dynamical systems are unpredictable, since their trajectories are extremely sensitive to their initial states. On the other hand, they may synchronize to a common chaotic trajectory if they are coupled to each other (Pikovsky et al., 2003; Kinzel et al., 2010). The generalized synchronization concept assumes that the behavior of several interacting individuals or subsystems can be strikingly different, but each one acts in function of the others. Müller et al. used this concept to investigate the influence of rhythmic auditory stimulation (RAS) on soccer performance. The authors provide quantitative evidence that the connectivity between teammates, expressed by fast and precise pass sequences with a minimal number of ball contacts for each player, and the scoring rate of male soccer teams improve significantly when playing under the influence of collective RAS. They conclude that results can be explained in terms of the dynamical system theory, non-linear resonances, and dynamic attention theory.

Synchronization in a team or group was also explored in a multi-person adaptive metronome study by Fink et al. using a specific assistive device (adaptive metronome) in five different experiments. The authors found that in all experiments, tapper synchronization with the metronome was significantly enhanced with 25–50% metronome adaptivity (percent correction based on the immediately preceding tap-metronome asynchrony), compared to no adaptation (Fairhurst et al., 2013). Furthermore, synchronization with the metronome reached 70–100% adaptivity in group experiments with auditory feedback. It was also shown that individuals who tapped less variably than the group felt more in the groove, a unified rhythmic effect or feeling that compels one to move and that is generally regarded as pleasurable (Janata et al., 2012). Moreover, subjective ratings of being in the groove, in synchrony with the metronome, in synchrony with others, liking the task, and task difficulty loaded onto one latent factor, which was termed enjoyment. Prediction of enjoyment required an interaction between auditory feedback and metronome adaptivity, with increased enjoyment at optimal levels of adaptivity (with auditory feedback only) and a marked decrease in enjoyment at higher levels of adaptivity, especially without feedback. The authors conclude that the adaptive metronome system holds promise for helping groups of people to achieve better motor and psychological alignment or synchrony in a variety of contexts.

There is neurophysiological evidence that constraints operating at both individual and joint scales have reciprocal effects: intrapersonal constraints affect processes of both intrapersonal and interpersonal coordination, and likewise interpersonal constraints (Ramenzoni et al., 2011; Miyata et al., 2017). This is in line with the joint forward model for interpersonal action coordination (cf. Figure 1), functional system theory, as well as the notion of circular causation of self-organized systems (Müller et al., 2021). Laroche et al. perturbed interpersonal sensorimotor communication in violin players of an orchestra and examined how this affected the musicians' intrapersonal movement coordination by using the motion capture of head and bow kinematics. The authors found that altering the usual interpersonal coupling scheme increased intrapersonal coordination and that the perturbation induced smaller yet more complex head movements. Moreover, the perturbation differentially increased intrapersonal coordination across different timescales. In general, the present study illustrates the sensitivity of intrapersonal body coordination to interpersonal coupling constraints in the complex and ecological context of a music ensemble.

In line with the aforementioned joint forward model (see Figure 1 for details), besides intra- and inter-personal sensory-motor coordination, action prediction for self and other play an essential role in social interaction, in general, and in the ensemble performance of music, in particular (Keller et al., 2014; Müller et al., 2021). Klein et al. asked professional violinists to play along with recordings of two folk pieces and investigated the information flow in the sounds. They used Granger causality to measure information flow and cross-correlation to measure synchronization between their performances and the recording sounds. The authors found that information flow from the recording to the musicians was much greater than vice versa, indicating that musicians can learn to predict how another musician will play next on the basis of the sounds they have just produced. In addition, they found that this information flow decreased as the violinists became more familiar with the recordings over trials. This was also accompanied by increased synchronization between the violinists over trials. The authors conclude that investigating information flow between the sound outcomes of live performing musicians could be a useful tool in more diverse and ecologically valid performance contexts.

Musical ensemble performances provide an ideal environment and a perfect model to study and gain insights into complex human group interactions (D'Ausilio et al., 2015). Synchronization patterns and emerging network structures can reflect specific roles of individual performers and a higher level of organization of all performers as a superordinate system or superorganism with a robust interplay between network topology and function (Bashan et al., 2012; Müller et al., 2021). Lange et al. investigated group dynamics of choral singing with and without physical contact (i.e., touching each other's shoulder or waist), using hyperscanning of respiratory and cardiac responses from eight professional singers. The idea of singing with touch was motivated by historical depictions of ensembles originating from the 14th to 17th centuries (cf. Figure 1). In line with previous studies (Müller and Lindenberger, 2011; Müller et al., 2018a, 2019), the authors found a significant increase in synchronization of respiratory and cardiac outcomes during singing as compared to rest (baseline). Most importantly, this synchronization in respiration across singers was stronger among different frequencies when singing with touch, with the effect of touch being stronger when all singers were singing in comparison to the partial ensemble. The findings suggest a higher level of organization of singers in the choir functioning as a superordinate system or superorganism when singers share the same goal.

Tomashin et al. used multidimensional recurrence quantification analysis on cardiac Interbeat Intervals (IBIs) to assess dyadic and group-level interactions during a drumming and a decision-making task, and compared these with the resting state baseline. The authors found that IBIs synchrony between group members was significantly higher than during baseline and also significantly higher in actual than in pseudo-groups (false-pair surrogates). Interestingly, synchrony during baseline was not significantly higher than in false-pair surrogates. Most importantly, the change in IBI synchrony from baseline to group interaction predicted a psychological sense of group cohesion measured by using cohesion questionnaire. This result was evident at both the individual and the group levels and was independent of the interaction task. However, it should be noted that the positive cohesion effect was found only for change from baseline to group interaction, whereas no significant results for cohesion were found for the groups' synchrony during the task and the effect of baseline synchrony on cohesion was significantly negative. Thus, cohesion is considered as an emergent or dynamic state that is socially modulated by group experiences or relationships and represents a multilayered construct with intertwined coupling dynamics (Marks et al., 2001; Konvalinka et al., 2011).

As mentioned above, there is neurophysiological evidence that positive emotions or pleasure may facilitate neural or physiological synchrony within a group of people (Konvalinka et al., 2011; Chabin et al., 2022). Smykovskyi et al. investigated group interaction in triads of people engaged in a movement improvisation task and explored the effect of emotional feedback on behavioral, psychological, and physiological levels. The participants were instructed to create complex, varied, and interesting movements with their right hand to express themselves. The authors showed that positive and negative emotions differently alter spontaneous human synchronous behavior (movement synchrony). On the psychological level, a significant effect of emotion was obtained on pleasure but not on arousal scores. On the physiological level, no significant effects of emotions on the cardiac activity of the triad were found. This result partially contradicts the previous findings (e.g., Konvalinka et al., 2011) and therefore, further research is required for clarification.

Psychotherapy, music therapy, and neurodynamics of healthcare teams

As mentioned above, synchronization within and between brains appears to be crucial for interpersonal action coordination and is an important element of neural communication systems during an interaction (Müller et al., 2021; Shamay-Tsoory, 2021). Such synchronization is important not only in daily life, but also in therapy, as it gives the patient and the therapist access to each other's inner states and facilitates mutual understanding and emotional exchange (Koole and Tschacher, 2016). In their review paper, Sened et al. propose that therapy improves patients' ability to achieve such synchrony through inter-brain plasticity, i.e., recurrent activation of specific brain regions in the patient and therapist in close succession (compare the "hyper-brain cell assembly hypothesis" suggested by Müller). This can lead to a long-term improvement in the ability to synchronize and to generalize to other interpersonal relationships and other situations, ultimately leading to a reduction in symptoms. This review suggests that the inter-brain plasticity model offers a novel biological framework for understanding relational change in psychotherapy, and the enhanced capacity for synchronization and generalization underlies some of the beneficial effects of psychotherapy.

Music therapy is tied to the process of creating and experiencing music together through improvisation, listening, and reflection (Fachner, 2014). Despite the diversity of techniques and models in music therapy, they all have one thing in common in that music and the relationships developed within it are the foundation for change (Millard and Carr, 2021). Yap et al. investigated non-verbal synchrony or coordination of body movement between patient and therapist using Motion Energy Analysis (MEA) from a video source and subsequent calculation of cross-correlation between the MEA time series. This analysis revealed an increase in motion synchrony and patient leading after the music intervention, possibly due to greater familiarity between therapist and patient, as they had already spent some time together in a music therapy session, as well as improved self-regulation, thus empowering the patient. This presents a novel method for investigating non-verbal synchrony in music therapy in neuro-rehabilitation.

Healthcare team members jointly regulate their activities and operate at the collective behavioral level while coordinating their actions and interacting dynamically, interdependently, and adaptively toward common goals. Stevens and Galloway investigated the differential neurodynamics of seven two-person healthcare teams across time and brain regions during autonomous (taskwork) and collaborative (teamwork) segments of simulation training. The authors used a neurodynamic information (NI) EEG measure, describing the pauses and hesitations associated with individual uncertainty, and interbrain coherence (IBC), which is an inevitable component of social interactions. No correlation was found between NI and IBC measures, and second-by-second dynamic comparison indicated mutual exclusivity. The authors observe that the sustained expression of NI and IBC did not occur simultaneously, suggesting that team members may find it difficult to maintain synchrony between brains while reducing their individual uncertainties.

With noteworthy diversity of topics and research questions explored, the studies in this Research Topic emphasize the important mechanisms and functions of interpersonal action coordination and social interaction. They confirm that the neuronal dynamics during interpersonal interaction is brain- or system-wide, i.e., it is based on common neuronal activity synchronized across brains or, more generally, on coupled physiological and sensorimotor systems including brains. These results highlight future avenues for applications in basic research and therapeutic areas, and specify the role of hyperscanning research in the growing field of social neuroscience.

Author contributions

All authors contributed to the writing of this editorial and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Neural Synchrony and Network Dynamics in Social Interaction: A Hyper-Brain Cell Assembly Hypothesis

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Mounting neurophysiological evidence suggests that interpersonal interaction relies on continual communication between cell assemblies within interacting brains and continual adjustments of these neuronal dynamic states between the brains. In this Hypothesis and Theory article, a *Hyper-Brain Cell Assembly Hypothesis* is suggested on the basis of a conceptual review of neural synchrony and network dynamics and their roles in emerging cell assemblies within the interacting brains. The proposed hypothesis states that such cell assemblies can emerge not only within, but also between the interacting brains. More precisely, the *hyper-brain cell assembly* encompasses and integrates oscillatory activity within and between brains, and represents a common hyper-brain unit, which has a certain relation to social behavior and interaction. Hyper-brain modules or communities, comprising nodes across two or several brains, are considered as one of the possible representations of the hypothesized *hyper-brain cell assemblies*, which can also have a multidimensional or multilayer structure. It is concluded that the neuronal dynamics during interpersonal interaction is brain-wide, i.e., it is based on common neuronal activity of several brains or, more generally, of the coupled physiological systems including brains.

Keywords: neural synchrony, hyper-brain network dynamics, within- and cross-frequency coupling, multiplex and multilayer networks, graph-theoretic approach, social interaction

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INTRODUCTION

As noted by György Buzsáki (2006, p. 5), "Nature is both periodic and perpetual. One of the most basic laws of the universe is the law of periodicity. This law governs all manifestations of living and nonliving. In its broadest definition, periodicity refers to the quality, state, or fact of being regularly recurrent: a repeating pattern or structure in time or space. What goes up must come down. The sun rises and sets, and the days wax and wane. Without periodicity, there is no time; without time, there is no past, present, or future. In living systems, the periodicity of individual lives gives rise to the continuity of life on Earth. Our existence has meaning only when experienced in time." The most common expression of periodicity is an oscillation. As indicated in several studies, most biological, and also social systems, are oscillatory in nature (Stankovski et al., 2015; Cao et al., 2016; Wilson and Cook, 2016; Müller et al., 2018a). Oscillations form a basis for communication between different components or subsystems at different organizational levels and between them. In line with synergetics and a system dynamics approach, complex natural phenomena can best be described by the interaction of several subsystems (Forrester, 1968; Haken's, 1983; Haken, 1984). When viewed in isolation, each of these subsystems has its own (often relatively simple) dynamics; however, the complex behavior of the entire system is due to corresponding coupling mechanisms within and between these subsystems that can be considered as a superordinate system imposing boundary conditions on its constituents (Buzsáki, 2006; Haken, 2006, 2016; Noble, 2012; Haken and Portugali, 2016, 2021; Müller et al., 2018a, 2019a, 2021a). As noted by Arkady Pikovsky and colleagues (Pikovsky et al., 2003, pp. xvii–xviii), "Our surroundings are full of oscillating objects. Radio communication and electrical equipment, violins in an orchestra, fireflies emitting sequences of light pulses, crickets producing chirps, birds flapping their wings, chemical systems exhibiting oscillatory variation of the concentration of reagents, a neural center that controls the contraction of the human heart and the heart itself, a center of pathological activity that causes involuntary shaking of limbs as a consequence of Parkinson's disease—all these and many other systems have a common feature: they produce rhythms. Usually, these objects are not isolated from their environment, but interact with other objects, in other words, they are open systems." As the authors then concluded: "**This adjustment of rhythms due to an interaction is the essence of synchronization**. . ." (Pikovsky et al., 2003, p. xviii).

Such relations between things or systems are also crucial for our social life. In everyday life, people often have to coordinate their actions with each other in time and space. Such interpersonal interaction is also essential for the development of congruent goals, which are generally decisive for social behavior, although not always necessary for the mutual alignment of minds and bodies (Gallotti and Frith, 2013; Gallotti et al., 2017; Müller et al., 2021a). As proposed by Hasson and Frith (2016, p. 2), ". . .interactions with other members of a group can fundamentally shape the way we behave in the world, and alignment is a ubiquitous feature of such interactions." Such an alignment presupposes different types of synchronization and/or temporal (and also spatial) coordination.

In biological studies of collective behavior, interactions among individual insects, and between them and their environment, result in swarm behavior that is often considered a "superorganism" (Trianni et al., 2011). The concept of superorganism was proposed by the American entomologist William Morton Wheeler (1911) in his seminal work "The ant-colony as an organism" (cf. Hoffecker, 2013). The ability to function as a whole and to take collective decisions is also a representative feature of other organisms or societies (e.g., fish schools, bird flocks, packs or herds of mammals) as well as human group behavior (Detrain and Deneubourg, 2006; Gelblum et al., 2015; Müller et al., 2021a). Such societies are self-organizing and auto-regulating systems. Self-organization is defined as a process where a spontaneous order or a spatiotemporal pattern arises from local interactions between parts of an initially disordered system, mostly triggered by random fluctuations and amplified by positive feedback. The self-organizing pattern of order is an emergent property of the system that arises unexpectedly from interactions among the system's components (Haken's, 1983; Haken, 1984, 2006; Haken and Portugali, 2016, 2021). As noted by Ilya Prigogine and colleagues, self-organization typically takes place in non-linear systems, which are far from their thermodynamic equilibrium state (Nicolis and Prigogine, 1977; Prigogine and Stengers, 1984). Ross Ashby (1952) also suggested that a dynamical system (far from an equilibrium state) always tends to evolve towards a stable equilibrium state or towards an attractor in a phase space.

The present article aims at providing a conceptual review of neural synchrony and network dynamics in social interaction. First, I will review synchronization phenomena in general and how they emerge in social interaction and interpersonal action coordination in particular. Second, different types of neural coding (e.g., rate and temporal codes) and their roles in emerging cell assemblies will be discussed in relation to brain oscillations and underlying coupling dynamics. Third, after considering the intra- and inter-brain synchronization processes with a reference to hyper-brain activity, a *Hyper-Brain Cell Assembly Hypothesis* will be postulated or suggested. Fourth, neural and hyper-brain network dynamics will be considered in terms of cross-frequency coupling and multiplex or multilayer networks. Hyper-brain modules or communities will be considered as one of the possible representations of hypothesized *hyper-brain cell assemblies*, which can also have a multilayer or multidimensional structure. Fifth, network physiology and neural network dynamics will be inspected in their unified interplay. Investigating the hyper-brain networks in their close connections with physiological systems and subsystems is crucial for understanding the mechanisms of social interaction and interpersonal action coordination. Finally, ways of proving the hyper-brain cell assembly hypothesis will be provided and discussed.

SYNCHRONIZATION PHENOMENA AND THEIR ROLE IN SOCIAL INTERACTION

The German biologist and physiologist Erich von Holst arguably made the most important contribution to the topic of synchronization and coordination. His fundamental work established the concepts of absolute and relative coordination drawing on the example of motion sequences in animals (von Holst, 1936a,b, 1938a,b, 1939a,b). The generic term of fixed or *absolute coordination* denotes all movement types in which the frequency and amplitude of a movement remain constant and the individual limbs or segments maintain a certain phase relationship characteristic of the form of coordination in question. Its counterpart, sliding or *relative coordination*, is fundamentally different from absolute coordination, as the characteristics of constancy of frequency, amplitude, and/or phase relations do not apply. In relative coordination, the different moving parts (at least some of them) have a different working cycle and correspondingly changing mutual phase relations; in addition, one or the other rhythm usually shows a more or less distinct periodic change of amplitude and frequency. Formally this largely corresponds to the periodic forms of harmonic or quasi-harmonic oscillations (cf. von Holst, 1939a,b). The so-called "magnet effect" was considered to be the central mechanism of relative coordination (von Holst, 1936b). It states that two (or more) rhythms can influence each other in different ways. These interactions can show different behavior that mostly depends on the strength of one or the other rhythm. If, for example, the effect is only transferred from one rhythm to the other, the one exerting the effect while remaining uninfluenced itself is described as attracting and the other as attracted. If the effect is very strong, it can ultimately lead to absolute coordination, with the attracted rhythm completely taking over the oscillation frequency of the attracting rhythm. If both rhythms influence each other, one speaks of a mutual attraction. Normally, a mutual attraction slows down the faster rhythm and accelerates the slower one (von Holst, 1936b, 1938a,b, 1939a,b). As Erich von Holst has shown, the frequency relationships are not "rigid" and change continually. A comparably simple model for frequency adaptation of populations of coupled oscillators was proposed by Ott and Antonsen (2017). Despite the fact that von Holst's main ideas about absolute and relative synchronization were derived from the motion sequences in animals, they are highly transferable to neuronal and other (e.g., social) processes.

A further interesting point about oscillatory synchrony was made by György Buzsáki (2006): "The paramount advantage of synchronization by oscillation is its cost-effectiveness. No other known mechanism in the physical world can bring about synchrony with so little investment. What do I mean by declaring that synchrony by oscillation is cheap? Let me illustrate the cost issue first with a few familiar examples from our everyday life. You have probably watched leisurely strolling romantic couples on a fine evening in a park or on the beach. Couples holding hands walk in perfect unison, whereas couples without such physical links walk out of step" (Buzsáki, 2006, p. 168). Cost-effectiveness is probably the most important factor that made oscillatory synchrony ubiquitous. As suggested by Karl Friston and colleagues, oscillatory synchrony is an emergent property of free energy minimization (Friston, 2010; Friston and Frith, 2015; Palacios et al., 2019). A further familiar example from our everyday life is synchronized clapping or applause, which provides a striking example of social self-organization (Néda et al., 2000a,b). Néda et al. (2000a) describe it as follows: "Our measurements offer an insight into the mechanism of synchronized clapping: during fast clapping, synchronization is not possible owing to the large dispersion in the clapping frequencies. After period doubling, as mode II clapping with small dispersion appears, synchronization can be and is achieved. However, as the audience gradually decreases the period to enhance the average noise intensity, it slips back to the fast clapping mode with larger dispersion, destroying synchronization" (Néda et al., 2000a, p. 849). Thus, the two main desires and intentions of the spectators (i.e., optimal synchronization and maximal applause intensity) cannot both be fulfilled at the same time (Néda et al., 2000b). It is obvious that synchronized clapping saves us costs while applause intensity is more costly. In accordance with the free-energy principle, any self-organizing system that is at equilibrium with its environment must minimize its free energy (Friston et al., 2006; Friston, 2010; Bruineberg et al., 2018; Palacios et al., 2019). Moreover, this switching between maximal applause intensity and optimal synchronization is also a good example of phase transition and the emergence of order from chaos or enhanced fluctuations (cf. Prigogine and Stengers, 1984; Haken, 2006; Haken and Portugali, 2016, 2021). It also shows the way self-organization may occur.

Another interesting aspect of the applause scenario is that synchronous clapping is also rhythmic. For a short moment, there is competition among the different individual rhythms, but very quickly people "agree" on a certain rhythm that is compatible with their state and corresponds to the specific situation (Kriz, 2001). In everyday life, rhythm plays an important, often even a central role, not only for applause or such rhythmic behavior as music, speech, or dancing (Brown, 2018; Kotz et al., 2018; Savage et al., 2021), but also in architecture, poetry, cinema, theater, arts, and many other domains of human life (Chan, 2012; Cureton, 2015; Thapa, 2017; Mohamed, 2018). Rhythm is omnipresent and represents a basic anthropological principle that determines the bodily-sensory experience of space and time and is considered a fundamental *organizing principle* of social interaction (Iberall and McCulloch, 1968, 1969; Warner et al., 1987; Warner, 1988).

NEURAL CODING, CELL ASSEMBLIES, BRAIN OSCILLATIONS, AND COUPLING DYNAMICS

Neural Coding and Oscillatory Activity

From the neural point of view, oscillations reflect rhythmic synchronous firing of neuronal elements or cells. Adrian (1926a,b), Adrian and Zotterman (1926a,b), and Adrian and Bronk (1928, 1929) showed that the intensity or salience of a stimulus is often coded as the rate of nerve action potentials over time. This is commonly referred to as the "rate code" (Gerstner et al., 1997; Mehta et al., 2002; Panzeri et al., 2015; Li and Tsien, 2017). An alternative coding concept, known as "temporal coding," considers the exact timing of neural spikes and is also relevant for the coding of sensory and motor events (Gerstner et al., 1997; Mehta et al., 2002; Li and Tsien, 2017). Temporal coding becomes more robust with experience and drives synaptic plasticity in cortical networks (Mehta et al., 2002; Hestrin and Galarreta, 2005). It has been shown that the rate and temporal codes can be highly correlated (Mehta et al., 2002) or also independently adjustable (Singer, 1999). As suggested by Singer (1999, p. 56), "…fast synchronization codes and more sustained rate codes could ultimately coexist and perhaps even optimally complement one another." Thus, internal or external information is encoded by not only modulating the firing rate of individual neurons but also by temporally synchronized spiking across different neurons. They mostly participate in synchronously oscillating assemblies and give rise to the robust real-time population or cell-assembly code (Singer, 1999; Li and Tsien, 2017). A candidate mechanism for representation of neural coding at the macroscopic level is oscillatory brain activity such as hippocampal theta or gamma oscillations (Buzsáki and Draguhn, 2004; Siapas et al., 2005) or cortical and thalamocortical alpha oscillatory activity (Buzsáki, 2006; Klimesch, 2012; Becker et al., 2015).

The basic characteristics of an oscillation are its amplitude, phase, and frequency, changing across time. These changes are a result of different neural coding strategies that complement each other. If the amplitude of the signal is coded by the firing rate or "rate code," its temporal structure or phase is instead reflected by the "temporal code". The frequency of an oscillation is an indicator of change or rate of change, i.e., it shows how many cycles per second occur. Important characteristics of neural coding mechanisms are synchronization, in general, and phase synchronization among temporally linked processes, in particular (Llinás et al., 2005).

The electroencephalogram (EEG) offers a rich source of information about neural coding dynamics (Nunez's, 1995; Nunez, 2000). Neuronal oscillations in mammalian cortical networks can be observed across a wide frequency range from approximately 0.05 to 500 Hz and have been regarded as a key mechanism in neural communication and cognitive brain function (Buzsáki and Draguhn, 2004; Buzsáki, 2006). Enhanced oscillatory activity in the delta frequency range (0.05–3.5 Hz) during cognitive tasks is often considered an indicator of attentional task demands (Harmony et al., 1996, 2001; McEvoy et al., 2001). In contrast, in the absence of cognitive tasks, delta oscillations have been associated with slow-wave sleep and anesthesia (Blake and Gerard, 1937; Chauvette et al., 2011; Nir et al., 2011; Hagihira, 2015). In addition, phase-amplitude coupling between delta and high-frequency oscillations was observed during sub-anesthetic and general anesthetic sevoflurane treated brain states; thus, delta brain oscillations may modulate high-frequency brain activity in respective manners (Chamadia et al., 2019). Furthermore, coherent large-scale delta oscillations play a crucial role during decision-making (Nácher et al., 2013). Theta oscillations (4–7 Hz) are particularly prominent, with possible functional roles covering a wide range of behavior from arousal, attention, and memory to the orienting reflex, conditioning, and learning, including different binding and information processing mechanisms as well as large-scale integrative processes (Buzsáki, 2005, 2006; Müller et al., 2009). In contrast to delta and theta frequencies, alpha (8–13 Hz) and partly also beta (14–28 Hz) rhythms tend to respond to a stimulus and/or task demands either with a decrease or increase in amplitude/power, termed event-related desynchronization and synchronization, respectively (Klimesch, 2012). These rhythms decrease or desynchronize, for example, in response to the perceptual decision and memory tasks (Pfurtscheller and Lopes da Silva, 1999). At the same time, brain regions associated with task-irrelevant and potentially interfering processes exhibit event-related synchronization, especially in the alpha band, emphasizing the inhibitory function of alpha oscillations (Pfurtscheller and Lopes da Silva, 1999; Klimesch, 2012). However, it has also been suggested that local and inter-areal alpha phase synchronization may play a role in active task-relevant neuronal processing and support attentional, executive, contextual functions, and consciousness (Palva and Palva, 2007, 2011). Moreover, alpha oscillations can be synchronized in terms of cross-frequency coupling with theta, beta, and gamma oscillations in response to cognitive demand, attention, and sensory awareness (Palva et al., 2005; Schack et al., 2005; Palva and Palva, 2007). Gamma band oscillations (>30 Hz) have been demonstrated to play an important role in perception, perceptual binding phenomena, memory, and synaptic plasticity (Tallon-Baudry and Bertrand, 1999; Singer, 2001; Fries et al., 2007; Van Vugt et al., 2010; Zarnadze et al., 2016; Bocchio et al., 2017; von Lautz et al., 2017; Galuske et al., 2019). In cortical networks, a dynamic balance between excitation and inhibition leads to a series of network oscillations involving neuronal populations of different sizes (Buzsáki, 2007). In general, network oscillations may functionally bias stimulus selection, support transient bindings of neuronal assemblies, and facilitate synaptic plasticity (Bibbig et al., 2001; Fries et al., 2007; Zarnadze et al., 2016; Bocchio et al., 2017; Galuske et al., 2019).

Varela et al. (2001) distinguished between local synchrony (on a spatial scale of less than 1 cm and conduction delay of 4–6 ms) and global or large-scale synchrony (on a spatial scale of more than 1 cm and conduction delay of 8–10 ms) providing neural integration on different organization levels. In agreement with Nunez's (1995) dynamic theory, it will be distinguished between local processes (with a dominance of functional segregation) and global ones (with a dominance of functional integration) that are in steady interaction (Nunez's, 1995; Nunez, 2000). In line with the dynamic core hypothesis proposed by Tononi and Edelman (1998, p. 1848), "...the distributed neural process underlying conscious experience must be functionally integrated and at the same time highly differentiated." Neural processes with high functional segregation and integration reveal high neural complexity (in terms of the mutual information between subsets of the system's units). However, complexity can also be low when the components of a system are either completely independent (segregated) or completely dependent (integrated). It has been shown that certain structural characteristics of the brain, such as a high density of connections, strong local connectivity, patchiness in the connectivity among neuronal groups, and a large number of reentrant circuits, are associated with high neural complexity and conscious experiences (Tononi et al., 1994; Tononi and Edelman, 1998). Buzsáki (2007) also suggested that the local-global relations of the cerebral cortex and the ongoing, self-organized complex dynamics are necessary ingredients for subjective experiences. He argued that understanding and distinguishing between normal and dysfunctional processes in the cerebral cortex can be enabled by linking local and global patterns of activity on behaviorally relevant time scales. In line with Haken's (1983) principles of synergetics, "...emergence through self-organization has two directions. The upward direction is the local-to-global causation, through which novel dynamics emerge. The downward direction is a global-to-local determination, whereby a global order parameter "enslaves" the constituents and effectively governs local interactions. There is no supervisor or agent that causes order; the system is self-organized. The spooky thing here, of course, is that while the parts do cause the behavior of the whole, the behavior of the whole also constrains the behavior of its parts according to a majority rule; it is a case of circular causation. Crucially, the cause is not one or the other but is embedded in the configuration of relations" (Buzsáki, 2006, p. 14; see also Haken's, 1983; Haken, 2006).

The Neural Cell Assembly Approach

Self-organization is also an important element in the cell assembly approach or Hebbian learning (Hebb, 1949). In the early 1920s, Karl Lashley began his historical work on memory traces (engrams) in the cerebral cortex. He showed that distribution of active and inactive synapses provided evidence for learning or memory processes (Lashley, 1924, 1931). Lashley's student, Donald Hebb, developed his so-called theory of cell assemblies, which he published in 1949 in his well-known book, *The Organization of Behavior*. He postulated: "*When an axon of cell* A *is near enough to excite a cell* B *and repeatedly or persistently takes part in firing it, some growth process or metabolic change takes place in one or both cells such that* A*'s efficiency, as one of the cells firing* B*, is increased*" (Hebb, 1949, p. 62). Hebb (1949) used the concept of "reverberating circuits" or "closed self-reexciting chains", proposed by Lorente de Nó (1933, 1938) to describe a mechanism for maintaining activity in the cortex after the initial stimulus has ceased. This led him to the concept of the *cell assembly*, a complex reverberating circuit that can be created during an experience/behavior by certain changes in the synapses. Once activated, such a circuit can maintain excitation in the neural system, whereby each neuron in the cell assembly receives excitation from and transmits it to other neurons of the same assembly. When most of the neuronal elements in such a cell assembly become active, the whole cell assembly fires, i.e., the cell assembly represents an entity (according to the Hebbian rule: "what fires together, wires together"). The formation and development of cell assemblies are closely related to plastic ("Hebbian") excitatory cell systems with a rapid activation time constant. The velocity component is very important because the cell assemblies must have the property to ignite explosively as a whole. As mentioned above, a dynamic balance between excitation and inhibition is important to ensure that information from excitatory cells controlled by inhibitory interneurons flows to just the right place at just the right time (Buzsáki, 2007). Thus, a cell assembly forms a functional unit within the entire neuronal network and can provide a neural representation of objects, concepts, thoughts, and various behavioral patterns (cf. Birbaumer et al., 1995; Müller et al., 2011). As figuratively expressed by Pulvermüller et al. (2014, p. 575) "…cell assemblies may be the neurobiological vehicles of perception, action, attention, memory, decision, concepts, language and thought…". Moreover, as stated by Buzsáki: "…flexible cooperation among local and distant cell assemblies is believed to underlie nearly all cognitive behaviors" (Buzsáki, 2006, p. 48). Buzsáki also discussed the importance of neuronal synchronization in the formation of functional cell assemblies and concluded that "synchronization by oscillation is the simplest and most economic mechanism to bring together discharging neurons in time so that they can exert a maximal impact on their targets" (Buzsáki, 2006, p. 137). Cell assemblies active within an oscillation cycle can represent an integrated entity (e.g., a neural "letter") and the chaining of such assemblies (Hebb's "phase sequences") would provide the basis for complex cognitive processes (e.g., neural "words"). Hence, there is an intrinsic relation between oscillatory activity, neural cell assemblies, and behavioral or cognitive entities (Buzsáki, 2006, 2010). As suggested by Varela et al. (2001, p. 229), "… the emergence of a specific neuronal assembly is thought to underlie the operation of every cognitive act."

INTRA- AND INTER-BRAIN SYNCHRONIZATION AND THE HYPER-BRAIN CELL ASSEMBLY HYPOTHESIS

Intra- and Inter-Brain Synchronization as a Hyper-Brain Activity

A recently emerging view in cognitive neuroscience with regard to hyperscanning methods holds that interpersonal action coordination or social interaction (e.g., playing music in duets or groups, dancing, acrobatics, competitive sports, movement imitation, etc.) requires strong inter-brain synchronization (synchronized neuronal activities in multiple brains) and specific hyper-brain network activity to support such coordination or interaction (Lindenberger et al., 2009; Astolfi et al., 2010, 2020; Dumas et al., 2010, 2012, 2020; Sänger et al., 2012, 2013; Müller et al., 2013, 2018b; Acquadro et al., 2016; Müller and Lindenberger, 2019, 2022; Czeszumski et al., 2020). Synchronization both within and between brains seems to be crucial for interpersonal interaction and is an inevitable element of neuronal communication systems within and between individuals or agents (Sänger et al., 2011, 2012, 2013; Yun et al., 2012; Dumas et al., 2012; Müller et al., 2013, 2018b, 2021a; Müller and Lindenberger, 2014, 2019, 2022; Szymanski et al., 2017b; Hu et al., 2017; Ahn et al., 2018; Stone et al., 2019; Astolfi et al., 2020; Balconi et al., 2020). In our view, both these forms of synchronization (i.e., intra- and inter-brain synchronization), reflecting the common integrated state of interactors known as *hyper-brain network* activity, are of paramount importance. This hyper-brain network activity is enhanced during periods of high demand on interpersonal interaction, and exhibits temporal and structural changes in response to the current situation and social circumstances (Sänger et al., 2012, 2013; Yun et al., 2012; Müller et al., 2013, 2018b; Filho et al., 2016; Toppi et al., 2016; Müller and Lindenberger, 2019, 2022; Astolfi et al., 2020). In an EEG hyperscanning study on fingertip movement, it has been shown that the overall number of significant phase synchrony in theta and beta frequency bands increased after cooperative interaction training in inter-brain connections, but not in intra-brain connections (Yun et al., 2012). In a computerized joint action task including interactive and non-interactive conditions, hyper-brain EEG activity was investigated using graph-theoretical approach (GTA) measures (Astolfi et al., 2020). Results of this study indicated that all the GTA indices were modulated by the interaction task, and returned a significantly stronger integration of hyper-brain networks in the interactive vs. non-interactive conditions. The authors compared also GTA indices derived from hyper-brain and intra-brain networks and showed that the former differentiated better between the conditions at lower frequencies (theta and alpha) and the latter differentiated better at higher frequencies (beta and gamma). The hyper-brain GTA indices were also modulated in accordance with the degree of cooperation or successful interaction between subjects (Astolfi et al., 2020). Filho et al. (2016) investigated within- and between-brain connectivity during a dyadic juggling task. Although the study was carried out with only one dyad of jugglers, the data showed some interesting synchronization patterns both within and between brains as well as corresponding changes in hyper-brain network dynamics in the theta and alpha frequency bands, which vary as a function of task difficulty (i.e., three, four, five, or six balls juggled). In another study with 13 jugglers divided into seven pairs (one juggler participated in two different pairs), Stone et al. (2019) found that at the intra-brain level, global efficiency was reduced for less-skilled jugglers and increased for more skilled jugglers during paired juggling as compared to solo juggling. No significant results were found at the inter- or hyper-brain levels in this study (Stone et al., 2019). Within- and between-brain connectivity, as well as the corresponding hyper-brain network structure and topology dynamics, were found to change as a function of playing condition, musical situation, and musical role (e.g., leader vs. follower) as well as the oscillation frequency in guitarist duets and quartets (Sänger et al., 2012, 2013; Müller et al., 2013, 2018b; Müller and Lindenberger, 2019, 2022). However, there is a large gap between neural and behavioral data—we neither know exactly how intra- and inter-brain synchronous activity influence or promote each other and how this interaction, resulting in hyper-brain network activity, is related to social behavior nor whether and to what degree internal state variables contribute to inter-brain dynamics (cf. Kingsbury and Hong, 2020). Recently, it has been suggested that within-brain activity and connectivity reflect an individual state of the interacting agent, while the adjustment of these activity states during interpersonal interaction can only be facilitated by between-brain connectivity or synchrony (Müller et al., 2021a). Thus, interpersonal interaction is locked into steady communication between the cell assemblies within the interacting brains and continual adjustment of these dynamic neuronal states between the brains (Müller et al., 2021a; Shamay-Tsoory, 2021).

However, we have to keep in mind that there is an essential difference between intra- and inter-brain synchronization. While synchronization within the brain is mostly (but not always) bound to the neuronal substrate, synchronization between brains is substrate-free (in the sense that there are no physical connections between the brains) and presumably relies on the common timing of the interactors. It has also been suggested that inter-brain synchronization could be a result of shared perceptual input and/or equal motor output, but nevertheless, there is evidence that a certain amount of inter-brain synchronization has intrinsic attraction and is not necessarily (directly) caused by common systems' input or output (Lindenberger et al., 2009; Sänger et al., 2012, 2013; Szymanski et al., 2017b; Gvirts and Perlmutter, 2020; Müller et al., 2021a; Novembre and Iannetti, 2021; Reinero et al., 2021; Gugnowska et al., 2022). This becomes particularly clear when we consider, for example, the coupling between brains and sounds elicited by musical instruments (guitars), as illustrated in the work by Müller and Lindenberger (2019). **Figure 1** shows the coupling between brains and musical instruments in a guitarist duet during free improvisation. To investigate phase coupling between EEG and auditory signals, the amplitude of the auditory signal was firstly averaged within the four frequency ranges: low (50–250 Hz), middle (250–500 Hz), high (500–2,000 Hz), and whole range (50–2,000 Hz). Thereafter, directed coupling measured by the Integrative Coupling Index (ICI) was determined between EEG and transformed auditory signals in four frequencies of interest (1.25, 2.5, 5, and 10 Hz; see Müller and Lindenberger, 2019, for more details). **Figure 1A** shows the ICI within (left panel) and between (right panel) the brains and instruments of the guitarists' A and B at the delta frequency (1.25 Hz). To clarify, brain maps were created that are influenced by the signals from individual guitars and also display reciprocal effects of the two musicians' brains on each other. Out- and in-strength were calculated as a sum of outgoing (from one node to all others) and incoming (to one node from all others) connections, respectively. Brain maps of out-strength (**Figure 1B**) and in-strength (**Figure 1C**) distribution within and between the brains as well as an in-strength distribution from the guitar to the brain (**Figure 1D**) and an out-strength distribution from the brain to the guitar (**Figure 1E**) are depicted. For this representation, the four guitar nodes were added together. It can be seen that connections from brain A to brain B go from temporoparietal regions in A to temporoparietal and above all right- and mid-frontal regions in B, while the connections from brain B to brain A go from right temporal regions in B to left temporoparietal regions in A. At the same time, the brain of guitarist A receives the connections from guitar A in frontotemporal regions (especially left) and at temporoparietal brain regions from guitar B, whereas the brain of guitarist B receives the connections from both guitars in temporoparietal and occipital brain regions. Thus, the guitars address brain regions in the two brains that are interconnected as well as those that are not. In addition, there are connections between brain regions that are not connected with the guitars. This could indicate that areas that are connected between brains are not affected by the guitars. It is evident that the two guitars have different effects on the two brains and that the reciprocal effects of the two brains on each other are different. This challenges the claim that synchronization between brains is simply a result of a common perceptual input and/or a common motor output. Recently, in pianist duets, while keeping sensory input and movements comparable across conditions as well as during musical pauses without sensory input or movement, it has been shown that inter-brain synchrony does not merely depend on shared sensorimotor impact but can also emerge endogenously, from aligned cognitive processes supporting social interaction (Gugnowska et al., 2022).

Interesting evidence found in an EEG hyperscanning study on analgesia is related to social touch, where romantic partners were assigned the roles of the target (pain receiver) and observer (pain observer). It has been found that hand-holding during pain administration increases the brain-to-brain coupling between the central regions of the pain receiver and the right hemisphere of the pain observer (Goldstein et al., 2018). This increase in

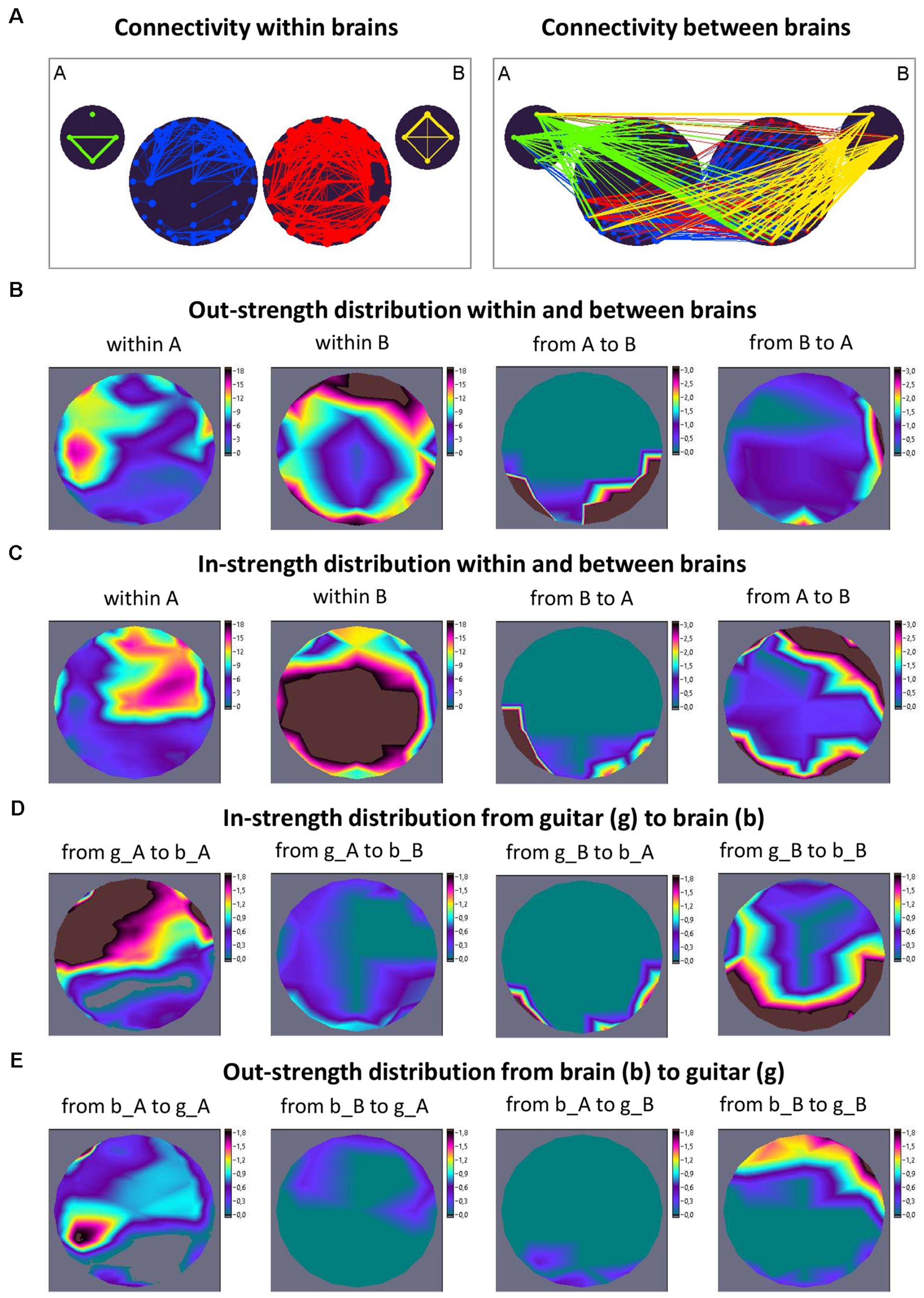

FIGURE 1 | Connectivity within and between the brains and instruments and corresponding strength distributions during free guitar improvisation. **(A)** Connectivity maps. The left panel represents the connectivity between the guitars and brains, and the right panel represents the connectivity between the guitars and brains. The strength of the nodes (sum of all out-going connections) is coded by circle size, and the strength of edges is coded by line thickness. The different parts of the network are color-coded: guitar A, green; guitar B, yellow; guitarist A's brain, blue; guitarist B's brain, red. The guitars comprise four nodes each, indicating different frequency ranges of auditory signals ordered clockwise from top: low, middle, high, and whole range (see text). The brains comprise 40 nodes (electrodes) each. **(B)** Out-strength distribution within and between brains. The two maps on the left represent the topological distribution of the out-strengths within the brains of the two guitarists, and the ones on the right display the topological distribution of the out-strengths going from guitarist A's brain to guitarist B's brain and *vice versa*. **(C)** In-strength distribution within and between brains. The two maps on the left represent the topological distribution of the in-strengths within the brains of the two guitarists, and the ones on the right display the topological distribution of the in-strengths coming from guitarist B's brain to guitarist A's brain and *vice versa*. **(D)** In-strength distribution from the guitar (g) to the brain (b). The strength distribution maps from left to right represent the topological distribution of the in-strengths coming from guitar A to brain A, from guitar A to brain B, from guitar B to brain A, and from guitar B to brain B. **(E)** Out-strength distribution from the brain (b) to guitar (g). The strength distribution maps from left to right represent the topological distribution of the out-strengths coming from brain A to guitar A, from brain B to guitar A, from brain A to guitar B, and from brain B to guitar B. It can be seen that the guitars address brain regions in the two brains that are interconnected as well as those that are not. In addition, there are connections between the brains that are not connected with the guitars (adapted from Müller and Lindenberger, 2019).

brain-to-brain coupling cannot be explained through a common sensory input, because the pain was administered to only one participant. It was also found that brain-to-brain coupling correlated significantly with the target's analgesia magnitude and the observer's empathic accuracy (Goldstein et al., 2018). In other words, enhanced inter-brain synchrony resulted in two distinct subjective experiences, that is, analgesia in one case and empathy in the other. Recently, this evidence was also confirmed in hyperscanning animal studies using different approaches (Kingsbury et al., 2019; Omer et al., 2019; Zhang and Yartsev, 2019). In a mouse study with microendoscopic calcium imaging to record neural activity from thousands of neurons, two animals, showing high interbrain correlations between the dorsomedial prefrontal cortex (dmPFC) neurons during social vs. non-social behavior, significantly reduced interbrain synchrony when tested within the same physical environment (constant ambient noise and lighting) with a barrier abolishing social interaction (Kingsbury et al., 2019). In another study using extracellular electrophysiology recordings in two bats, high inter-brain synchrony measured by local field potential correlations between two bats persisted even when one of the bats was only observing the interaction of his companion with a third bat that shared their enclosure (Zhang and Yartsev, 2019). Interestingly, Kingsbury and Hong (2020) hypothesized that "...a subject's attentional state may be compared with the estimated attentional state of an interacting partner by some circuit. By computing the synchronization of self and inferred attentional states across individuals, such a circuit could shape behavior based on the estimated synchrony of their attentional states. Although such a mechanism has not been tested, it is possible to determine whether any neural components encode the inter-brain synchronization of specific neural processes" (Kingsbury and Hong, 2020, p. 663). It is an interesting hypothesis, and perhaps such circuits do exist, but I would expect hyper-brain assemblies to be initially heterogeneous, distributed over the entire brain, and generally supportive of any kind of social behavior (cf. Prounis and Ophir, 2020). Nevertheless, further research in this direction is needed to properly understand the dynamics and origins of inter-brain synchronization and to effectively address the challenges of brain-to-brain interaction.

Interestingly, in a recent hyperscanning neurofeedback study, it has been shown that participants can learn to adjust their brain activity by using inter-brain synchrony as a neurofeedback feature (Müller et al., 2021b). Moreover, Basso et al. (2021) recently proposed the *synchronicity hypothesis of dance*, which states that humans dance to enhance both intra- and inter-brain synchrony. In other words, enhancement of intra- and inter-brain synchrony is supposed to be the desired result of a coordinated action, namely dancing. Thus, the authors hypothesized that dance evolved as a spontaneous process to drive coherent neural activity between brain regions within the brains of dancers and also between their brains. At the same time, dance is controlled or affected by the brain and thus emerges from the brain (Basso et al., 2021). This is in line with the aforementioned study on synchronization between musicians and instruments by Müller and Lindenberger (2019), where the authors stated that "...the instrument's sound is a result of the musician's behavior, which is based on sensorimotor synchronization and action. At the same time, this sound influences the behavior of musicians through auditory sensory pathways and is in this sense an actor. In our view, music improvisation and interaction can be understood only when considering both bidirectional influences" (Müller and Lindenberger, 2019, p. 9). As hypothesized by Novembre and Keller (2014), *action-perception coupling* when playing music in an ensemble facilitates the capacity to generate predictions of the respective musician's own as well as others' actions and to form representations of actions produced by others, and to integrate them with self-generated actions in real-time.

The Inter- or Hyper-Brain Cell Assembly Hypothesis

From everyday life, we know that social activities, such as making music, dancing, acrobatics, etc., can and must be learned and practiced to be effective and smooth. During learning (by repeated social activity), unnecessary degrees of freedom of interpersonal interaction are eliminated, with positive effects on smooth movement and motor skills. As mentioned above, there is an intrinsic relation between oscillatory activity, neural cell assemblies, and behavioral or cognitive entities. This relation also concerns inter-brain oscillatory activity or synchrony. In this context, we suggest an *inter- or hyper-brain cell assembly hypothesis* that states that cell assemblies can be formed between brains as well, following roughly the same rules as within brains. Probably, I would rephrase the Hebbian rule in accordance with this context: "what wires together, fires together" ("wire" here in the sense of inter-brain connectivity or synchrony), indicating that cell assemblies that are interconnected between the brains by means of inter-brain synchrony ignite simultaneously or synchronously within these brains. This also means that cell assemblies within brains that form during an interaction and are synchronized with each other through between-brain interaction or synchrony will also gain precedence during repeated joint activity. This leads to the formation of the so-called inter-brain or rather *hyper-brain cell assemblies* (because both intra- and inter-brain connections are involved), which interconnect the two (or more) brains and lead to the joint firing of neuronal elements in these brains or in the common hyper-brain cell assembly. We also assume that such hyper-brain cell assemblies can be generalized with respect to other individuals or brains, albeit with some interpersonal variability.

In the studies with guitarist duets (Sänger et al., 2012; Müller et al., 2013) and quartets (Müller et al., 2018b), so-called *hyper-brain modules* comprising nodes in two or more brains were found. Such hyper-brain modules or communities, in which the connections within the modules are the strongest, will be considered as one of the possible representations of the hypothesized hyper-brain cell assemblies. As an example, consider a guitarist duet during free improvisation. **Figure 2** shows two different 2-s sequences during the improvisation. Analogous to the previous example (**Figure 1**) directional coupling (ICI) was calculated within and between the brains in the delta (1.25 Hz) frequency. The entire hyper-brain network was then examined using modularity analysis. The modules are labeled in different colors. In the first sequence (**Figure 2A**), the hyper-brain network consists of three modules, while one of them (marked in blue) consists of nodes within one brain (guitarist A), and the other two modules (red and green) are hyper-brain modules that are represented in both brains. But what is striking here is the different network structures in the two hyper-brain modules. If the electrodes or the nodes in the green module are strongly connected both within and between the brains, the connections in the red module within the brain of guitarist A (temporal nodes) are very weak, but these nodes send strong connections to the brain of guitarist B, which is itself strongly interconnected. In other words, the red module comes about through the strong connections between the brains and through the strong connections within the brain of guitarist B. In the second sequence (**Figure 2B**), there are also three modules, but this time all three are hyper-brain modules. Notably, all three modules show strong connections either within the brain of guitarist A or within the brain of guitarist B. The remaining nodes in these modules are weakly connected within the brains but respectively connected to a different brain as if these nodes play a subordinate role within the brains but a connector role between the brains. As indicated by the brain maps of out-strength distribution, the fronto-central and temporal regions play a leading or important role in both sequences. By definition, the connections between the nodes within the modules are the strongest, so the hyper-brain modules or communities comprising nodes located in different brains must have an important functional meaning (Müller et al., 2021a). These strong connections within the hyper-brain module(s) are important for information transfer between the brains (and also within them) and for simultaneous and probably synchronized firing ignition of neural cells within these brains. As shown, these hyper-brain modules can have different modularity structures, which change in time dependent on the situation or interaction circumstances. Hyper-brain modules are not equal to hyper-brain cell assemblies, but nevertheless, such hyper-brain modules may represent a prototype of cell assemblies that can play a central role in inter- or hyper-brain communication.

Similar ideas were recently conveyed in a hypothesis article by Shamay-Tsoory (2021). She refers to *interbrain plasticity* or *interaction-based learning*, where the term *interbrain plasticity* is used as a metaphor representing the capacity of the inter-brain networks (based also on intra-brain connectivity) to rearrange their functional structure in response to interaction-based learning. "Notably, if brain regions hold the capacity to coordinate their activity within a brain, it is possible that brain regions coordinate their activity *between brains*" (Shamay-Tsoory, 2021, p. 4). From a historical perspective, it is worth mentioning Varela's ideas or concept of interbeing (Varela, 1999) as well as the related concept of "genuine intersubjectivity" or "extended consciousness" (Froese, 2018; Valencia and Froese, 2020), which proposed inter-brain phase synchronization of neural oscillations as a candidate mechanism for the conscious extended mind, linking the idea of large-scale integration within brains to inter-brain synchrony.

In the aforementioned hyperscanning mouse study, Kingsbury et al. (2019) showed that interbrain activity correlations during competitive interaction arise from single-cell dynamics and that cells in dominant and subordinate mice encode subject and opponent information differently, whereby dominant mice exert a greater influence on interbrain synchrony than subordinates do. Moreover, neuronal cells in dominant animals respond more to subject behaviors compared to cells in subordinates, while cells in subordinates respond more to opponent behaviors compared to cells in dominants. The authors concluded that interbrain synchrony depends specifically on subsets of neurons that separately encode behaviors of the subject animal and those of the interacting partner (i.e., social behaviors of self and others) and allow each brain to represent a common repertoire of the behavior of both interacting animals (Kingsbury et al., 2019). Although the measurement method used in this study (i.e., microendoscopic calcium imaging) does not allow conclusions about neuronal firing to be drawn, the results of the study speak about correlated activity of cell assemblies in two brains of the test animals in social interaction. In this regard, the study by Zhang and Yartsev (2019), in which electrophysiological local field potentials were measured in bats, is more informative with respect to neuronal firing. They observed that the 30–150 Hz local field potential was linked to aggregate local spiking activity and that the degree of interbrain neural correlation covaried with the extent of social interactions (Zhang and Yartsev, 2019). Both these studies indicate correlated neural activity on the cell level. It remains to be seen whether cell assemblies that are interconnected between brains *via* inter-brain synchrony or correlated neural activity ignite simultaneously or synchronously within these brains. The suggested hyper-brain cell assembly hypothesis predicts or assumes a simultaneous firing of neural cells in two (or more) brains.

From a synergetic point of view, a hyper-brain assembly represents a system or superordinate system that is controlled at the macro level by certain order parameter(s). The order parameter determines the behavior of the neuronal elements in a hyper-brain assembly and thus "enslaves" the behavior of the individual parts. At the same time, the individual parts on the micro-level of neuronal elements (neurons or synapses) can influence the structure and dynamics of hyper-brain assembly as a whole in accordance with the *circular causation* rule (Haken, 2006, 2016). Importantly, this principle of circular causation works not only within individual brains but also in a hyper-brain network or assembly binding two or more brains together that function as a superordinate system or superorganism (cf. Müller et al., 2021a).

WITHIN- AND CROSS-FREQUENCY COUPLING AND RELATED HYPER-BRAIN ASSEMBLY

It has already been shown that synchronization by oscillation and related binding phenomena play a crucial role in neural communication. Neural interaction can occur at the same or at different frequencies and can be indexed by within-

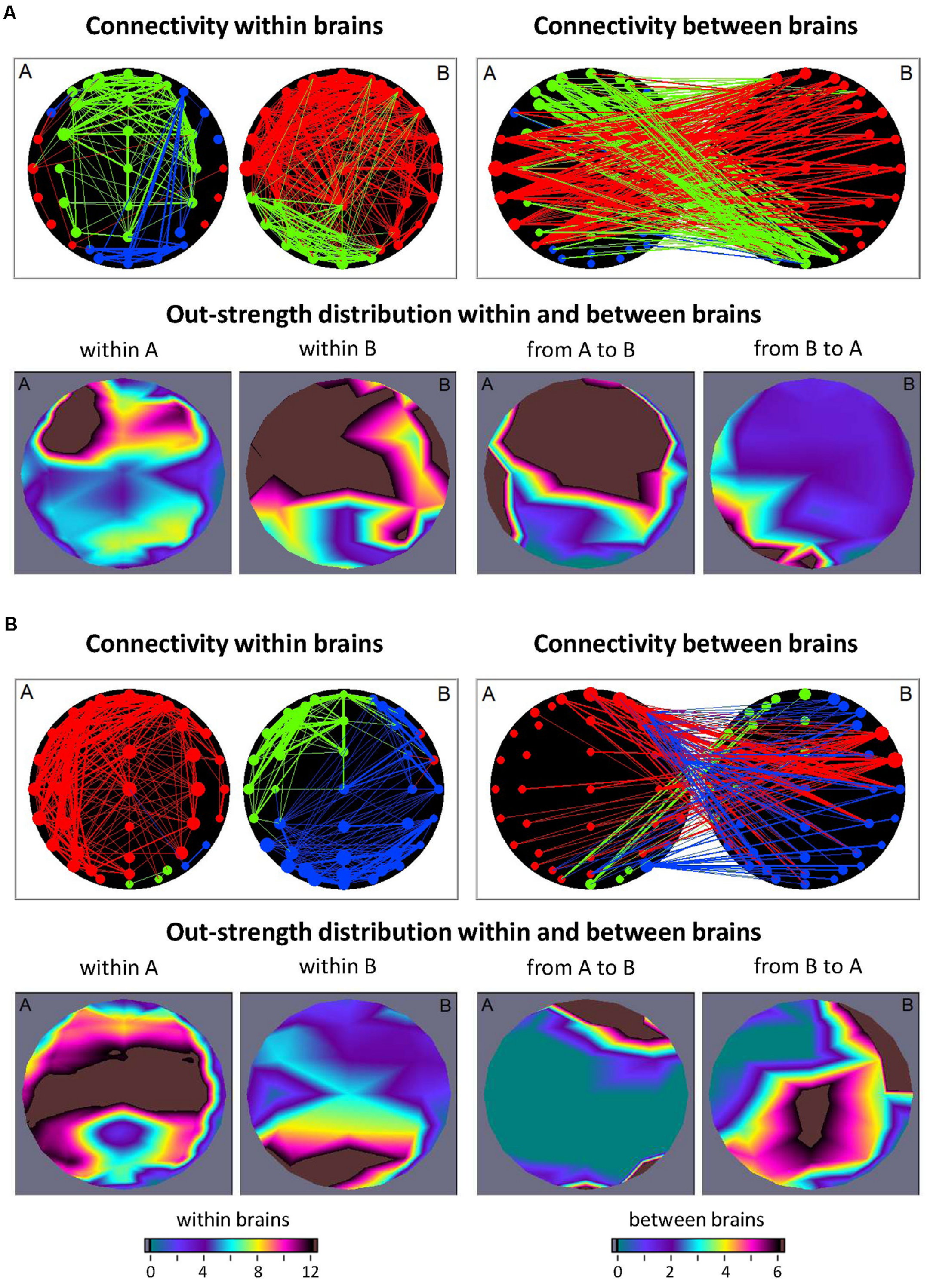

FIGURE 2 | Connectivity within and between the brains and corresponding out-strength distributions during free guitar improvisation. **(A)** Connectivity maps and out-strength distributions in the first time window. In the first row, the left panel represents the connectivity within the brains, and the right panel represents the connectivity between the brains. The size of the circles represents the strength of the nodes (electrodes) and connectivity strength is coded by line thickness. The three different modules are coded by color. In the second row, the two maps on the left represent the topological distribution of the out-strengths within the brains of the two guitarists, and the right ones display the topological distribution of the out-strengths going from guitarist A's brain to guitarist B's brain and *vice versa*. **(B)** Connectivity maps and out-strength distributions in the second time window. Connectivity maps within and between the brains and corresponding out-strength distribution maps are represented in the same way as in **(A)**.

and cross-frequency coupling (WFC and CFC, respectively). It has been suggested that WFC and CFC can represent information flows within and between neural cell assemblies, respectively (Buzsáki and Draguhn, 2004; Buzsáki, 2006; Müller et al., 2016, 2019b). The interaction between different characteristics of the signals indicated by different WFC and CFC measures adds another dimension to understanding complex neural dynamics and neuronal networks (Jirsa and Müller, 2013). As reported by Buzsáki and Draguhn (2004), neuronal cell assemblies oscillating synchronously at different frequencies provide an efficient basis for integrative processes in the brain. CFC, allowing accurate timing between different oscillatory rhythms, maybe one of the mechanisms underlying the re-integration of these separated information flows and allowing for communication between different cell assemblies (Canolty et al., 2006; Klimesch et al., 2008; Doesburg et al., 2009; Canolty and Knight, 2010). As suggested by Buzsáki, "…frequency locking can occur between any two or more oscillators with an integer period relationship. In principle, virtually infinite numbers of combinations are possible but the limited number of classes of oscillators that can be simultaneously present in the same neuronal substrate puts severe constraints on the possible numbers of combinations" (Buzsáki, 2006, p. 354). It should be added here that besides the aforementioned *phase-to-phase* CFC with an integer period relationship, there are other CFC forms that can play an important role in neuronal and other biological or social interactions (cf. Jensen and Colgin, 2007; Jirsa and Müller, 2013; Hyafil et al., 2015), such as: (i) *power-to-power*; (ii) *phase-to-power*; (iii) *phase-to-frequency*; (iv) *envelope- (*or *amplitude-) to-frequency*; and (v) *frequency-to-frequency* CFC. These CFC types are schematically presented in **Figure 3** (cf. Jirsa and Müller, 2013).

There is increasing evidence that the phase-amplitude modulation occurs most often—it has been found both in animals and humans in the entorhinal and prefrontal cortices, in the hippocampus, and in distributed cortical areas (Mormann et al., 2005; Canolty et al., 2006; Tort et al., 2008, 2009, 2010; Cohen, 2008; Osipova et al., 2008; Cohen et al., 2009a,b; Colgin et al., 2009; Axmacher et al., 2010a,b; Voytek et al., 2010; Munia and Aviyente, 2019). In particular, it was observed that the phase of low-frequency oscillation (e.g., theta) modulates power in high-frequency oscillations (e.g., gamma), with stronger modulation mostly occurring at higher theta amplitudes (Canolty et al., 2006; Jensen and Colgin, 2007; Cohen, 2008; Tort et al., 2008, 2009; Doesburg et al., 2009; Canolty and Knight, 2010; Kendrick et al., 2011; Colgin, 2015; Amemiya and Redish, 2018). Besides the CFC between low-frequency phase and high-frequency amplitude (e.g., theta-gamma), there is evidence that phase-amplitude CFC also exists between the low-frequency bands (e.g., delta-theta, delta-alpha, and theta-alpha; see Witte et al., 2000; Lakatos et al., 2005; Schack et al., 2005; Cohen, 2008; Isler et al., 2008). Furthermore, it was reported that the high-frequency gamma amplitude can also be modulated by the alpha phase (Jensen and Colgin, 2007; Cohen et al., 2009a; Voytek et al., 2010). Lakatos et al. (2005) found that the delta (1–4 Hz) phase modulates theta (4–10 Hz) amplitude, and the theta phase modulates gamma (30–50 Hz) amplitude in the primary auditory cortex of awake macaque monkeys. Based on their findings, the authors introduced a hypothesis on the "hierarchical" organization of EEG oscillations suggesting that the amplitude of the oscillations at a characteristic frequency is modulated by the oscillatory phase at the lower frequency (Lakatos et al., 2005). Furthermore, as mentioned above, there is also clear evidence that not only the amplitude of the high-frequency oscillations is modulated by the oscillatory phase at a lower frequency but also that phases of both these oscillations can be related to each other (e.g., theta-gamma phase-to-phase coupling; see Schack et al., 2002; Schack and Weiss, 2005). Moreover, other types of CFC (e.g., amplitude-to-amplitude or envelope-to-envelope, frequency-to-frequency, and amplitude/envelope-to-frequency) may occur and have indeed been observed (De Lange et al., 2008; Witte et al., 2008, 2011; Jirsa and Müller, 2013; Hyafil et al., 2015). All these interaction patterns exist simultaneously in biological signals and thus provide a more complete picture about information processing in the brain or other biological systems and subsystems (Jirsa and Müller, 2013). It is worth noting here that all these CFC forms are associated with, or implicated in, the relative coordination described above with respect to the important work by Erich von Holst many decades ago (cf. Müller et al., 2011).

It is also justified to assume that hyper-brain cell assemblies can make use of CFC. An example of a hyper-brain cell assembly based on WFC and CFC could be the so-called theta-alpha networks detected when couples kissed (Müller and Lindenberger, 2014). This is displayed in **Figure 4**. It can be seen that 5- and 10-Hz oscillation nodes are strongly interconnected within (**Figure 4A**) and especially between (**Figure 4B**) the partners' brains. Modularity analysis revealed a hyper-brain module comprising these oscillation nodes in both brains (indicated in green in **Figure 4C**), which also shows different strength distributions in the two brains (see **Figure 4D** for details). Interestingly, hyper- and especially inter-brain strength determined for 5-Hz oscillation nodes (**Figure 4E**, left and mid panel, respectively) correlated significantly positively with partner-oriented kissing satisfaction, and intra-brain strength determined for 10-Hz oscillation nodes correlated significantly positively with self-reported kissing quality (**Figure 4E**, right panel). In other words, the main parts of the theta-alpha subnetwork (i.e., theta and alpha oscillatory nodes) have certain relations to the subjective feelings of the kissing subjects, that is, the hyper-brain module or cell assembly and its parts (intra- and inter-brain connection strengths) are related to social behavior outcomes. This hyper-brain assembly or theta-alpha subnetwork is based on phase-to-phase WFC and CFC, comprising connections both within and between the brains. The question that arises here: Can a subnetwork (i.e., the theta-alpha subnetwork) identified using modularity analysis be equated with a cell assembly? If we assume that neural cells within cell assemblies communicate with each other at the same frequency and that the CFC is responsible for the communication between the cell assemblies, then it can be supposed that the theta-alpha subnetwork contains (at least) two hyper-brain cell assemblies oscillating at theta and alpha frequencies that are strongly interconnected and form hierarchically organized structure or

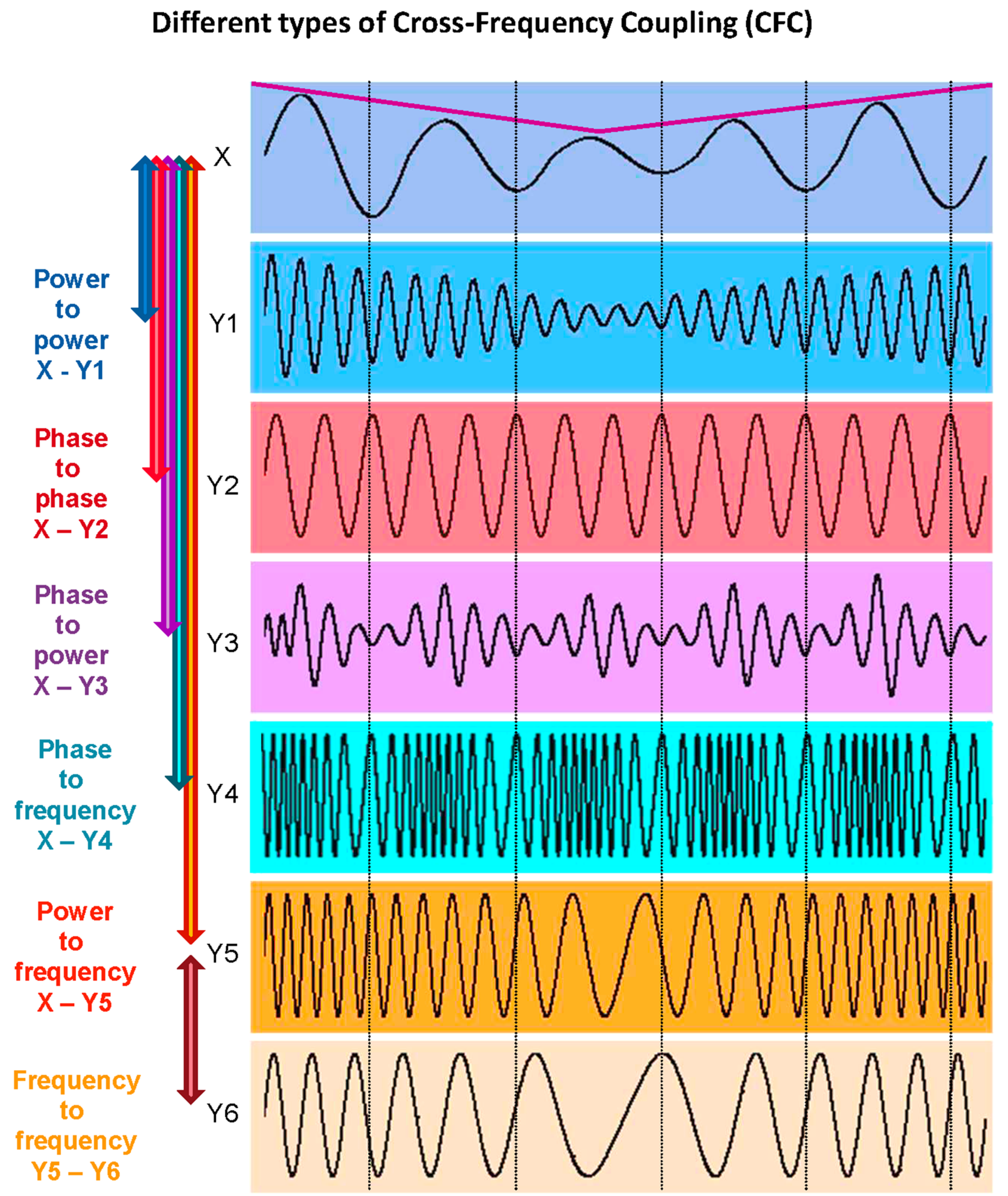

FIGURE 3 | Different types of cross-frequency coupling (CFC). *Power-to-power CFC* can be identified between signals *X* and *Y1*: Signal *Y1* about five times higher frequency than that of signal *X* shows slow amplitude modulations over time like signal *X* (indicated by the purple line). *Phase-to-phase CFC* can be identified between signals *X* and *Y2*: Signal *Y2* shows 3:1 phase-to-phase coupling with signal *X*, i.e., one oscillation period of signal *X* corresponds to three periods of signal *Y2*. *Phase-to-power CFC* can be identified between signals *X* and *Y3*: Signal *Y3* shows fast amplitude modulations that are related (or coupled) to the phase of signal *X*. *Phase-to-frequency CFC* can be identified between signals *X* and *Y4*: Signal *Y4* shows frequency modulations that are coupled with phase changes of signal *X*. *Power-to-frequency CFC* can be identified between signals *X* and *Y5*: Signal *Y5* shows frequency modulations that are related to, or coupled with, the slow amplitude modulations of signal *X* (purple line). *Frequency-to-frequency CFC* can be identified between signals *Y5* and *Y6*: Signal *Y6* shows slower but similar frequency modulations as the signal *Y5*. The different types of CFC are not mutually exclusive (cf. Jensen and Colgin, 2007). For instance, slow amplitude modulations of signal *X* are coupled not only with the amplitude changes of signal *Y1* but also with frequency changes of signals *Y5* and *Y6*, which are coupled in their frequency modulations at the same time (adapted from Jirsa and Müller, 2013).

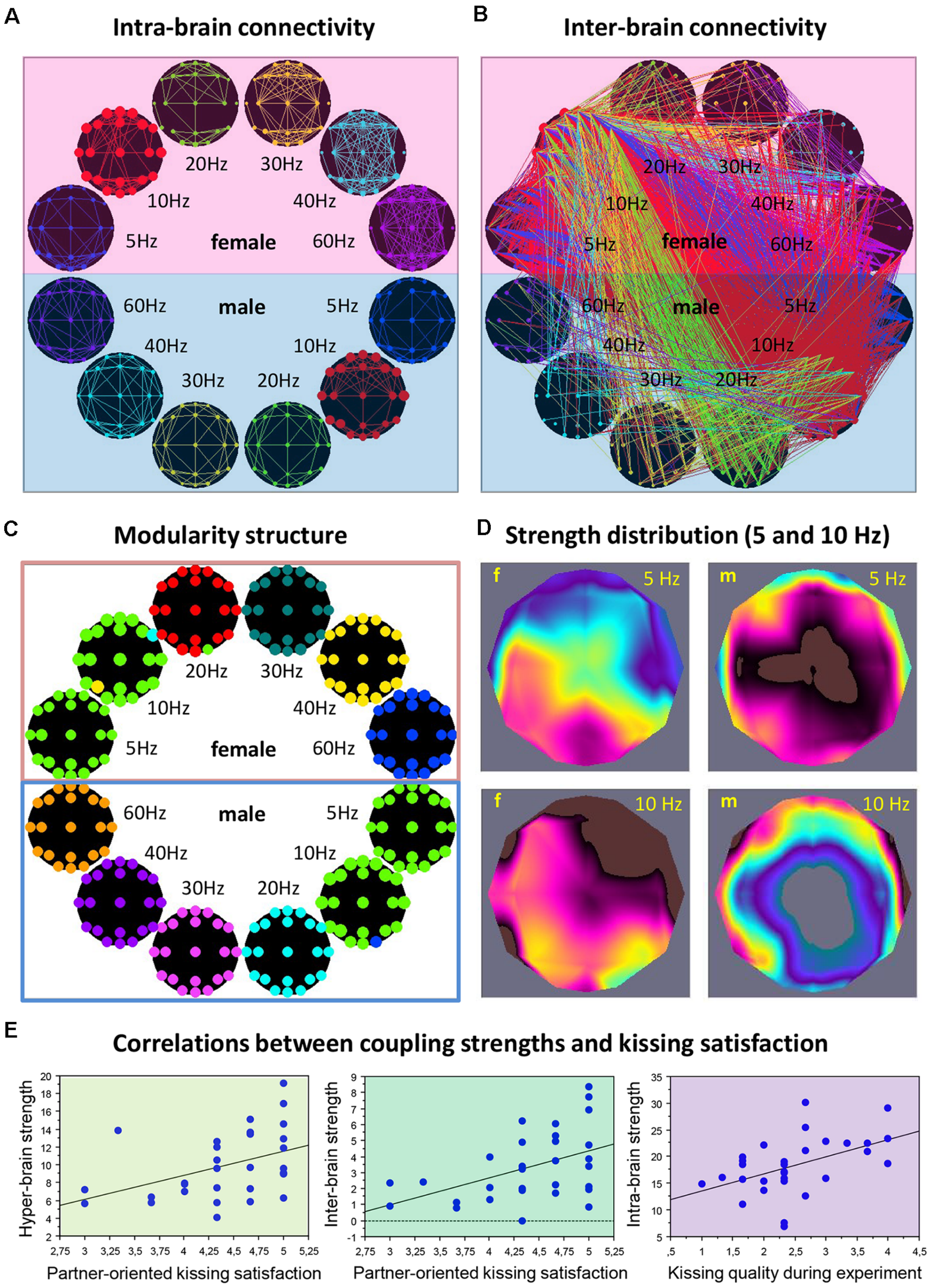

FIGURE 4 | Representation of the hyper-brain network and the theta-alpha subnetwork during kissing. **(A)** Intra-brain connectivity. The brain maps represent connectivity at six different frequencies within the female and male partners' brains, respectively. **(B)** Intra-brain connectivity. The brain maps represent the between-brain connectivity within and between the six frequencies. It can be seen that the strongest connections are found in the theta (blue) and alpha (red) frequency bands, and between them. **(C)** Modularity structure. Modularity analysis revealed nine different modules. The biggest module is the so-called theta-alpha module or subnetwork comprising 5- and 10-Hz nodes in both female and male brains. Other modules represent different frequencies in both brains separately. **(D)** Out-strength distribution of theta (5 Hz) and alpha (10 Hz) nodes within the female and male brains. The topological distribution of coupling strength represents the overall within- and cross-frequency connectivity within the theta-alpha subnetwork for female and male brains, respectively. **(E)** Correlations between coupling strengths and kissing satisfaction and kissing quality. Partner-oriented kissing satisfaction correlated significantly positively with the hyper- and especially inter-brain strengths determined for 5-Hz oscillation nodes. Kissing quality during the experiment correlated significantly positively with intra-brain strength determined for 10-Hz oscillation nodes (adapted from Müller and Lindenberger, 2014 and Müller et al., 2021a).

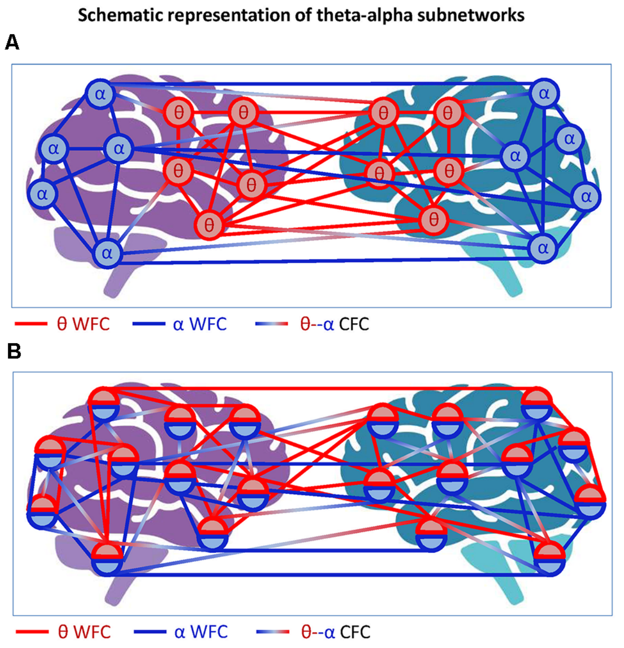

FIGURE 5 | Schematic representation of theta-alpha subnetworks. **(A)** Theta-alpha subnetwork as two hyper-brain modules oscillating at different frequencies. The two hyper-brain modules oscillating at different frequencies (θ and α) are coded by colors (blue and red). The coupling within the modules is given by WFC and the coupling between the modules by CFC. **(B)** Theta-alpha subnetwork with nodes oscillating at two different frequencies each. The two hyper-brain modules oscillating at different frequencies (θ and α), also coded in blue and red, are distributed across two brains, whereby each node belongs to both modules. The coupling within the modules is given by WFC and the coupling between the modules by CFC.

the theta-alpha subnetwork. Such a situation is schematically represented in **Figure 5A**.

Another possible scenario is depicted in **Figure 5B**, where each electrode or node contains two oscillations. In this case, we can speak of a common theta-alpha subnetwork comprising all nodes with their WFC and CFC links. This scenario, which probably corresponds more to the situation outlined in **Figure 4**, will be discussed in the next section with respect to multilayer networks, which are more suitable for such situations. At this point, we only note that if we consider the concept of hierarchical modularity or modularity at multiple topological scales (cf. Meunier et al., 2009, 2010), the scenarios shown in **Figure 5** or mixed scenarios would or could occur.

Next, an example of phase-amplitude cross-frequency coupling with respect to the hyper-brain cell assembly hypothesis should be discussed. **Figure 6A** represents a scenario in which the amplitude of signal X in the brain on the left is coupled to the phase of signal Y in the brain on the right. If we follow the literature (Lisman, 2005; Buzsáki and Wang, 2012) and assume that the period of gamma activity is closely related to the firing activity of neurons, then one could speculate that the activity of spiking cells in the left brain occurs during certain periods of the theta phase in the right brain. **Figure 6B** represents another scenario of phase-amplitude cross-frequency coupling between two brains. In this case, signals X and Y (in the brains on the left and right, respectively) are gamma oscillations, which are mostly out of phase (indicated by the vertical dotted lines in the middle) but their amplitude or envelope is modulated by the common theta rhythm (cf. Buzsáki and Wang, 2012). Presumably, this theta rhythm could be located in the brain or brains (e.g., in the hippocampus) and accordingly induce the gamma oscillation cycles in two brains, or it could be purely virtual or originate from the environment. Importantly, in this case, the hyper-brain cell assembly activity represented by high-frequency gamma oscillation cycles is synchronized *via* the modulating activity of low-frequency theta oscillation. Recently, in a hyperscanning EEG study on pianists jointly performing duets, inter-brain synchrony was calculated by extracting the amplitude envelopes in five frequency bands (delta: 1–3 Hz, theta: 4–7 Hz, alpha: 8–12 Hz, beta: 13–30 Hz, and gamma: 30–40 Hz), band-pass filtering these envelopes in the frequency range of pianists' planned and actually performed musical tempi (1–3 Hz), and finally by extracting the phase of these envelopes to calculate the aforementioned inter-brain synchrony indices. Practically, this approach corresponds to the scenario shown in **Figure 6B**, with the difference that the delta-gamma (instead of theta-gamma) phase-amplitude CFC was calculated, although the authors do not speak of CFC in their work (Gugnowska et al., 2022). Please note that gamma (and also other frequency) oscillations were modulated by the delta rhythm (the pianists' planned and performed musical tempi), which can be induced either endogenously or exogenously.

In general, the combination of WFC and CFC has a stronger explanatory power because cortical, and more generally, biological systems never operate at only one frequency. Different modulations that take place continually in complex systems are interconnected and influence each other in order to adapt and sufficiently react to the constantly changing environment. An important question that exists and needs to be answered in this context is the question of the relationship between oscillatory and firing or spiking neuronal activity. However, as discussed earlier and indicated by Buzsáki (2010, p. 366): "Oscillators are also natural parsing and chunking mechanisms of neuronal activity because they have well-defined onsets and offsets with characteristic maximum and minimum spiking activity of the information-transmitting principal cells."

HYPER-FREQUENCY AND MULTILAYER NETWORKS

Networks including both types of couplings, WFC and CFC, were called hyper-frequency networks (HFNs) and were found within (Müller et al., 2016, 2019b) and between brains (Müller and Lindenberger, 2014) as well as in complex networks emerging during choir singing (Müller et al., 2018a, 2019a). Complex networks (e.g., HFNs) can be described as multiplex or multilayer networks that have a specific multidimensional or multilayer network organization (De Domenico et al., 2013, 2015, 2016; Boccaletti et al., 2014; Kivelä et al., 2014; De Domenico, 2017; Pilosof et al., 2017; de Arruda et al., 2018). Basically, multiplex networks can be considered as a special case of multilayer

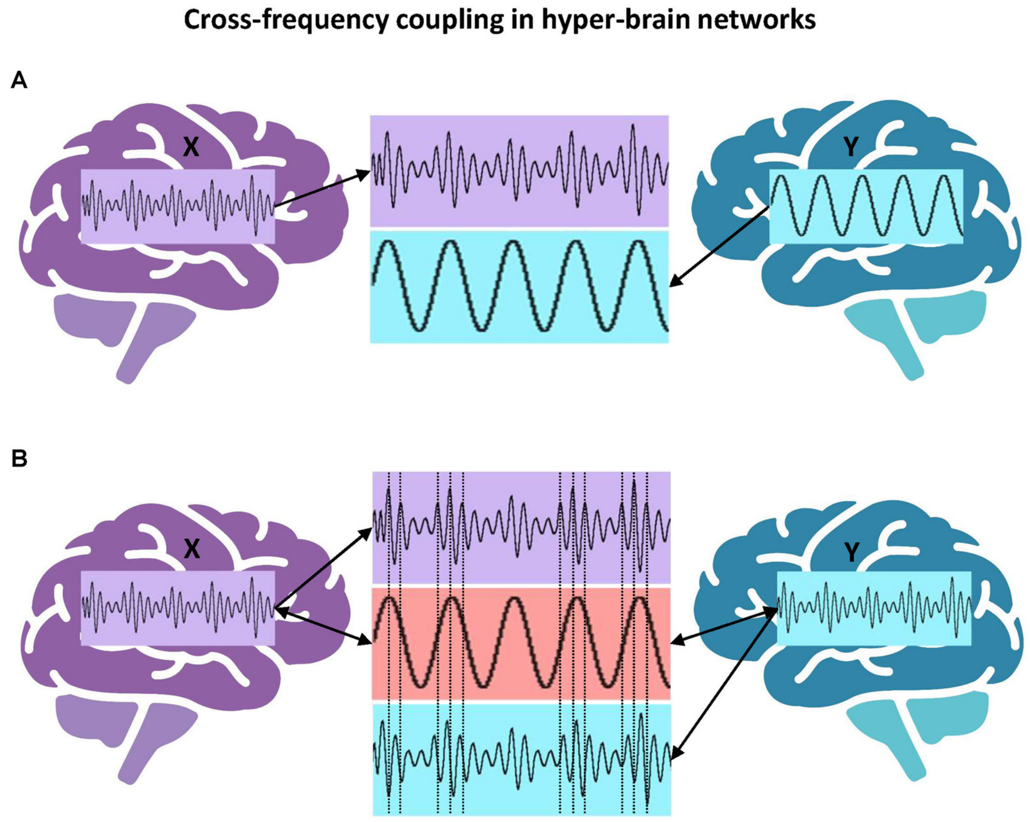

FIGURE 6 | Cross-frequency coupling in hyper-brain networks. **(A)** Hyper-brain theta-gamma phase-amplitude CFC, scenario 1. The amplitude or envelope of signal X in the brain on the left is coupled to the phase of signal Y in the brain on the right. **(B)** Hyper-brain theta-gamma phase-amplitude CFC, scenario 2. Signals X and Y (in the brains on the left and right, respectively) are gamma oscillations, which are mostly out of phase (indicated by the vertical dotted lines in the middle) but their amplitude or envelope is modulated by the common theta rhythm, which can be either endogenous or exogenous.

networks. In multiplex networks, the set of nodes in each layer is usually the same (but not always), and the nodes are connected within the layer but not between layers (e.g., in conventional functional connectivity analyses, the WFC at different frequencies can represent different layers that are not connected to each other). Multilayer networks are characterized by the existence of connections not only within the layers but also between them (e.g., by means of CFC). In the literature, there is no unified conceptualization of multiplex and multilayer networks. I present my view on these phenomena here and am mainly oriented towards the applicability of these concepts with regard to neuroimaging and hyperscanning research. In this context, HFNs can be described as multilayer networks, where WFC represents communication within different layers and CFC depicts communication between the layers (Brookes et al., 2016; Tewarie et al., 2016, 2021; De Domenico, 2017; Buldú and Porter, 2018; O'Neill et al., 2018; Tenney et al., 2021). **Figures 7A,B** exemplarily show complex two-layer single-brain networks in the form of multiplex (**Figure 7A**) and multilayer (**Figure 7B**) networks. It can be seen that in multilayer networks as compared to multiplex networks, there are connections between the layers that can be accomplished by CFC. In the case of hyper-brain multilayer networks, there are, in addition, connections between the brains that can occur both within and between frequencies (see **Figure 7C** for details). The two layers of persons A and B and the two layers within their brains, representing WFC at different frequencies, can be regarded as two different *aspects* or *features* of the multilayer network (cf. Kivelä et al., 2014). To avoid confusion, the four layers in **Figure 7C** are also called *elementary layers*, indicating the affiliation to different aspects or features of the multilayer network (Kivelä et al., 2014). Furthermore, networks changing in time can also be considered as multiplex (if the temporal layers do not have any causal relationships or are not connected) or multilayer (if the temporal layers are causally dependent or interconnected) networks, as represented in **Figure 7D** (for simplicity, I have omitted the connections between the layers here so that the representation can be either multiplex or multilayer). These temporal or time-varying networks, whose edges have intrinsic dynamics with given characteristic time scales, represent the temporal evolution of a system or information spreading across time (Holme and Saramäki, 2012; Kivelä et al., 2014; Starnini et al., 2017; O'Neill et al., 2018).

There is a body of work in neuroscience on *functional connectivity dynamics* (FCD) or *network topology dynamics* (NTD) that uses temporal or time-varying connectivity networks

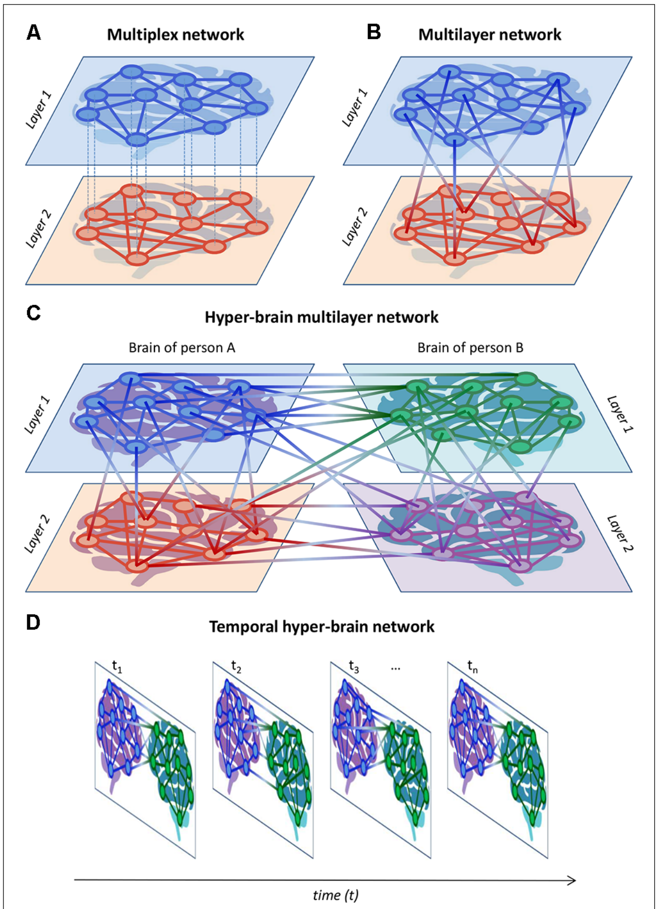

FIGURE 7 | Schematic representation of multiplex, multilayer, and temporal networks. **(A)** Multiplex network. A two-layer single-brain multiplex network is represented. The layers can represent, for example, different frequencies or other brain attributes (e.g., structural and functional connectivity). **(B)** Multilayer network. A two-layer single-brain multilayer network is represented, where the nodes are connected within and between the layers. The connections within the layers can be given by WFC and those between the layers by CFC. **(C)** Hyper-brain multilayer network. A two-layer hyper-brain multilayer network is represented, where the nodes are connected within and between the layers as well as within and between the brains. In the case of an HFN, connections within the layers are given by WFC, connections between the layers are given by CFC, and connections between the brains are given both by WFC and CFC. The two layers of persons A and B can be considered as two different *aspects*. **(D)** Temporal hyper-brain network. Network structures can change across time and can be considered multiplex (if the temporal layers do not have any causal relationships or are not connected) or multilayer (if the temporal layers are causally dependent or connected) networks. For simplicity, the connections between the temporal layers were omitted but they would appear if the network was multilayer.

to study changes in network structure and resulting network topology over time (Betzel et al., 2012, 2016; Chu et al., 2012; Calhoun et al., 2014; Hansen et al., 2015; Shen et al., 2015; Deco and Kringelbach, 2016; Müller et al., 2016, 2019b). This kind of connectivity network dynamics is also called *chronnectome*, focusing on identifying time-varying, but reoccurring, patterns of coupling among brain regions (Calhoun et al., 2014). It has been shown that the network structure and FCD or NTD are non-stationary and reveals a rich dynamic pattern, characterized by rapid transitions switching between a few discrete functional connectivity states (Betzel et al., 2012, 2016; Hansen et al., 2015; Shen et al., 2015; Müller et al., 2016, 2019b). Furthermore, analysis of the temporal fluctuations of HFN structure has revealed specific NTD, i.e., temporal changes of different GTA measures such as strength, the clustering coefficient (CC), characteristic path length (CPL), and local and global efficiency determined for HFNs in different time windows (Müller et al., 2016, 2019b). Moreover, it has been found that variability of these NTD metrics, measured by the standard deviation across time, correlated positively with perceptual speed scores, indicating that a more variable NTD increases performance in cognitive or at least perceptual-speed functioning and enhances adaptive capabilities of the system or individual (Müller et al., 2019b). A study comparing topological stability and graph characteristics of networks across time (ranging from 1 s to multiple hours) showed that functional networks were highly variable in the order of seconds and that stable network structures emerge after as little as 100 s duration. These conserved network structures or subnetworks were found to persist across different states and frequency bands, and the most common edges were markedly consistent, constituting a persistent network "core" (Chu et al., 2012). Networks changing in time can also be considered as assembly sequences; as hypothesized by Buzsáki (2010, p. 363): "…analogous to words and sentences in language, neuronal assemblies are organized by syntactical rules that define their first-order and higher-order relationships." Thus, neuronal cell assemblies not only have a hierarchical or multidimensional structure representing different levels of organization but also the temporal development of these assemblies itself is hierarchically organized by specific rules and regularities.

In a number of studies, it has been shown that multilayer networks and HFNs can also be represented as supra-adjacency matrices, where conventional GTA tools can be used to investigate the network properties (Kivelä et al., 2014; Müller and Lindenberger, 2014; Brookes et al., 2016; De Domenico et al., 2016; Müller et al., 2016, 2019b; De Domenico, 2017). **Figure 8** illustrates a supra-adjacency matrix of a hyper-frequency hyper-brain network emerging during kissing. Practically, it is another representation of the network depicted in **Figure 4** above. This matrix originally included 254 nodes (cf. Müller and Lindenberger, 2014) but, for simplicity, we removed two nodes indicating the two EMG lip responses of the female and male partners and reconstructed the matrix only on the basis of EEG signals oscillating at six different frequencies (5, 10, 20, 30, 40, and 60 Hz). Thus, the reconstructed supra-adjacency matrix (252 × 252) comprises all connections between 21 electrodes (organized in anterior-posterior order from left to right: Fp1, Fpz, Fp2,…, O1, Oz, and O2) and six frequencies within (brown and red quadrats) and between (green and purple quadrats) female and male brains, respectively (see **Figure 8A**). WFC connections between all electrodes within the female and male brains are distributed along the main diagonal of the matrix. WFC connections between the brains are distributed along diagonals within the green and purple quadrats. The 5- and 10-Hz nodes (indicated by the four yellow smaller squares) represent the so-called theta-alpha subnetwork (described above in **Figure 4**) comprising both WFC and CFC connections within and between brains, respectively. Moreover, the alpha-frequency (10 Hz) nodes have the most connections and serve a cleaving or pacemaker function in the common hyper-brain HFN. The six WFC subnetworks within the female and male brains represent the six layers of corresponding brains (see **Figure 8B**). The connections between the layers within the female and male brains are represented by the remaining edges in the brown or red quadrats in **Figure 8A**. The two other quadrants in **Figure 8A** (green and purple) comprise all connections (WFC and CFC) between the brains. As mentioned above, the multilayer network represented or organized in the form of a supra-adjacency matrix can be analyzed using the conventional GTA tools but also using other tools based on tensor algebra or tensor decomposition methods (Boccaletti et al., 2014; Kivelä et al., 2014; De Domenico et al., 2016; Cozzo et al., 2018; de Arruda et al., 2018).

In a choir study, it has been shown that physiological systems (respiratory, cardiac, and vocalizing) while singing are differently supported by WFC and CFC, whereby CFC connections are particularly strong when the choir sings a canon in parts, apparently supporting the interaction and coordination of the different canon entries. The balance between WFC and CFC provides effective HFN or multilayer network topology, allowing the choir to function as a superordinate system or superorganism (Müller et al., 2018a, 2019a). It has also been reported that HFNs, and thus multilayer networks, possess small-world network topology and exhibit different network topology dynamics, which can vary as a function of age, disease, or cognitive performance (Brookes et al., 2016; Müller et al., 2016, 2019b; Tewarie et al., 2016, 2021; De Domenico, 2017; O'Neill et al., 2018; Tenney et al., 2021) or with respect to different conditions of interpersonal action coordination (Müller and Lindenberger, 2014; Müller et al., 2018a, 2019a).

NETWORK PHYSIOLOGY AND NEURAL NETWORK DYNAMICS

As noted by Buzsáki (2010, p. 362), "With Hebb's cell assembly hypothesis, it appeared that cognitive neuroscience had established a comprehensive research program to link psychological and physiological processes." The biological system is an integrated network with different types of interaction between the elements or subsystems operating as a whole. These subsystems continuously interact through various feedback loops and across different spatio-temporal scales to optimize and coordinate their function (Bartsch et al., 2015; Ivanov, 2021). Physiological systems and organisms exhibit complex dynamics that transiently change over time under different physiological states (Faes et al., 2014; Liu et al., 2015; Ivanov et al., 2016; Rizzo et al., 2020; Ivanov, 2021). These physiological states are characterized by specific network structures and coupling strengths between systems and subsystems, demonstrating a robust interplay between network topology and function (Bashan et al., 2012). Plamen Ivanov and colleagues introduced the concept of time delay stability (TDS) to identify and quantify network connectivity among

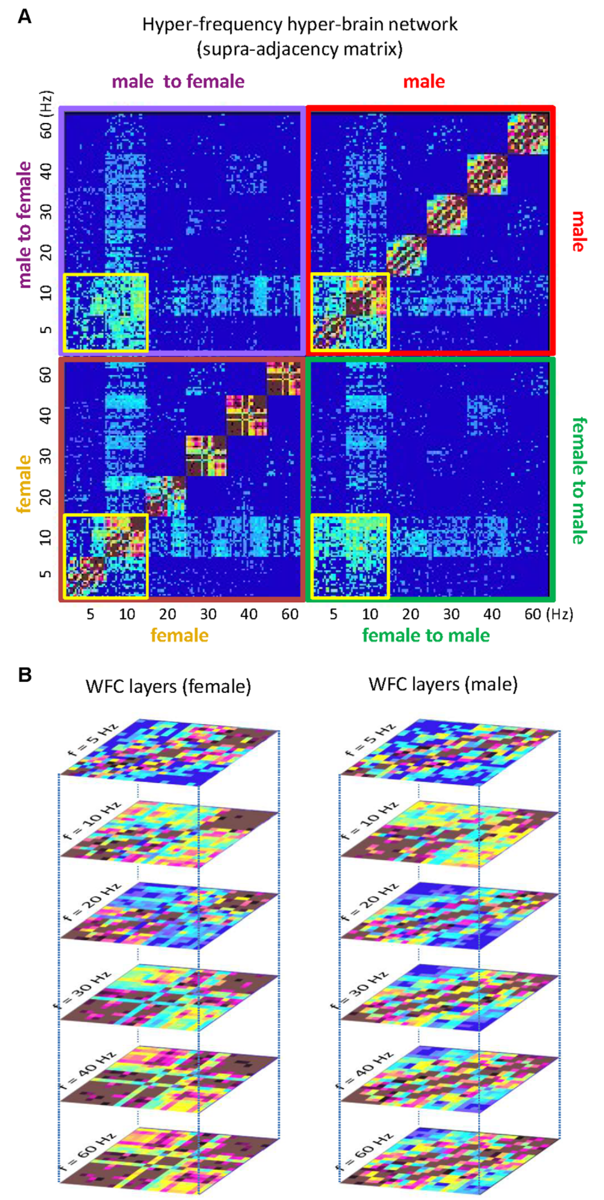

FIGURE 8 | Hyper-frequency hyper-brain network during kissing. **(A)** Supra-adjacency matrix of the common network. The supra-adjacency matrix (252 × 252) comprises all connections between 21 electrodes and six frequencies (5, 10, 20, 30, 40, and 60 Hz) within (brown and red quadrats) and between (green and purple quadrats) female and male brains, respectively. WFC connections between all electrodes within the female and male brains are distributed along the main diagonal of the matrix. The electrodes for each frequency are organized in anterior-posterior order from left to right: Fp1, Fpz, Fp2, . . .,O1, Oz, and O2. WFC connections between the brains are distributed along diagonals within the green and purple quadrats. The 5- and 10-Hz nodes (indicated by four smaller yellow squares) represent the so-called theta-alpha subnetwork. The alpha frequency (10 Hz) has the most connections and serves a cleaving or pacemaker function in the common network. **(B)** WFC layers of the female and male subnetworks or aspects. The WFC subnetworks are presented here in the form of a six-layer structure that is depicted in A along the diagonal. The connections between the layers within the female and male brains are represented by remaining edges in brown or red quadrats in A. The two other quadrants in A (green and purple) represent connections (WFC and CFC) between the brains.

physiological systems and proposed a system-wide integrative approach that may facilitate the development of a new field, Network Physiology (Bashan et al., 2012; Ivanov et al., 2016; Ivanov, 2021). In one study, they investigated dynamical network interactions between six physiological systems represented by 10 network nodes: cardiac and respiratory activity, chin muscle tone, leg and eye movements, and spectral brain activity in the five frequency bands: δ (0.5–3.5 Hz), θ (4–7.5 Hz), α (8–11.5 Hz), σ (12–15.5 Hz), and β (16–19.5 Hz) (Bashan et al., 2012). The authors found that transitions between physiological states were associated with changes in network topology: during deep sleep (DS), the network consisted mainly of brain-brain links, while with transition to light sleep (LS), links between other physiological systems emerged and the network became highly connected. In another study using the TDS measure, the coupling between cortical rhythms and peripheral muscle (chin and leg muscle tone) activation rhythms was investigated during sleep and awake states (Rizzo et al., 2020). They showed that cortico-muscular coupling was stronger during wake, weaker during rapid eye movement (REM) sleep and LS, and weakest during DS. Furthermore, they found that cortical rhythms (EEG) preferentially coupled with specific muscle rhythms (measured *via* electromyography, EMG) predominantly at the same frequency (i.e., WFC): (i) γ1 (20–33.5 Hz) and γ2 (34–98.5 Hz) brain and muscle rhythms strongly communicated with each other, particularly during wake and REM sleep; and (ii) slower rhythms (δ, θ, α, σ, and β) became strongly involved in the interaction between brain and muscles (both chin and leg) during REM sleep, LS, and DS. A pronounced transition from low brain network connectivity in DS and REM to high connectivity in LS and wake was also observed in a study by Liu et al. (2015). They also reported that different brain areas exhibited different network dynamics to achieve differentiation in function during different sleep stages, which was also frequency-specific (Liu et al., 2015). In another study using entropy-based measures to investigate the network dynamics of the heart and different spectral brain sub-systems (varying in the five frequency bands: δ, θ, α, σ, and β), it has been shown that the β EEG power node, acting as a hub in the brain–heart network, sent the largest part of the information coming from the brain–brain subnetworks to the heart and, at the same time, forwarded the information arriving from the heart system to the other brain subsystems (Faes et al., 2014).

In the aforementioned hyperscanning kissing study (Müller and Lindenberger, 2014), the coupling between the lip EMG and EEG brain waves was investigated within and between the individuals using WFC and CFC measures. The lip-brain coupling proved to be highest at the same frequency (i.e., 60 Hz) both within and between the individuals. Furthermore, the 10-Hz EEG oscillations, serving a cleaving or pacemaker function in the common hyper-brain network of the kissing couples, showed high CFC with the lip EMG of both participants (Müller and Lindenberger, 2014). However, the lip EMG nodes did not show any significant correlations with partner-oriented kissing satisfaction or self-reported kissing quality. Presumably, the theta-alpha subnetworks discussed above play a more prominent role in subjective feelings when kissing. Nevertheless, it is important to know how the cell assemblies or hyper-brain cell assemblies are related to other systems or subsystems. Due to the fact that different systems or subsystems in an organism (respiration, cardiac, etc.) function in a different (mostly lower) frequency range than the brain, the cross-frequency coupling may play an important role here.

In the choir study, with 11 singers and a conductor, directed coupling measures showed strong, mostly unidirectional influences of the conductor on the choir members, indicating that changes in the oscillatory activity of respiration and heart rate variability occurred in the conductor before the choir members, in accordance with the conductor's functional role. Furthermore, the choir members singing different parts of a song or canon could be partitioned into different modules or communities (in accordance with the parts sung, but not when singing these in unison; Müller and Lindenberger, 2011; Müller et al., 2018a). Thus, coupling strengths between systems and subsystems among the individuals involved in a coordinated activity (i.e., singing in a choir) also demonstrated a robust interplay between network topology and function (cf. Bashan et al., 2012). How such physiological systems or subsystems are linked to hyper-brain cell assemblies and how they contribute together to coordinated behavior remains to be seen.

FUTURE RESEARCH: PROVING THE HYPER-BRAIN CELL ASSEMBLY HYPOTHESIS ON DIFFERENT LEVELS

As shown, the hyper-brain networks based on intra- and inter-brain synchronization or coupling often have a complex and multilayer organization. This network organization is based on WFC and CFC, which also connect different systems and subsystems when two or more subjects interact or communicate with each other. It is proposed here that hyper-brain cell assemblies are capable of playing an important role in controlling the neural processes that take place in multibrain or multisystem interaction.

How can the proposed hyper-brain cell assembly hypothesis be tested? There are certainly different levels to test. The first level that comes to mind is the cellular level. But we must remember that although the theory proposed by Hebb (1949) was called cell assembly theory, he mainly argued that the synapses, their configuration, and cooperation play an important role in learning and other processes, known as "Hebbian Learning". He also assumed that a neuron can belong to different cell assemblies (Hebb, 1949). Buzsáki (2010), for instance, also talked about *"synapsembles"* as a constellation of current synaptic weights and as the constituents of the neural syntax. However, he admits: "Despite the expected critical role of synapsembles in neural syntax, experimental evidence supporting the role of synapsembles in combining and separating neuronal assemblies is scarce, largely because of the lack of tools to directly measure synaptic connectivity in the behaving animal" (Buzsáki, 2010, p. 372).

To test the hyper-brain cell assembly hypothesis on the *cellular level*, comprehensive hyperscanning studies on animals are needed. The primary goal of such studies should be to test whether neuronal elements fire synchronously in two or more brains during an interaction. The aforementioned studies in mice (Kingsbury et al., 2019) and bats (Zhang and Yartsev, 2019) provide very important information about neuronal cell activity during different interaction situations but are based on correlation data over time. Information about the spatiotemporal patterns of spiking behavior in hyper-brain assemblies is necessary to provide a better understanding of these phenomena. The study of spiking behavior in animals is also important in relation to the configuration and cooperation of synapses in multi-brain activity indicated above. It would be important to investigate how similar or dissimilar these synapse configurations are in the interacting brains. Moreover, there is evidence that molecular manipulations that cause an increase or decrease in the synaptic efficacy in dmPFC neurons in mice can trigger an upward or downward movement in social rank, respectively (Wang et al., 2011). The authors also found that dominance ranking in mice is transitive, relatively stable, and highly correlates with multiple features of dominance behaviors (e.g., aggressiveness, stress responsiveness, fearfulness, etc.). Therefore, such molecular or synaptic manipulations could be effective in combining and separating neuronal assemblies to understand how the behavioral specificity of these assemblies is generated by distinct synaptic weights and their configurations.

On the *brain oscillation level*, at least two techniques are currently attracting attention: multibrain stimulation (MBS) and multibrain neurofeedback (MBN). Both these methods allow the researcher to influence interacting brains in a hyperscanning experiment and change rhythmic activity in a predicted or hypothesized manner. Interestingly, these ideas have already received confirmation in animal studies. It has been shown that imposed interbrain synchrony shapes social interaction and social preference in mice (Kingsbury et al., 2019; Yang et al., 2021). Studies with MBS applications are currently still scarce and the results are inconsistent. Only a few studies have used transcranial alternating current stimulation in a hyperscanning setup (so-called hyper-tACS; see Szymanski et al., 2017a). In a dual finger-tapping task, it has been shown that the pairs improve their performance when their motor cortices are stimulated with beta band (20 Hz) in-phase currents (Novembre et al., 2017). In another hyper-tACS or MBS study, music instructor-learner dyads exhibited spontaneous and synchronized body movement and enhanced learning performance when stimulated with 6-Hz in-phase alternating currents (Pan et al., 2021). Remarkably, these effects were both phase- and frequency-specific: 6 Hz anti-phase stimulation or 10 Hz in-phase stimulation did not produce comparable results. In a study with synchronous dyadic drumming, contrary to the researchers' expectations, both the same-phase-same-frequency (6 Hz) and the different-phase-different frequency (5 Hz with 13 degrees offset in one participant and 7 Hz with 1 degree offset in the other) conditions were associated with greater dyadic drumming *asynchrony* relative to the sham (no brain stimulation) condition (Szymanski et al., 2017a). In an MBN study (Müller et al., 2021b), neurofeedback was provided either as two balls approaching each other (ball design), or as two pendula, each reflecting the oscillatory activity of one of the two participants (pendulum design). The delta (2.5 Hz) and theta (5 Hz) frequency oscillations were used as neurofeedback features. The participants proved able to increase inter-brain synchrony by using neurofeedback, especially when it was fed back at the theta frequency. Moreover, other oscillatory activities (e.g., power spectral density, peak amplitude, and peak frequency) also changed during the neurofeedback task compared with the rest. Importantly, all the measures showed specific correlations with the subjective post-survey item scores, reflecting subjective feeling and appraisal (Müller et al., 2021b). The disadvantage of the MBS studies presented above is that the brain stimulation took place either in-phase or anti-phase, whereas for the testing of the hyper-brain cell assembly hypothesis it would be essential to shift the phase only slightly in one subject relative to the other. In this way, it might be possible to test whether absolute or exact in-phase synchronization is important for social interaction and for the hyper-brain cell assembly to synchronously ignite cell assemblies in both brains and to integrate them. In the study by Szymanski et al. (2017a), such a phase shift was used, but the stimulation occurred at different frequencies (i.e., 5 and 7 Hz). Furthermore, hyper-tACS have so far only addressed a limited number of homologous brain regions (cf. Novembre and Iannetti, 2021) and all three aforementioned studies used different cortical sites and hemispheres for brain stimulation. Using heterologous stimulation electrodes would be more appropriate for the investigation of inter-brain synchronization during naturalistic social interactions (cf. Novembre and Iannetti, 2021), because inter-brain synchronization mostly concerns heterologous recording electrodes in two brains (e.g., frontal to central, frontal to parietal, etc.). The further disadvantage of the MBS approach is that the stimulation causes severe artifacts in EEG, making a precise examination of brain oscillations during stimulation difficult and sometimes impossible. The MBN approach is much better in this respect, as it does not cause EEG artifacts. Again, one could manipulate the temporal features of the neurofeedback presentation and see how its temporal shift in one subject relative to the other affects hyper-brain neurofeedback performance and the spectral or synchronization indices. As mentioned above, cortical and especially biological systems never operate at only one oscillation frequency. Therefore, it is preferable and more convincing to test the suggested hypothesis with a combination of WFC and CFC, which also involves the multilayer approach. The use of MBS or MBN approaches in different frequencies that have a certain relationship to each other would be particularly interesting, also in terms of phase-to-amplitude CFC or other CFC relationships. Note, however, that all these approaches might have a high potential impact on oscillatory activity modulation during the respective experiment, but such methods can provide only indirect evidence with regard to the suggested hyper-brain cell assembly hypothesis—they cannot substitute for testing the hypothesis at the cellular level as suggested above to examine the respective spiking behavior.

CONCLUDING REMARKS

Synchronization phenomena are ubiquitous and inevitable constituents or emergences of our universe. They are also crucial for our everyday social life, where people often have to coordinate their actions with each other in time and space. It is then also natural and self-evident that these phenomena take place in the brain controlling and mapping our behavior and relationships. Cell assemblies emerging within the interacting brains require a steady adjustment and tight cooperation to justify the interpersonal dynamics and interactive activity that very often operate at ms time scales. In this Hypothesis and Theory article, a *Hyper-Brain Cell Assembly* is hypothesized that encompasses and integrates oscillatory activity within and between brains, and represents a common hyper-brain unit responsible for social and interaction behavior. This hypothesis states that such hyper-brain cell assemblies emerge through joint and simultaneous ignition of neural cells within two or more brains supported by inter-brain synchronization patterns and their ongoing adjustment. Hyper-brain modules or communities comprising nodes across two or several brains and indicating strong relationships between these nodes or brain structures are considered as one of the possible representations of such hypothesized *hyper-brain assemblies*. These assemblies or hyper-brain community structures can also have a multidimensional or multilayer dynamic organization based on WFC and CFC within and between brains or physiological systems and subsystems. It is concluded that the neuronal dynamics during interpersonal interaction ae brain-wide and based on a common neuronal activity of different brain structures within and between brains operating in permanent interaction. Different approaches for testing the hyper-brain cell assembly hypothesis on different levels were proposed. Clearly further sophisticated research is needed to establish our view and deepen our understanding of these highly interesting and complex phenomena.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the ethics committee of Max Planck Institute for Human Development (Berlin). The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and has approved it for publication.

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Audience Interbrain Synchrony During Live Music Is Shaped by Both the Number of People Sharing Pleasure and the Strength of This Pleasure

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The study of interbrain coupling in a group of people attending a concert together is a favorable framework to estimate group emotions and more precisely emotional connection between people sharing situations in the same environment. It offers the advantage of studying interactions at the group level. By recording the cerebral activity of people from an audience during a concert using electroencephalography, we previously demonstrated that the higher the emotions and the physically closer the people were, the more the interbrain synchrony (IBS) was enhanced. To further investigate the parameters that shaped inter-brain synchronization in this context, we now focus on the emotional dynamics of the group as a whole by identifying specific moments in the concert that evoked strong or weak emotions, as well as strong or weak emotional cohesion between individuals. We demonstrated that audience interbrain synchrony is mainly associated with experiencing high musical pleasure and that the group emotional cohesion can enhance IBS, but alone is not the major parameter that shapes it in this context.

Keywords: EEG hyperscanning, cerebral coupling, emotional connection, emotional sharing, live performance, musical reward

1. INTRODUCTION

The study of cerebral coupling during social interactions through hyperscanning paradigms has shifted in recent years, with a huge volume of original research in various controlled (Leong et al., 2017; Mller et al., 2021) or more ecological settings and natural environments (Dikker et al., 2017; Chabin et al., 2021; Reinero et al., 2021). Although very challenging, natural environments offer the opportunity to further study direct (conversation, cooperation, etc.) as well as indirect (when people simply share a situation without explicit verbal or nonverbal communication) social interactions without simulating an experimental setting. Performing measurements in these conditions makes the environment naturalistic. It promotes participants' immersion in the experiment (Czepiel et al., 2021; Wald-Fuhrmann et al., 2021) and natural interactions with both environments and people. Interbrain synchrony (IBS) can be conceptualized "as a neural mechanism that causally facilitates social interaction"; supporting the hypothesis that the natural neural synchrony enhances social interaction, or conceptualized as the simple a consequence of neural entrainment elicited when sharing the same sensory inputs (Novembre and Iannetti, 2021). While is it still open to debate, recent data from hyperscanning studies suggest that IBS is not only shaped by simultaneous integration of similar external inputs (Novembre and Iannetti, 2021), but may have the potential to support social interactions. In brief, being in sync with peers could potentially modify the way we interact. For example, social interactions in rodents can be mediated by simultaneously synchronizing or desynchronizing populations of neurons in the brains of two individuals using intra-brain light stimulations (Yang et al., 2021). Also, visual cues have been reported to influence IBS when performing a face to face baseline before shared appraisal situations (Dikker et al., 2017) and during direct social interactions (Leong et al., 2017) in humans.

To investigate whether positive musical emotions, referred to as pleasure, can be shared between people even in indirect interactions (Chabin et al., 2021), our previous research aimed to estimate emotional neurophysiological synchronization by recording the brain activity of people attending a concert together using electroencephalography, while they were reporting their emotions in real-time (four levels to be reported from neutral = 1, low pleasure = 2, and high pleasure = 3 up to "musical chills" = 4). In the traditional frame of classical concerts, people are expected to minimize overt interactions toward others and are not expected to explicitly influence their peers' behavior (Tschacher et al., 2021). Nevertheless, we mainly demonstrated that IBS was enhanced when people felt similar and strong emotions, but also that the social context can influence IBS even in case of indirect communication. The closer the people were physically, the more similar their emotional reports were. More importantly, the closer they were, the higher was the cerebral synchrony (as well as the physiological synchrony measured using electrodermal activity) when they were reporting high levels of pleasure related to the music.

While our findings are correlational in nature, we defend the idea that sharing similar external inputs is not the only factor that explains these findings. We hypothesized that sharing a high level of pleasure related to music at the same time naturally elicits similar brain activity for several participants, thus enhancing IBS. Further, considering the relationship between physical proximity and IBS (Chabin et al., 2021), we propose that direct non-verbal communication elicited by the desire to share a pleasant emotion with others reinforces or sustains this effect through a retroactive loop. Reciprocally, we recently considered an alternative hypothesis that suggests that interbrain synchrony can shape social interaction to a certain extent, we can also consider that the specific cortical activities (in the frontotemporal areas in the theta frequency band Chabin et al., 2020) related to musical reward processing, shape IBS and enhance a natural implicit form of social interaction, in particular with peers that are physically close.

Since our design overcome the simple dyadic interaction, usually met in hyperscanning paradigms, we are now able to focus the analyses on the emotional dynamic of the overall group. Thus, we still wonder whether the global group emotional cohesion (GEC)–defined here by the reporting of the same emotions at the same time in a majority of people from the sample ($n = 15$), independently of the strength of emotion–was sufficient to elicit enhanced IBS, or concomitantly, whether the strength of emotions alone drove it. In other words, is IBS associated in the first place with being "on the same wavelength" as a group, and potentially in an unconscious way by perceiving a certain emotional closeness/connection with people? If yes, these results could argue for the social effect of IBS theory. This report aims to shed light on the way the emotion of the group plays a role in the global group IBS and, to a certain extent, estimate how the experiment is more than an aesthetic individual experience but also "a communal experience" (Tröndle, 2020) in the context of a concert audience. We expected that both the emotional cohesion and the strength of emotion would shape the IBS; the more the emotion and the number of people sharing it will be high, the more IBS should be high as well.

2. METHODS

Only a brief method section is provided here. Full details about procedures, recruitment, method, data processing, and analysis can be found in the methods section of our previous publication (Chabin et al., 2021).

2.1. Participants

Our participants were recruited among people who had bought a ticket for the semi final round of the International Competition for Young Conductors held in Besanon, France (september 2019). Our sample was composed of 15 participants (12 women) with a mean age of 55.7 years (SD = 18.9, range = 18–78; seven were musicians, including one professional). The study met the local ethical regulations as laid out in French law concerning non-invasive protocols involving healthy participants and was classified as an observational study outside the scope of the Jard law (Article R1121-1 of the French Law Code of Public Health amended by decree n 2017–884 of May 2017). It was submitted to the Ethics Committee CPP Est II, which exempted the study from the full ethics review process. Each participant was informed of the observational nature of the study and signed a non opposition notice designed for observational studies. The participants received no compensation for participation in the study.

2.2. Procedure

Participants were seated on the same row of seats, at the first balcony of the concert room. They were only instructed to enjoy the concert, to stay calm and quiet and to limit unnecessary movements. We used a unilateral emotional scale that was a gradient of positive pleasure. Participants reported in real time the pleasure related to music on a smartphone according to 4 levels of positive pleasure (neutral, low pleasure and high pleasure up to chill). They listened to 6 professional conductors who conducted in turn a full symphonic orchestra and choir, performing several extracts of Francis Poulenc Stabat Mater.

Twelve of the 15 participants were equipped with consumer-grade EEG headset.

2.3. Estimation of Interbrain Synchrony

We distinguished two main components for the estimation of IBS that were; group emotional cohesion (GEC) and group emotional state (GES).

-***Group Emotional Cohesion*** informs about whether the participants were emotionally aligned during the concert. When two participants reported the same level of pleasure, the value is 100%, 50% when participants reported levels of pleasure that differ by 1 point (e.g., high vs. low pleasure), 25% when participants reported levels of pleasure that differ by 2 points, and 0% for differences of more than 2 points. The final GEC index is an average of all 105 pairs GEC index, calculated at a temporal precision to the nearest second. We separated GEC in 3 sub components; High GEC corresponds to group synchrony higher than 70% (navy blue **Figure 1A**), Med GEC corresponds to group synchrony between 50 and 70% (cobalt blue **Figure 1A**), while Low GEC corresponds to synchrony lower than 50% (sky blue **Figure 1A**). A representation of GEC is given on the **Figure 1A**.

-***Group Emotional State*** represents the strength of the group pleasure related to music and is calculated by averaging the group emotional responses with a temporal precision to the nearest second. We separated GES in two subcomponents; High GES when the overall group reported a degree of pleasure higher than the low pleasure level and Low GES when the group reported a degree of pleasure lower than the low pleasure. A representation of the GES is given on the **Figure 1B**.

-***Theta*-Interbrain Synchrony:** EEG data have been recorded with two references on parietal sites (P3 (CMS) and P4 (DRL) with EMOTIV® EPOC+. The overall method for IBS estimation is a replication of the method of Dikker et al. (2017) and Chabin et al. (2021). In brief, EEG data were low- and high-pass filtered (Butterworth) between 1 and 30 Hz, with a notch filter fixed to 50 Hz using the Cartool software. We performed a principal component analysis (PCA) to avoid any rhythmical eye blink influence over IBS. Then we computed IBS defined as θ-IBS by performing a coherence calculation between the signals acquired on similar electrodes for two participants (over frontal, prefrontal and temporal electrodes; AF3, AF4, F3, F4, F7, F8, FC5, FC6, T7, T8 electrodes) using power spectral density (4–8 Hz). It informs about "the amount of mutual information between the two systems," with a value of 0 when signals are independent and 1 when there is a strong linear relationship between signals. The overall IBS index is an average of IBS estimated for each pair of electrodes for all pairs of participants. Phase and antiphase signals do not influence the result of the calculation. θ-IBS has been computed for High GES/High GEC (when a great number of people of the group shared a high emotional state related to music), for High GES/Low GEC (when a low number of people of the group shared a high emotional state related to music), for Low GES/Low GEC (when a low number of people of the group shared a low emotional state related to music). The low number of events and the minimum number of epochs free from artifacts required to include pairs did not allow us to calculate the condition High GEC/Low GES. We also computed θ-IBS when people from the group were highly (High GEC), moderately (Med GEC), or lowly (Low GEC) aligned in terms of emotional reports independently of the GES. Finally, the control condition corresponds to a random selection of music time periods. The number of epochs selected for the control condition was similar to the amount of epochs got in other conditions.

3. RESULTS AND DISCUSSION

As expected, θ-IBS estimation revealed that theta coherence was shaped by both GEC and GES, since our results revealed significant differences between each condition (Friedman test $\chi^2_{(2)} = 79.4$, $P < 0.0001$, Kendall's $W = 0.68$; for $n = 39$ pairs with enough common periods of signal free from artifacts, see **Figure 1C**). IBS was significantly higher when both GEC and GES were high, and this effect progressively decreased when the GEC decreased but the GES still high, and even more when both the GEC and GES were low ($p < 0.001$ in each case; Durbin Conover *post-hoc* test). As a control, we also estimated θ-IBS for High GEC, Med GEC or Low GEC only, independently of the strength of group emotion [Friedman test $\chi^2_{(3)} = 27.1$, $P < 0.0001$, Kendall's $W = 0.25$; for $n = 36$] and counterintuitively, simple emotional alignment did not increase θ-IBS. *Post-hoc* tests show a higher theta coherence for Low and Med GEC compared to High GEC (**Figure 1D**). We imputed the low θ-IBS for High GEC (compared to Med and Low Sync, $p < 0.01$) to the lower emotional ratings reported by the group (mean 1.64, SD = 0.067) that potentially influenced θ-IBS estimation.

This new set of results suggests that, in the context of the concert, audience interbrain synchrony is mainly associated with experiencing high musical pleasure. Considering our previous results which suggest that the IBS was higher when people share intense emotions (Chabin et al., 2021), mixed with the results presented on the **Figure 1D**, we suggest that the group emotional cohesion can enhance θ-IBS, but alone is not the major parameter that shapes it in this context. These findings also resonate with other recent studies that focused on group's collective physiological responses in the context of the concert. For example, Ardizzi et al. (2020) demonstrated that cardiac synchrony was spontaneously elicited by both the shared stimulations and shared/coherent explicit emotional experience. Czepiel et al. (2021) also demonstrated that specific moment of the concert linked with variations of musical characteristics and producing variations in arousal, engagement and familiarity elicited higher physiological synchrony and finally (Tschacher et al., 2021) suggested that "synchrony may yield an objective signature of aesthetic immersion at the collective level of a concert audience." We defend the idea that simply shared stimulation should not be the main component driving the θ-IBS here, while we recognize that it can play a role as well. Selected periods for our analyses were only based on emotional reports provided by

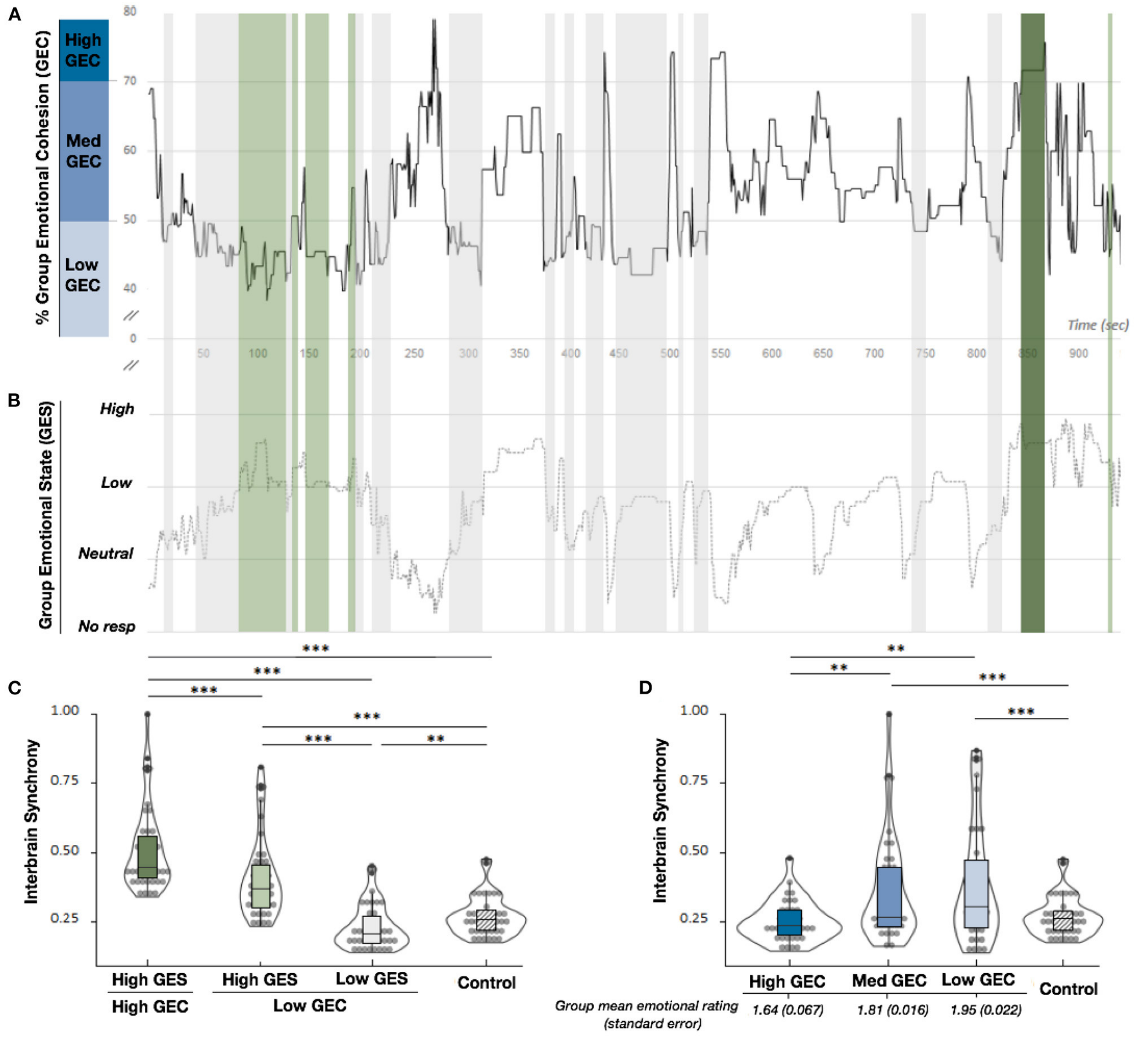

FIGURE 1 | (A) Representation of the averaged percentage of group emotional cohesion (GEC) ($n = 15$ giving 105 pairs) derived from behavioral reports for one conductor performance calculated at a temporal precision to the nearest second. This is only a representation, analyses have been conducted with data collected throughout the concert. High GEC is in navy blue **(A)**, Med GEC is in cobalt blue **(A)** and Low GEC is in sky blue **(A)**. **(B)** Representation of the average of the group pleasure reports ($n = 105$ pairs) on smartphones according to four levels; Neutral, Low pleasure and High pleasure up to chills. Colors correspond to a specific moment visible on the schematic representation of both group emotional state and group emotional cohesion; High GEC/High GES in dark green, Low GEC/High GES in light green, and Low GEC/Low GES in light gray. **(C)** Box plot of the theta coherence estimation calculated during High vs. Low group emotional cohesion for high group emotional state or low group emotional state related to music [see **(A,B)**, green/gray]. **(D)** Box plot of the theta coherence estimation calculated when the group had a High GEC [navy blue **(A)**], a moderate GEC [cobalt blue **(A)**], or a low GEC [sky blue **(A)**]. For both plots: $^{**}p < 0.01$, and $^{***}p < 0.001$.

participants, thus collective auditory/sensory inputs cannot be considered as the root cause producing the main effect. The control condition, through which auditory and sensory stimulations were the same for all participants as in other conditions, is significantly lower than both High GES conditions, thus providing a supplementary argument in favor of this hypothesis.

This exploratory work is a first step toward the investigation of a group emotional dynamic and aims to bring complementary results for our previous publication (Chabin et al., 2021). Several recent works also demonstrated that a perceiving a significant interaction or shared intentionality leads to exhibited marked IBS (Provolovski and Perlmutter, 2021). Here we seek to explore whether minimal interactions produce the same effect. We now wonder to which extent sharing high levels of emotions that elicit a higher θ-IBS, shaped the group emotional dynamic. In this case, interventional research studies should now investigate more deeply the social interactions at the group level to highlight not only correlational, but also causal evidence for IBS (Novembre and Iannetti, 2021).

DATA AVAILABILITY STATEMENT

The datasets generated for this study can be found in a figshare repository: https://doi.org/10.6084/m9.figshare.14401337.

ETHICS STATEMENT

Ethical review and approval was not required for the study on human participants in accordance with the local legislation and institutional requirements. The participants signed a non opposition notice designed for observational studies.

AUTHOR CONTRIBUTIONS

TC: conceptualization, data acquisition, formal analysis, writing original draft, writing—review, and editing. DG: conceptualization, data acquisition, formal analysis, and writing—review. LP and AC: conceptualization, data acquisition, and writing—review. All authors contributed to the article and approved the submitted version.

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BRIEF RESEARCH REPORT
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The Increasing Effect of Interoception on Brain Frontal Responsiveness During a Socially Framed Motor Synchronization Task

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This research explored the effect of explicit Interoceptive Attentiveness (IA) manipulation on hemodynamic brain correlates during a task involving interpersonal motor coordination framed with a social goal. Participants performed a task requiring interpersonal movement synchrony with and without a social framing in both explicit IA and control conditions. Functional Near-Infrared Spectroscopy (fNIRS) was used to record oxygenated (O2Hb) and deoxygenated hemoglobin (HHb) changes during the tasks. According to the results, the prefrontal cortex (PFC), which is involved in high-order social cognition and interpersonal relations processing, was more responsive when inducing the explicit focus (IA) on the breath during the socially framed motor task requiring synchronization, as indicated by increased O2Hb. In the absence of a broader social frame, this effect was not significant for the motor task. Overall, the present study suggests that when a joint task is performed and the individual focuses on his/her physiological body reactions, the brain hemodynamic correlates are "boosted" in neuroanatomical regions that support sustained attention, reorientation of attention, social responsiveness, and synchronization. Furthermore, the PFC responds significantly more as the person consciously focuses on physiological interoceptive correlates and performs a motor task requiring synchronization, particularly when the task is socially framed.

Keywords: interoceptive attentiveness, motor task, fNIRS, PFC, synchronization, social joint task

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INTRODUCTION

How does it feel to dance perfectly synchronized in front of an audience? How does it feel when you think about the sensations of your body while dancing or playing an instrument with another partner?

This ability to perceive, notice and pay attention to one's internal body state, including visceral feelings, consists of interoception. Precisely, the focused attention to a particular interoceptive signal for a specified time interval, such as the breath, has been previously defined as Interoceptive Attentiveness (IA) (Schulz, 2016; Tsakiris and De Preester, 2018).

Conceived of as a deliberate focus on the breath that underpins practices of controlled breathing, IA has been demonstrated to have an enhancing effect on various cognitive and emotional functions like prolonged attentional focus, cognitive control, and awareness (Boyadzhieva and Kayhan, 2021; Weng et al., 2021), negative emotion modulation (Arch and Craske, 2006; Paul et al., 2007; Varga and Heck, 2017; Balconi and Angioletti, 2021b), and the ability to recover from high-stress levels (Grossman, 2011). Regarding the enhancing effect of IA, it is worth noting that IA is not a static dimension of interoception, but can be trained by specific types of interventions, like brief relaxation practices, mindfulness approaches, or even short controlled breathing sessions (Farb et al., 2013; Weng et al., 2021).

According to previous neuroimaging evidence, the IA lays its foundations on a network of cortical and subcortical structures, which included the posterior right and left insula, right claustrum, precentral gyrus, and medial frontal gyrus (Schulz, 2016). Recent findings revealed greater activation in several cortical regions for interoception including the insula and sensorimotor regions (postcentral gyrus, inferior parietal lobule, paracentral lobule, precentral gyrus, supplementary motor area) and occipital cortex, temporal cortex, anterior cingulate cortex, and lateral prefrontal regions (Stern et al., 2017). An activation of posterior insula was found in relation to cardioception, with a right-hemisphere dominance processing the non-verbal inputs. While an increase in neural activation at the level of the PFC has been found in relation to both the distribution of top-down attention and the processing of interoceptive information, probably mediated through the claustrum (Schulz, 2016).

A significant activation of these areas was not only found in relation to interoception, but supports other processes, including attention and motor control. In particular, the dorsolateral portion of the PFC is involved in orienting and sustaining focused attention on the target while controlling internal and external interferences (Kondo et al., 2004). It also helps to better sustain focus on the breath by improving the person's awareness of when his or her mind wanders, allowing them to return their attention to the breath (Dickenson et al., 2013). In addition, this brain structure has been linked to social functions, by way of examples a fully conscious motor control and the adaptations to a changing rhythmic pattern (Stephan et al., 2002) or mutual cooperative interactions and interpersonal coordination (Balconi et al., 2017; Hu et al., 2021).

Nevertheless, to the best of our knowledge, there is no available evidence on how IA influences the prefrontal cortex (PFC) neural activity during interpersonal sensorimotor synchronization (interpersonal SMS), intended as movement among individuals that compels simultaneous occurrence, such as walking, drumming, playing an instrument, applause, or synchronized sports.

Interpersonal synchronization, in its widest terms, comprises a set of social communicative actions that encompasses joint attention, imitation, turn-taking, non-verbal social-communicative exchanges (Charman, 2011), and involves temporal and content synchronization (Delaherche et al., 2012). Interpersonal synchronization can occur either consciously when there is an explicit objective or unconsciously when the goal is absent. Motor synchronization is a subtype of interpersonal synchrony that focuses solely on non-verbal social-communicative exchanges and involves the synchronization of two people engaged in a social interaction (Fitzpatrick et al., 2017).

Former single-person synchronization studies showed the striato-thalamo-cortical system was involved in the timing process, and the coupling of motor and sensory areas engaged in rhythm perception. The cerebellum was critical to prediction and error correction, and activation of prefrontal and parietal areas was found in complex SMS tasks due to the high cognitive control demand (Repp and Su, 2013; Keller et al., 2014).

Regarding the social influence on synchronization performance, Dai et al. (2018) conducted a real-person joint-tapping hyperscanning experiment and found interpersonal SMS performance was better in a bidirectional than in unidirectional condition, suggesting bidirectional condition can be considered as more cooperative than unidirectional condition. Interestingly, two-person studies showed the right PFC of two interactive individuals exhibited synchronization during joint-tapping tasks (Cheng et al., 2015; Baker et al., 2016; Pan et al., 2017). It is, therefore, possible that even a simple motor task if openly socially framed can affect the neural activation of the participants engaged in the synchronization task.

Concerning the distinction between PFC and premotor cortices (PMC) activations, Bien et al. (2009) studied the functional separation between automatic and intentional imitation by using functional magnetic resonance imaging (fMRI): they found that frontal cortices transfer neural input about response inhibition to the PMC, which is engaged in automatic imitation. In line with the present understanding, the PFC seems to play a key role in social activities demanding synchrony (Sänger et al., 2011; Liu and Pelowski, 2014; Cheng et al., 2015), sustained attention (Khoe et al., 2020), and shared intentionality (operationalized as the joint attention to the stimulus with a mutual goal of problem-solving through interaction; Fishburn et al., 2018).

Notwithstanding, the influence of IA manipulation on tasks requiring interpersonal SMS has never been tested before. Furthermore, there is no observation of the effect of IA on synchronization when the task is not simply motor but has a declared social frame.

To investigate the potential positive impact that the manipulation of the attentional focus on the body could have on human social interactions can be an important research topic also in terms of promotion and intervention. In fact, an increased attentional focus on one's body could promote the self-regulation of the individual and consequently obtain better performance also during a dynamic of social motor synchronization, such as sports, arts, but also in basic learning processes. IA is relevant for motor synchronization since interoceptive processes inform motor planning, making predictions about a partner's movements, and motor coordination with the social partner (Farmer and Tsakiris, 2012). Also, previous studies suggested a link between controlled breathing and motor synchronization, stating the first plays a special role in mediating respiration-entrained brain synchrony enhancing motor activity (McKay et al., 2003) and synchrony in the motor cortex (Herrero et al., 2018).

Despite even basic interpersonal SMS, like for example rhythm tapping activity or walking, being shown to promote social bonds between partners (Wiltermuth and Heath, 2009; Vicaria and Dickens, 2016), as well as a self-reported sense of joint agency (Bolt et al., 2016), it remains still unexamined whether the PFC activation can be enhanced by consciously focused attention on the breath and by explicit social framing.

As a result, the aim of this work is to observe how intentional IA manipulation affects hemodynamic correlates of a motor synchronization task when it is or is not socially framed. In this experiment, the social framework applied to the motor task consisted only of explicitly requiring shared intentionality by the participants. Indeed, in the socially framed motor task, participants were told that they had to try to synchronize to develop greater teamwork skills. Therefore, the innovativeness and relevance of this task consist in maintaining the bidirectionality in interpersonal SMS and at the same time in emphasizing the mutual goal of the motor task.

In line with previous evidence supporting the positive impact of IA on cognitive processes (Weng et al., 2021), it was assumed that IA could magnify PFC correlates during the synchronized motor tasks, independently from the frame, compared to the control condition. Secondly, given the role of PFC in supporting social cognition and shared intentionality (Fishburn et al., 2018), an increased PFC activation for the socially framed motor task, compared to the simple motor task, is expected. Finally, given the involvement of PFC in promoting sustained attention (Khoe et al., 2020) and shared intentionality (Fishburn et al., 2018), we expect the PFC activation will be boosted in the socially framed motor task by the explicit IA condition.

METHODS

Participants

For this fNIRS research, a total of eighteen healthy volunteers [14 females and four men; age mean (M) = 27.05; Standard Deviation (SD) = 3.18] were recruited from among university students with a non-probabilistic convenience sampling approach. Because the phenomenon under investigation is relatively new in the field of social neuroscience, and the literature does not provide systematic repeated evidence, previous references could not be used to estimate the extent of expected significant effects. As a result, we ran an *a priori* power analysis for repeated measures ANOVA and found that a total sample size of 17 (with alpha error probability = 0.05 and power 0.80) is the minimum for detecting a significant within effect or factor interaction [G*Power 3.1 software (Faul et al., 2007)].

Exclusion criteria included physiologic disorders such as chronic or acute pain, severe medical and chronic diseases, seizures, traumatic brain damage, pregnancy, previous meditation experience, and any mental or neurologic disorders. Participants were right-handed and with normal visual acuity. All subjects signed a written informed consent form prior to the experiment, and they were informed no compensation was provided. The Department of Psychology at the Catholic University of the Sacred Heart of Milan, Italy, gave its consent to the study, which was carried out in conformity with the Declaration of Helsinki.

Study Procedure

Participants were introduced in a room with dimmed light and asked to sit next to an experimenter in charge of giving the experimental instructions and carrying out the synchronization tasks, together with the participant as a member of the dyad. Before starting with the experimental tasks, a 120-s resting baseline was recorded by using fNIRS.

Regarding IA manipulation, each participant performed the motor synchronization tasks in two distinct conditions: the explicit IA condition and a control condition (Balconi and Angioletti, 2021a,b). The explicit IA condition requested participants to focus on their body while executing the task, as it follows: *"During this task, we want you to focus your attention on your breath. As you execute the task, try to notice how you feel and whether there are any changes in your breath."* Instead, in the control condition, participants were given instructions to complete the task, but no explicit request to concentrate on their interoceptive correlates was provided. The order of task execution was randomized and counterbalanced to prevent potential biases due to sequence effects. At the end of the four tasks, a set of manipulation checks were conducted for checking both their IA and social framing manipulations. Participants were asked to rate the attention they paid to themselves during the task on a Visual Analog Scale (VAS) with the following item "From 0 to 10, how much attention you paid to yourself during the task?," the average score was for all the participants above 5 points (*M* = 7.88; SD = 1.62).

The entire experiment took less than 40 min (**Figure 1A**).

Motor Synchronization Tasks

The participants were required to perform a different version of the same motor synchronization task consisting of a simple finger movement task [modified version of the task adopted in a previous study (Jobbágy et al., 2005)]. For a total of 3 min, subjects were required to synchronize their finger movements with the experimenter sitting in front of them (**Figure 1B**).

For the finger movement task, the participants were told to position their dominant hand on the table in the prone position in front of the experimenter, with the fingers about one cm apart and elbows on the table. They were then asked to raise the fingers of their hand and tap the table with their little, ring, middle, index, and thumb. They were not told to perform the action at a specified tempo or raise their fingers as high as possible; instead, they were told to synchronize with the experimenter's movement in front of them.

For the socially framed motor task, the task consisted of the same motor synchronization task previously described (i.e., the finger movement task), but it was socially framed by specifying that they need to synchronize during the motor task in order to develop greater teamwork skills. Our goal was to develop two experimental tasks: one in which subjects completed a motor task that supported shared intentionality and another in which

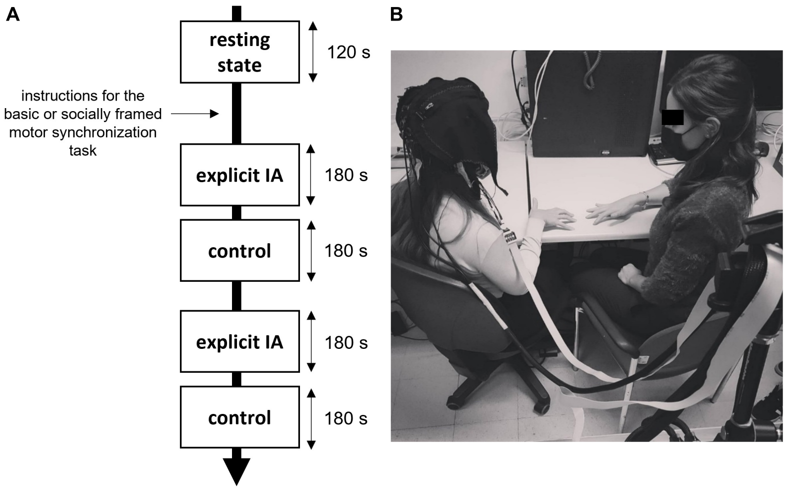

FIGURE 1 | (A,B) Experiment setting and procedure. **(A)** Duration and timing of the motor tasks requiring synchronization, the instructions were provided both for the explicit IA and control conditions and for the type of the motor task (socially framed or not). **(B)** An example of an experimental setup with a fNIRS recording device and the experimenter performing the motor task.

the subjects completed the identical motor task, but the sharing of intention was not declared or emphasized. The order of the motor synchronization task execution was randomized and counterbalanced to prevent potential biases due to sequence effects (by computer-generated randomization).

At the end of the tasks, there was a debriefing phase in which participants declared their perceived sense of synchrony that was at the 98%. In the manipulation checks, the following item was included: *"From 0 to 10 how much do you think you were synchronized with your partner*?," the average score was for all the participants above 5 points ($M = 8.13$; $SD = 0.27$).

Functional Near Infrared Spectroscopy Montage

For this study, oxygenated hemoglobin (O2Hb) and deoxygenated hemoglobin (HHb) variations were recorded by applying a six channel optodes matrix from a NIRScout System (NIRx Medical Technologies, LLC, Los Angeles, CA, United States). A fNIRS Cap was used to position four light sources/emitters and four detectors over the head in accordance with the standard international 10/5 system (Oostenveld and Praamstra, 2001). The emitter-detector distance was kept constant at 30 mm for consecutive optodes, and a near-infrared light with two wavelengths was used (760 and 850 nm). The fNIRS setup was consistent with a prior fNIRS research on IA (Balconi and Angioletti, 2021a) and in **Figure 2** are reported the following six channels derived by optodes positioning: Ch1 (AF3-F3), Ch2 (AF3-AFF1h), Ch3 (F5-F3), that correspond to the left DLPFC, and Ch4 (AF4-F4), Ch5 (AF4-AFF2h), Ch6 (F6-F4) consistent with the right DLPFC (Brodmann Area, BA09). A probabilistic atlas implemented in the software fOLD [fNIRS Optodes' Location Decider (Zimeo Morais et al., 2018)], based on the automated anatomical labeling atlas Brodmann (Rorden and Brett, 2000), was used for the correspondence between brain regions and channels.

Hemodynamic Data Analysis

For fNIRS data acquisition and processing, the same procedural steps described in Balconi and Angioletti (2021a) were adopted. During the baseline (120 s) and the tasks, the hemodynamic signals (O2Hb and HHb) were acquired continuously with the NIRStar Acquisition Software. Each participant performed the two tasks in the two conditions one time. The average number of trials for each condition was no less than 45 for the 3 min, therefore 45 trials per each condition were considered. The signals from the six channels were collected at a sample rate of 6.25 Hz, then processed and analyzed by employing the nirsLAB software (v2014.05; NIRx Medical Technologies LLC, 15 Cherry Lane, Glen Head, NY, United States) based on their wavelength and position, yielding mmol*mm values related to the variations in O2Hb and HHb for each channel.

A digital band-pass filter was adopted to filter the raw data at 0.01–0.3 Hz (Balconi et al., 2015; Pinti et al., 2019). To detect noisy channels due to motion artifacts or amplitude changes raw time-series were visually inspected subject-by-subject both during the experimental phase and the signal analysis. 3% of the data was eliminated for artifacts. During this visual inspection channels with poor optical coupling and absence of ∼1 Hz heartbeat oscillations were excluded (Pinti et al., 2015). To preserve the frequency related to the task, a Mayer's frequency was included in the filtering range which corrupts the optical cortical response estimation. In this regard, future research could adopt different methods to overcome this limitation. Moreover, a linear-phase FIR filter on respiration (0.3 Hz), that allows obtaining the symmetric-impulse-response, was used (Naseer and Hong, 2013; Naseer et al., 2014). For each channel, the average O2Hb and HHb were calculated and extracted for the

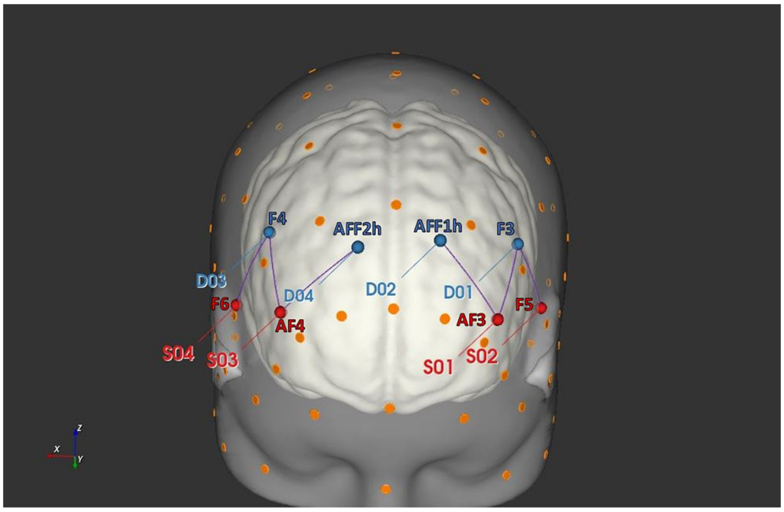

FIGURE 2 | fNIRS head probe placement. The head rendering has been generated with the software NIRSite (NIRx Medical Technologies LLC) and it displays the position of the fNIRS sources (in red) and detectors (in blue).

two tasks performed in the two experimental conditions. **Figure 3** shows the plots of the time course of O2Hb and HHb for all channels under the four conditions.

Following the data pre-processing, the average concentrations in the time series for each channel and individual were used to calculate the effect size in each condition. The following formula was adopted to calculate the effect sizes (Cohen's d). They were calculated by dividing the difference between the baseline and trial means by the baseline standard deviation (SD): $D = (m1-m2)/s$, where m1 and m2 represent the baseline and trial mean concentration levels, respectively, and s represents the baseline SD. Unlike raw fNIRS data, which were originally relative values that could not be directly averaged across subjects or channels, normalized effect size data were averaged regardless of the unit because effect size is unaffected by differential pathlength factor (DPF). A preliminary step of the statistical analysis also included the single channels as a variable. However, since it was not significant anytime, the "Lateralization" as a variable created by grouping the frontal left (Ch1-Ch2-Ch3) and right (Ch4-Ch5-Ch6) homologous channels, was added to the successive statistical analysis to maintain a higher statistical power.

Statistical Analysis

A set of repeated measures ANOVAs with independent within factors Condition (2: explicit IA, control) × *Task* (2: motor, social motor) × *Lateralization* (2: right, left) was applied to D-dependent fNIRS data (O2Hb and HHb concentration values). In the case of significant effects, pairwise comparisons were employed to check simple effects for significant interactions, and Bonferroni correction was utilized to decrease multiple comparisons possible biases. The degrees of freedom have been adjusted using Greenhouse-Geisser epsilon where suitable for all ANOVA tests. In addition, the normality of the data distribution was checked using the kurtosis and asymmetry indices. Partial eta squared (η^2) indices were computed to determine the extent of statistically significant effects.

RESULTS

Hemodynamic (O2Hb) Evidence

The statistical tests performed on D-dependent values for oxygenated and de-oxygenated concentrations yielded the outcomes reported below.

A first significant main effect for the *Task* was detected for O2Hb values [$F(1,17) = 8.04$, $p = 0.01$, $\eta^2 = 0.411$], for which higher mean values were found in the socially framed motor task compared to the basic motor task (**Figure 4A**).

A second main effect was found for the *Condition* [$F(1,17) = 6.43$, $p = 0.01$, $\eta^2 = 0.367$], revealing significantly higher mean values of O2Hb in the PFC for the explicit IA condition compared to the control condition (**Figure 4B**).

Thirdly, a significant interaction effect *Condition* × *Task* was identified for O2Hb values [$F(1,17) = 7.01$, $p = 0.01$, $\eta^2 = 0.397$]. According to pairwise comparisons significant higher mean values were found in the socially framed motor task compared to the basic motor task in the explicit IA condition [$F(1, 17) = 7.04$, $p = 0.01$, $\eta^2 = 0.402$] (**Figures 4C,D**).

No significant effects were found for the lateralization factor.

Regarding the analysis conducted on the de-oxygenated D values, no significant results were detected.

DISCUSSION

This fNIRS research explored the effect of the explicit Interoceptive Attentiveness (IA) manipulation on hemodynamic brain correlates during a task involving interpersonal motor coordination framed with a social goal. According to the results,

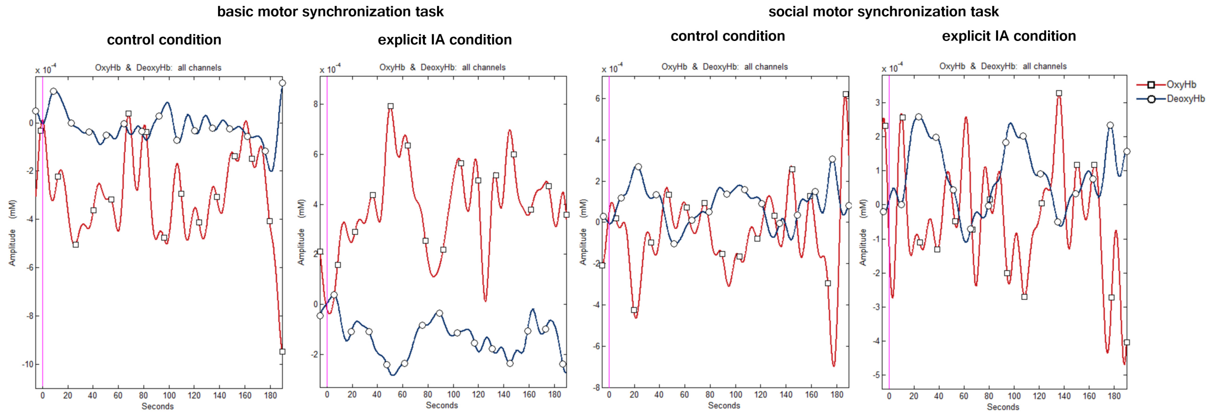

FIGURE 3 | Hemodynamic signal time course under the four conditions. The figure shows the time course plots of O2Hb (red) and HHb signal (blue) when performing the following tasks: the basic motor synchronization task and the socially framed motor synchronization task during the control and explicit IA condition.

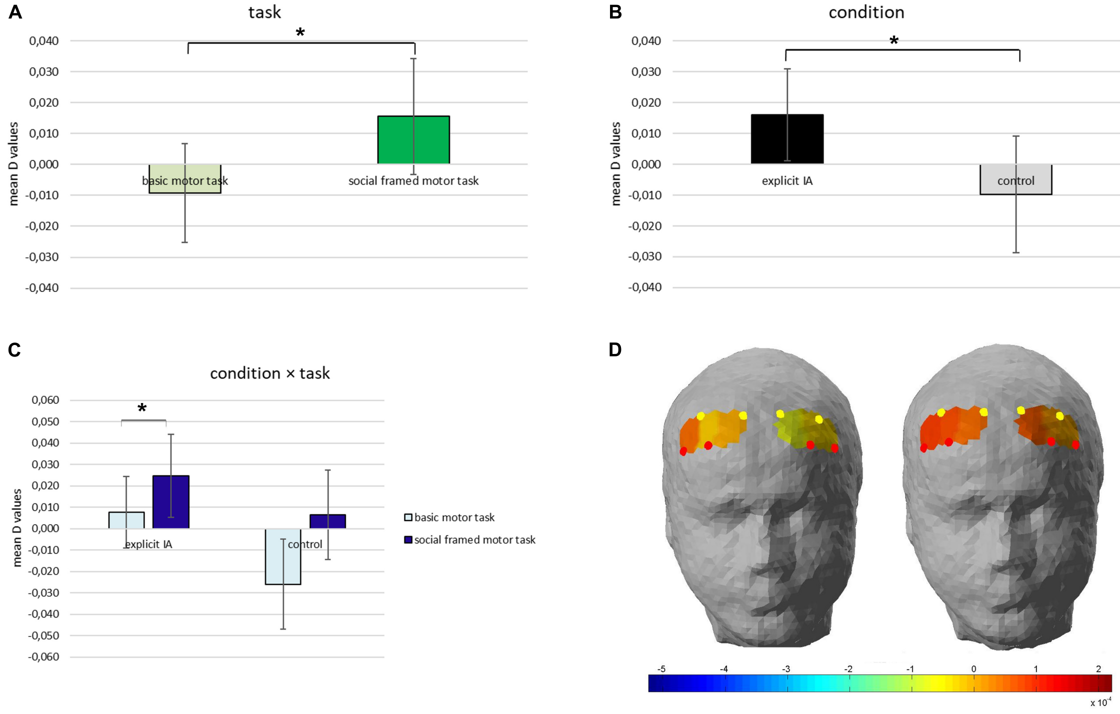

FIGURE 4 | **(A–D)** Oxygenated hemoglobin (O2Hb) evidence. **(A)** The graph displays O2Hb modulation [**(D)** values] as a function of the Task, which is significantly increased for the social framed motor task compared to the basic motor task. **(B)** The bar chart shows significantly higher O2Hb values in the explicit IA confronted with the control condition. **(C)** The bar graph shows the significant interaction effect Condition × Task detected for the O2Hb values. **(D)** In the head renderings, it is represented the significant interaction effect for which the red color corresponds to the higher O2Hb values found in the socially framed motor task (right head) compared to the basic motor task (left head) in the explicit IA condition. All data are represented as mean ± SE; all asterisks mark statistically significant differences, with $p \leq 0.05$.

the PFC, which is involved in high-order social cognition and the processing of interpersonal relations, was more responsive, first of all, when inducing the explicit focus (IA) on the breath during the motor task requiring synchronization and secondly when the motor synchronization task was socially framed compared to the basic motor task, as indicated by increased O2Hb. Thirdly, in the explicit IA condition, this increase of O2Hb mean values in the PFC was found in the socially framed motor task compared to the basic motor task. In the absence of a broader social frame, this effect was not significant for the basic motor task.

Starting from the first evidence, increased O2Hb in the PFC was found when inducing the explicit focus (IA) on the breath during the motor task requiring synchronization. Former studies suggested the enhancing effect of IA on various cognitive and emotional functions like prolonged attentional focus, cognitive control, and awareness (Weng et al., 2021). This amplification effect seems to be mediated by the activation of the PFC, which, in tasks that require the interoceptive focus, is responsible for the distribution of top-down attention, the processing of interoceptive information (Schulz, 2016).

However, it is worth noting the task adopted in this study did not consist of an interoceptive task only, but also of a motor synchronization task. Before, the PFC has been linked to social functions, by way of examples a fully conscious motor control and the adaptations to a changing rhythmic pattern (Stephan et al., 2002) or mutual cooperative interactions and interpersonal coordination (Balconi et al., 2017; Hu et al., 2021). Therefore, it is plausible to state that IA plays a role in affecting the mental representation of the synergic task based on the PFC activation. In other words, the present study suggests that when a joint task is performed and the individual focuses on his/her physiological body reactions, the brain hemodynamic activation is significantly enhanced in neuroanatomical regions that support sustained attention, reorientation of attention, social responsiveness, and synchronization.

As a second effect, significantly higher mean O2Hb values were found in the socially framed motor task compared to the basic motor task. This effect could be deemed as a "social effect" that recalibrates the basic motor synchronization task.

In terms of the impact of social factors on synchronization performance, a previous hyperscanning study suggested that a more cooperative and bidirectional condition has a positive impact on interpersonal SMS performance (Dai et al., 2018). It is thus conceivable that even simple motor activity if openly socially framed, can have a distinct "social" impact on the PFC activation during a synchronization task. Notably, the PFC is involved in social activities demanding synchrony (Sänger et al., 2011; Liu and Pelowski, 2014; Cheng et al., 2015) and shared intentionality, meant as a shared focus on a task with the common purpose of problem-solving *via* the interaction (Fishburn et al., 2018). Therefore, this result is in line with our hypothesis that if there is a declared social purpose, then there is a massive effect of activating the PFC.

Finally, significantly higher mean O2Hb values were found in the socially framed motor task compared to the basic motor task in the explicit IA condition. Although basic interpersonal SMS tasks have also been shown to promote social bonds between partners (Wiltermuth and Heath, 2009; Vicaria and Dickens, 2016), as well as a self-reported sense of agency joint (Bolt et al., 2016), findings suggested that consciously focused attention on breathing in a condition with an explicit social framework could enhance neural activation of PFC areas that support shared intentionality, attentional focus, and high-order social processes. Interestingly, this effect was not found for the control condition.

Thus, we may suppose that combined effect of IA and a social frame, that is the condition in which the subjects are aware of their body changes, and they are mentally representing the social relevance of their motor synchronization, was related to the most significant PFC activation. In the other cases, the effect was absent or less significant in terms of PFC activation. Therefore, the innovative aspect of this study is that there a significant activation of the PFC as a person consciously focuses on its physiological interoceptive correlates and performs the socially framed motor synchronization task.

It should be noted that no significant effect was found for the lateralization factor in this study, perhaps suggesting that the effect of the combination of IA and a social purpose in this context does not recruit a significantly unbalanced hemispherical process. This result is interesting because it is partially in contrast with previous neuroscientific research has demonstrated activation of different portions of the right hemisphere during the execution of interoceptive attention/awareness (IAA) tasks (Farb et al., 2007; Zheng et al., 2019; Balconi and Angioletti, 2021a).

Thus, compared to previous studies, for the first time, the effect of IA manipulation on synchronization was observed not only when the task is simply a motor task, but also when it is framed with a social purpose requiring shared intentionality. It is as if the focus on yourself and your breath while dancing in a synchronized manner with a partner, in order to demonstrate excellent performance in front of an audience, activates more the neural basis that supports the performance.

Some relevant applications can be suggested for the social, clinical domain and, potentially, for rehabilitation contexts. For example: in socially mediated sports disciplines, through practices that involve self-perception, it could be possible to strengthen the sense of belonging and teamwork between the players. Or, in rehabilitation, the sense of awareness of one's own body reactivity and the impact it has at the level of the central nervous system could be a target of therapy, in order to manage consciously (when possible) mental or neurophysiological deficits, developing a joint relationship with tutors or clinicians.

The current study holds potential for innovation, nonetheless, there are the following caveats to consider. First, this work used a simplest type of interpersonal SMS requiring finger tapping and not more complex motor synchronized activities (like dancing or playing an instrument). Complex situations, such as ecological tasks, multi-person groups, or tempo changes should be investigated by further studies, paying attention to controlling the amount of cognitive load. However, the present study used the simplest model of interpersonal SMS as an example to evaluate the effects of the explicit IA manipulation and the social frame on the PFC.

Secondly, the social framework applied to the motor task consisted only of explicitly requiring shared intentionality to the participants (operationalized as the instruction to synchronize to develop greater teamwork skills). However, distinct instructions, less artificial and contextually closest to the synchronization task could be given to the participants to increase the ecological validity of the results. For example, in the case of a motor synchronization task that requires participants to playing an instrument, the social framed condition might request them to synchronize to develop their duet skills. In this way, we could observe the effect of the interoceptive manipulation on the neural responses connected to a more ecological social framing condition.

Thirdly, fNIRS was only used on the PFC and not on the complete brain, including somatosensory cortical areas and subcortical structures (Balconi and Molteni, 2016), such as PMC and the claustrum. These two structures play a role in intentional imitation (Bien et al., 2009) and interoceptive processing (Schulz, 2016) respectively, thus their role deserves further deepening by future works. On a methodological level, prospective research could also implement fNIRS layouts that include short channels, as method that can help to eliminate non-specific hemodynamic trends and minimize noise (Brigadoi and Cooper, 2015).

In order to generalize these findings, the sample size should be enlarged by recruiting more participants, and gender should be balanced in future studies.

Also, specific manipulation checks to make sure the participants only focused on their breath and not on other modalities (e.g., skin temperature or heartbeat) could be added in future studies. Otherwise, it will be required to control the voluntary component of the respiratory rate, which could affect the overall outcomes of this research, and to examine the differences between tasks that require a focus on breathing and tasks that require a focus on cardiac activity.

To sum up, future research should consider exploring the influence of IA and social framing in more realistic situations such as dancing and playing an instrument. Most importantly, on a methodological level, collecting the brain activity of a dyad while executing these activities could be valuable (for instance by applying the hyperscanning paradigm) for grasping the interbrain coherence of the partners and observing the neural dynamic of the two subjects synchronizing with each other, rather than the responses of the single subject synchronizing with the experimenter. This would allow us to explore how the increasing effect of interoception on the PFC functions in the dyad at the neural level during a socially framed motor synchronization task.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Ethic committee of the Department of Psychology, Catholic University of the Sacred Heart, Milan, Italy. The patients/participants provided their written informed consent to participate in this study. Written informed consent was obtained from the individual(s) for the publication of any potentially identifiable images or data included in this article.

AUTHOR CONTRIBUTIONS

MB and LA contributed to the conception and design of the study, wrote the first draft, and contributed to the manuscript revision. Both authors read and approved the submitted version.

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Dynamic Inter-Brain Networks Correspond With Specific Communication Behaviors: Using Functional Near-Infrared Spectroscopy Hyperscanning During Creative and Non-creative Communication

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Social interaction is a dynamic and variable process. However, most hyperscanning studies implicitly assume that inter-brain synchrony (IBS) is constant and rarely investigate the temporal variability of the multi-brain networks. In this study, we used sliding windows and k-mean clustering to obtain a set of representative inter-brain network states during different group communication tasks. By calculating the network parameters and temporal occurrence of the inter-brain states, we found that dense efficient interbrain states and sparse inefficient interbrain states appeared alternately and periodically, and the occurrence of efficient interbrain states was positively correlated with collaborative behaviors and group performance. Moreover, compared to common communication, the occurrence of efficient interbrain states and state transitions were significantly higher during creative communication, indicating a more active and intertwined neural network. These findings may indicate that there is a close correspondence between inter-brain network states and social behaviors, contributing to the flourishing literature on group communication.

Keywords: inter-brain synchrony, dynamic inter-brain networks, creative communication, hyperscanning, fNIRS (functional near-infrared spectroscopy)

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INTRODUCTION

Humans are inherently social animals with a natural desire to communicate. Therefore, many researchers in the field of human neuroscience have been making every effort to understand the multi-brain neural mechanisms of social communication. In recent years, hyperscanning technology has attracted lots of attention and has been acclaimed as a "game changer" in social interaction studies (Gvirts and Perlmutter, 2020). Hyperscanning is a measurement that records brain activity of two or more individuals at the same time (Montague et al., 2002; Li et al., 2009). By using hyperscanning, researchers can measure the strength of inter-brain neural coupling (termed inter-brain synchrony, IBS), which provides a tool for revealing the basis of multi-brain neural mechanisms behind complex social activities.

Previous hyperscanning studies showed that inter-brain synchrony (IBS) arises when individuals communicate with each other, inferring others' intentions, and cooperate to achieve common goals (Cui et al., 2012; Jiang et al., 2012; Nozawa et al., 2016). For instance, Cui et al. (2012) measured brain activity of paired participants when they were performing two different tasks: a cooperation task where the participants try to press the button at the same time, and a competition task where the participants try to press the button as fast as possible. Results showed significantly higher IBS in the superior frontal cortex under the cooperation task than in the competition task. Lu and Hao (2019) measured brain activity of three-person groups where two of the members are real participants and one is a confederate, and found that IBS between the real participant pairings is significantly higher than the pairs between real participants and confederates. In addition, researchers also found that IBS emerges during natural social communication (Nozawa et al., 2016). Based on these results, IBS has been seen as an effective neural mark of inter-brain information transmission and shared intentionality (Fishburn et al., 2018).

Social communication is a complex and dynamic system. During social interaction, people constantly update information and adjust communication strategies, and their inter-brain neural networks change accordingly. However, most hyperscanning studies implicitly assume that IBS is steady throughout the entire recording procedure and rarely investigate the temporal variability of the multi-brain networks. Recently, Li et al. (2021) presented a novel approach based on sliding windows and k-mean clustering to capture the dynamic modulation of IBS patterns during cooperation tasks and found different IBS states occurred at different stages of the task. Here we followed their methods using sliding windows and k-mean clustering to characterize dynamic IBS (dIBS) states during group communication and applied multiple behavioral indices to explore the connection between different dIBS states and social behaviors. By calculating the graph-based network parameters and temporal occurrence of the dIBS states, as well as associating them with behavioral indices, we analyzed the variability and flexibility of the dynamic inter-brain networks during different social communication tasks.

Creative communication (i.e., communication and brainstorming in creative collaborations) is a special type of communication. It involves a distinct constellation of communication challenges, such as sharing generated ideas, understanding and evaluating others' ideas, and integrating personal novelty into collaborative work (Jordan and Babrow, 2013); all in order to produce novel and applicable products (Vera and Crossan, 2005; Paulus and Brown, 2007; Runco and Jaeger, 2012). It is an indispensable driving force for the development of modern society. Therefore, in this study, we implemented two different tasks to explore the similarities and differences of the dIBS states between creative and non-creative group communication tasks.

Previous studies have found that IBS can occur in multiple brain regions, such as the prefrontal cortex (PFC), right temporal-parietal junction (r-TPJ), superior temporal gyrus (STG), and medial temporal gyrus (MTG). These areas are deeply involved in production and comprehension of conversation, "reading" other minds, and anticipating their future actions, all of which contributed to social communication (Rizzolatti and Craighero, 2004; Frith and Frith, 2007). For instance, the PFC are important to tasks involving cooperation and social interactions (Decety et al., 2004; Cui et al., 2012; Baker et al., 2016). IBS in this area may be related to inferring others' goals and intentions (Stephens et al., 2010; Silbert et al., 2014). Previous studies also found that the r-TPJ is associated with understanding meanings of the conversation, and the increased IBS in this area was observed during group collaborations and storytelling (Jung-Beeman, 2005; Redcay et al., 2010; Hari et al., 2015). Besides, in some sensory or motor-related areas, IBS can also be induced by shared external stimulus (Hasson and Frith, 2016). Accordingly, these areas were selected as regions of interest in the present study (see details in **Figure 1D**) to explore the dynamic inter-brain networks during group communication.

Compared to functional magnetic resonance imaging (fMRI) and electroencephalography (EEG), functional near-infrared spectroscopy (fNIRS) has its unique advantages. During the recording procedure, fNIRS allows participants to perform small movements and has great adaptability to various environments, which benefits to recording brain activities in natural social scenes. Therefore, many researchers applied fNIRS-based hyperscanning technology to explore multi-brain neural interactions during real-life social communication (Jiang et al., 2012; Lu et al., 2019). In the present study, we also used fNIRS-based hyperscanning to track brain activity in pairs of participants during group communication tasks. Fifty-four individuals were randomly assigned as 27 dyads and were required to complete a creative communication task (alternative uses task; AUT) and a common communication task (object characteristic task; OCT). We adopted wavelet transform coherence, sliding windows, and k-mean clustering to describe participants' dIBS states. By calculating the graph-based network parameters and temporal occurrence of the dIBS states, as well as associating them with behavioral indicators, we analyzed the variability of the inter-brain networks during different group communication. We hypothesized that in both communication tasks, different dIBS states will appear alternately and periodically, and the occurrence of dense efficient dIBS states will be associated with better group communication performance. Moreover, considering that creative communication has its distinct social challenges, we hypothesized that compared to the non-creative communication, the inter-brain network will be more flexible during the creative communication.

MATERIALS AND METHODS

Participants

Fifty-four participants (all female, age: 21.2 ± 2.0 years) were randomly assigned as 27 dyads. Participants were recruited through online advertising and were each paid ¥40 for their participation. Before the experiment, informed consent was provided. The study procedure was approved by the University

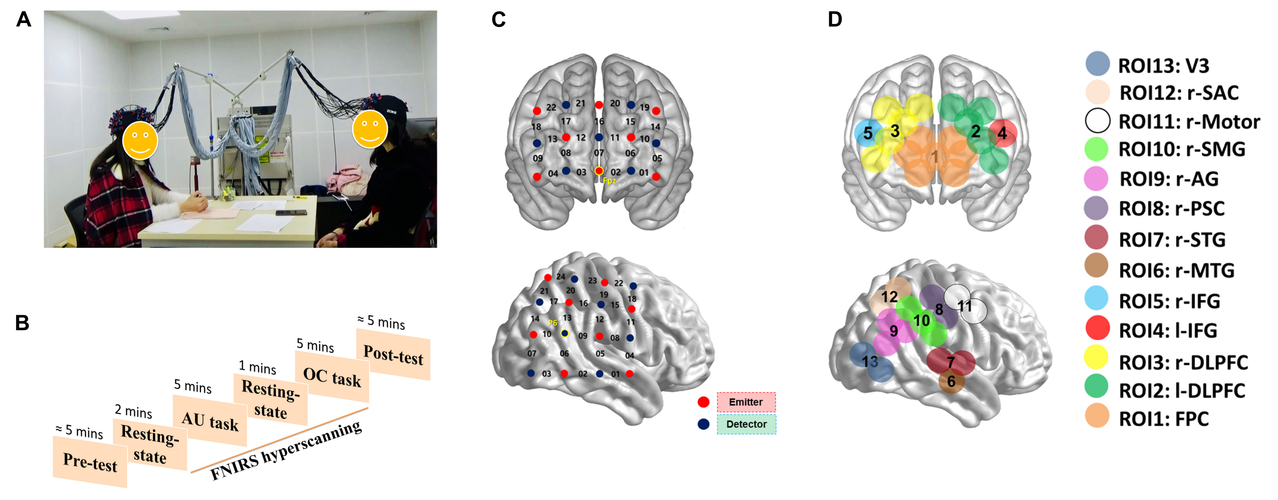

FIGURE 1 | The experimental settings of the current study. **(A)** Two participants were communicating with each other during the tasks. "AU task" means alternative uses task; "OC task" means object characteristic task. **(B)** The experiment procedure. **(C)** The optode probe sets. **(D)** Regions of interest.

Committee on Human Research Protection of East China Normal University.

Procedures

This study consisted of a one factorial design (Task: AUT vs. OCT), with Task as the within-subject factor. The sequence of the AUT and OCT was counterbalanced. The experimental procedure consisted of a 2-min rest session, two 5-min task sessions, and another 1-min rest session (see details in **Figure 1**). Before each task session, the rules of communication and task instructions were presented. During the AUT session, participants were asked to report as many unusual and original uses as possible for an ordinary item. During the OCT session, participants were asked to generate as many relevant characteristics as possible of a common item. During both communication tasks, participants were asked to take turns to report, one idea at a time. If a participant cannot think of any idea during their turn, they can say "pass" and present the idea in the next turn.

Pre- and Post-experimental Tests

Prior to the experiment, participants were asked to complete the self-assessment manikin scale to rate the valence and arousal of their emotional states (Bradley and Lang, 1994; Kirsch et al., 2005; Coan et al., 2006). Immediately after the experiment, participants were asked to rate their emotional state again. They then rated feelings of difficulty, depletion, and enjoyment when performing each task on scales ranging from 1 ("not at all") to 5 ("very much").

Behavioral Assessments

Participants' performance on the AUT was measured from three dimensions: fluency, originality, and flexibility (Guilford, 1967). The fluency score was the total number of non-redundant responses. The originality score was accessed using an objective method. If a response was statistically infrequent (i.e., 5% or fewer participants in the sample presented the response), it scored 1, and all the other frequent responses (i.e., 95% or more participants in the sample presented the response) scored zero. The originality score was the total number of statistically infrequent responses. The flexibility score was coded according to the number of categories of generated responses (e.g., decorations, weapons, toys, etc.). To compensate for the effect of fluency, the final flexibility score was defined as the number of categories divided by the fluency. Two trained raters independently assessed the originality and flexibility scores for each participant. The inter-rater agreements of originality [internal consistency coefficient (ICC) = 0.89, calculated as Cronbach's α] and flexibility (ICC = 0.82) were satisfactory. The ratings of the two raters were averaged. The score for each dyad was the sum of the two members.

Participants' performance on the OCT was scored by fluency, and the scoring procedure was the same as the AUT.

The index of cooperation (IOC) was calculated based on the number of combined ideas, which reflects the perspective-taking behaviors (Larey and Paulus, 1999). First, the responses of the two participants were listed in chronological order. From the first idea to the last, when a response pertained to the same category as the previous response, it scored "1." The total number of responses scored "1" was defined as the "converge." The IOC value for each dyad was then obtained using the following equation: IOC = converge/(group fluency—converge). Therefore, this index could demonstrate the extent to which the group members combined their ideas with others, and reveal the level of cooperation between group members (Lu et al., 2019, 2022).

Functional Near-Infrared Spectroscopy Data Acquisition and Pre-processing

The concentrations of oxyhemoglobin (HbO) and deoxyhemoglobin (HbR) were recorded continuously using an ETG-7100 NIRS system (Hitachi Medical Corporation) for each dyad. Based on the abovementioned studies showing the important contributions of the PFC and right temporal-parietal-occipital regions (r-TPO) to social communication, we placed two optode probe sets on each participant's PFC (3*5 optode probe set; 22 measurement channels) and r-TPO areas (4*4 optode probe set; 24 measurement channels). The registration of the probe sets was based on the 10–20 system of EEG. The MNI coordinates of the CHs in a typical participant are presented in **Supplementary Table 1**.

Considering that the HbO signal is more sensitive to changes in cerebral blood flow than the HbR signal, we focused on the HbO signal (Hoshi, 2007; Jiang et al., 2012). The data were pre-processed using a principal component spatial filter algorithm to eliminate the effects of systemic components such as blood pressure, respiratory variation, and blood flow variation on the fNIRS data (Zhang et al., 2016). We also used a correlation-based signal improvement method to remove motion artifacts (Cui et al., 2010). Besides, the initial and last 30-s periods of each task session were removed to obtain data within the steady period, leaving a total of the 480-s period for two task sessions.

Functional Near-Infrared Spectroscopy Data Analysis

The dynamic IBS analysis was conducted by three processes: (1) IBS computation using wavelet transform coherence, (2) temporal segmentation using sliding windows, and (3) characterization of dIBS states using k-means clustering (Li et al., 2021).

Inter-Brain Synchrony Computation

We used wavelet transform coherence (WTC) to assess the cross-correlation (i.e., IBS) between two HbO time series (Grinsted et al., 2004). Fisher's r-to-z transformation was applied to IBS values before further analysis (Cui et al., 2012; Simony et al., 2016). In each dyad, we calculated the IBS of all ROI combinations between two participants. The IBS between the same ROI pairings was then averaged. For example, the IBS between IFG-1 (participant 1's IFG) and AG-2 (participant 2' AG) was averaged with the IBS between AG-1 (participant 1'AG) and IFG-2 (participant 2' IFG) (Li et al., 2021), which led to a total of 91 ROI combinations per dyad.

To identify the frequency band of interest (FOI) in this study, we conducted paired sample t-tests to compare IBS between the task period and rest period of each ROI combination along the full frequency range (0.01–0.7 Hz). The IBS was averaged across the different task periods prior to the aforementioned t-test to prevent bias (Lu et al., 2019; Pan et al., 2020). Data over 0.7 Hz were not taken into account to exclude higher frequency noise, such as cardiac activity (0.8–2.5 Hz). Data below 0.01 Hz were also excluded to avoid fluctuations at very low frequencies (Barrett et al., 2010). The t-test results were thresholded at $P < 0.000005$. No further corrections were applied since this analysis was only used to identify the FOI rather than to obtain the final results (Dai et al., 2018; Zheng et al., 2018). Significant P-values which survived the thresholding were observed at frequencies between 0.10 and 0.19 Hz (corresponding to the period between 5.2 and 10.5 s), which means in this frequency band, the IBS of the task period was significantly higher than that of the rest period. Therefore, this band was selected as the FOI, and the IBS of each ROI combination was averaged across the selected FOI.

Clustering Analysis (Sliding Windows and k-Means Clustering)

To quantitively compare the dIBS states between different group communication, the dynamic IBS network of the AUT and OCT were clustered together. First, we used a sliding window approach to obtain a series of windowed IBS matrices along the 480 s task period (see details in **Figure 2**). The window size was set to 10 s and moved in an increment of 1 s throughout the task. The IBS values were then averaged between the same ROI combinations within each time window to obtain the corresponding IBS matrix. The 480 s task duration was then split into a series of windowed IBS matrices (13 ROIs × 13 ROIs × 471 windows) for each dyad.

Next, we averaged these chained IBS matrices across groups and applied a k-means clustering method in MATLAB to assess the similarity between the windowed IBS matrices and obtain the representative dIBS states (i.e., clusters). We chose the number of clusters using the elbow criterion of the cluster validity index, which is the ratio between within-cluster distance to between-cluster distance (Allen et al., 2014; Fang et al., 2020; Li et al., 2021). Specifically, the validity index for different k values were computed and plotted as a function of cluster number, then the number of clusters is chosen at the elbow of the curve to best balance the cost of clustering (i.e., minimize the within-cluster distance and maximize the between-cluster distance) and the number of clusters. In addition, previous research found that the Manhattan distance is a more effective similarity measure than the Euclidean distance for high-dimensional neuroimaging data (Aggarwal et al., 2001), therefore we used the Manhattan distance to calculate the similarity between the windowed IBS matrices. Finally, after iterated 1,000 times to decrease the chances of escaping local minima, the cluster centroids (i.e., the representative dIBS states in **Figure 3A**) were obtained. These cluster centroids derived from the group-averaged IBS matrices were then used as the initial centroids for the cluster analysis of individual dyad to obtain the final dIBS states of each dyad.

Statistical Analysis

The dIBS states were characterized by the following metrics: the occurrence rate of each state, number of transitions between states, and network parameters of each state (Allen et al., 2014; Li et al., 2021). The occurrence rate of each state means the percentage of total windows each dIBS states account for. The number of transitions stands for the total number of switches between any two states. Moreover, we also implemented network analyses in MATLAB using GRETNA to calculated graph-based metrics, such as global efficiency (globE) and shortest path length (Lp), of each dIBS state (Achard and Bullmore, 2007; He et al., 2009; Wang et al., 2015). globE is an important network parameter that measures the global efficiency of parallel information transfer in the network. It is the inverse of the

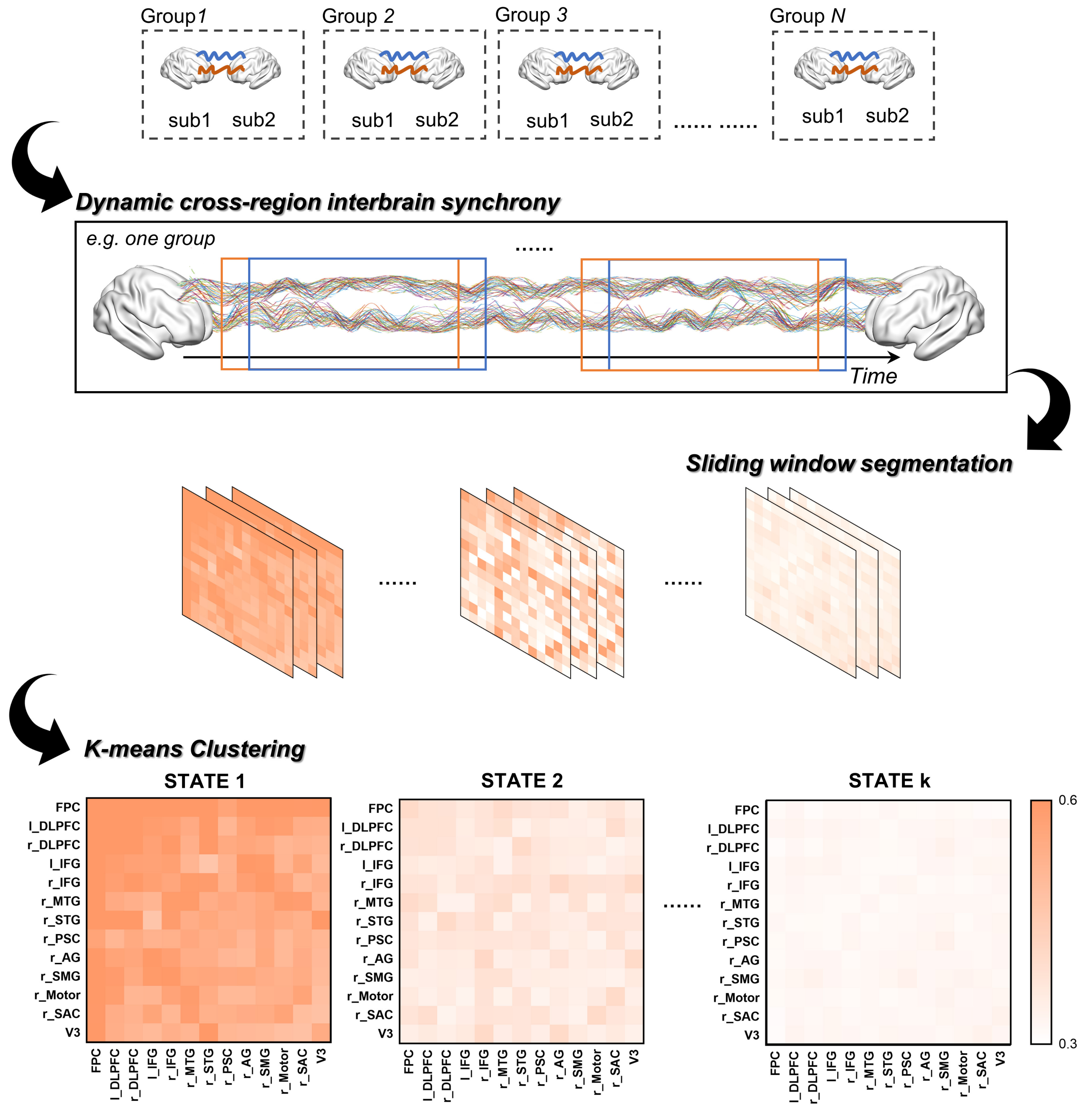

FIGURE 2 | The procedure of clustering analysis.

harmonic mean of the characteristic path length between each pair of nodes within the network. As for Lp, it quantifies the ability for information propagation in parallel over the whole network, computed as a harmonic mean length between all pairs of nodes. Repeated measure ANOVA was used to assess whether there were significant differences between the characteristics of these dIBS states. Repeated measure ANOVA was also used to assess whether there were significant differences between AUT and OCT in terms of the occurrence rate of three dIBS states and the number of state transitions. In addition, we also examined the Pearson correlation between the properties of each dIBS state and the behavioral group communication performance.

RESULTS

Dynamic Interbrain Synchrony States in Group Communication

To quantitatively compare the dynamic inter-brain networks between different group communication tasks, the dIBS of the

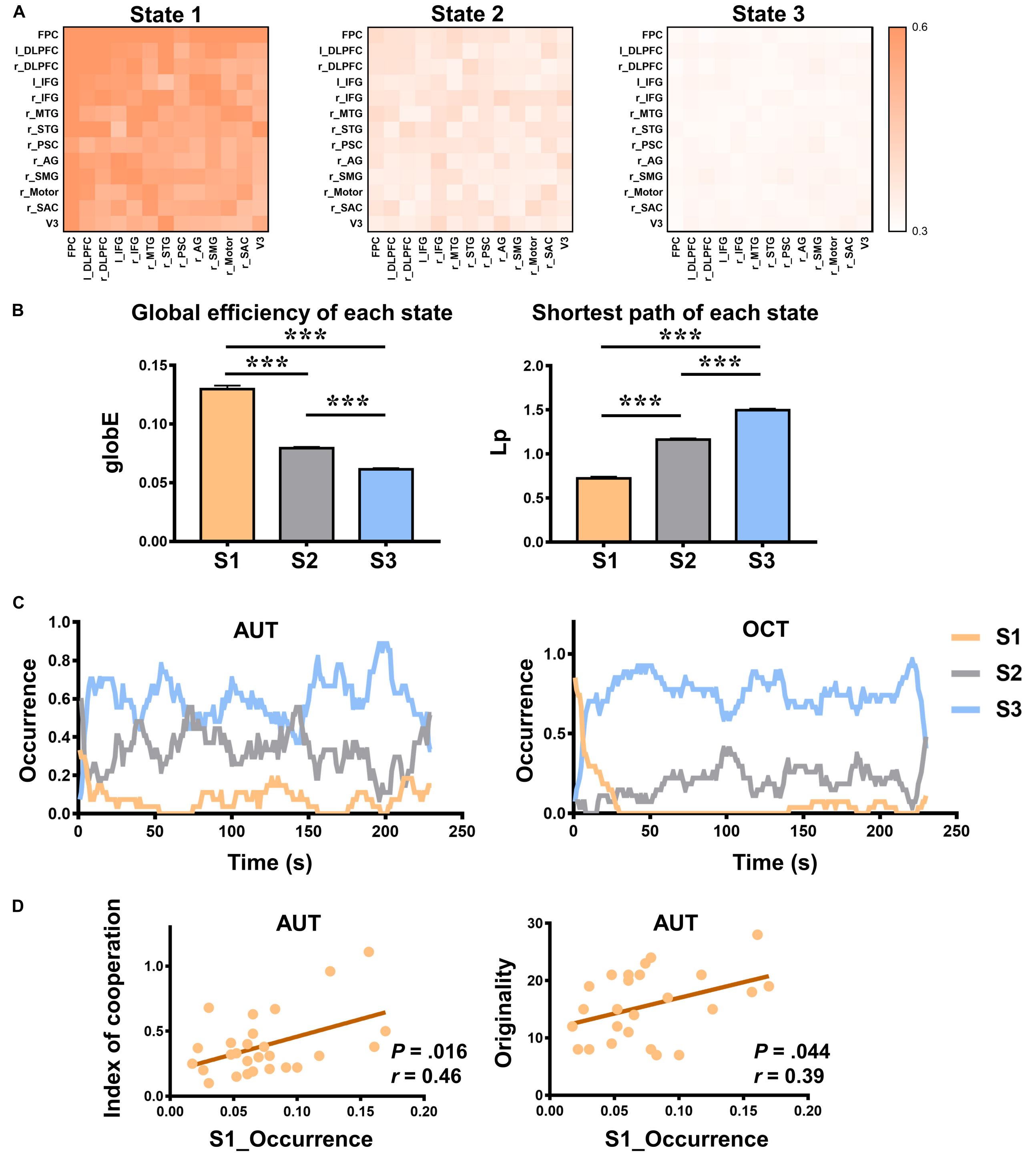

FIGURE 3 | The properties of dynamic inter-brain synchrony (dIBS) states. **(A)** The 13 × 13 matrix of dIBS states. The horizontal and vertical coordinates are ROIs. Color represents the IBS value. **(B)** The global efficiency (globE) and shortest path (Lp) of each dIBS state. Error bars indicate standard errors of the mean. ***$P < 0.001$. **(C)** The temporal occurrence of each dIBS state during the AUT and OCT. **(D)** Pearson correlations between the occurrence rate of State 1 and the index of cooperation as well as AUT originality. S1 means State 1; S2 means State 2; S3 means State 3.

AUT and OCT were clustered together. During the entire group communication, three distinct dIBS states were obtained using the k-means clustering analysis (see details in **Figure 3A**). Then we calculated graph-based network parameters such as globE and Lp of each state in MATLAB using GRETNA (Achard and Bullmore, 2007; He et al., 2009; Wang et al., 2015).

Repeated measure ANOVA was used to assess whether there were significant differences between these dIBS states. Results showed that State 1 had significantly higher globE and significantly lower Lp than State 2 and State 3, and State 2 had significantly higher globE and significantly lower Lp than State 3 [see details in **Figure 3B**; globE: $F_{(2,\ 26)} = 328.47$, $P < 0.001$, $\eta_p{}^2 = 0.96$, $M_{s1} = 0.13$, $M_{s2} = 0.08$, $M_{s3} = 0.06$; Lp: $F_{(2,\ 26)} = 588.16$, $P < 0.001$, $\eta_p{}^2 = 0.98$, $M_{s1} = 0.72$, $M_{s2} = 1.16$, $M_{s3} = 1.50$; *post hoc* Bonferroni correction was used to account for multiple comparisons].

Repeated measure ANOVA was also used to assess whether there were significant differences between the occurrence rate of these dIBS states. Results showed that in both AUT and OCT, State 1 occurs significantly less than States 2 and 3, and State 2 occurs significantly less than State 3 [AUT: $F_{(2,\ 26)} = 261.64$, $P < 0.001$, $\eta_p{}^2 = 0.95$, $M_{s1} = 0.08$, $M_{s2} = 0.33$, $M_{s3} = 0.59$; OCT: $F_{(2,\ 26)} = 482.66$, $P < 0.001$, $\eta_p{}^2 = 0.97$, $M_{s1} = 0.06$, $M_{s2} = 0.19$, $M_{s3} = 0.75$; *post hoc* Bonferroni corrected]. It may indicate the difficulty of entering into a state where group members experiencing efficient interbrain information transmission during both creative and non-creative social communication.

Moreover, in **Figure 3C**, we displayed the temporal occurrence of each dIBS state. Intuitively, it can be seen that different states appeared periodically and alternately during both creative and non-creative communication. We also examined the Pearson correlation between the occurrence rate of each dIBS state and the collaborative behaviors as well as the group performance. Results showed that the occurrence rate of State 1 was positively correlated with group originality and index of cooperation (see details in **Figure 3D**; AUT originality: $r = 0.39$, $P = 0.044$; IOC: $r = 0.46$, $P = 0.016$).

Differences Between the Creative Communication and Non-creative Communication

Repeated measure ANOVA was used to assess whether there were significant differences between the occurrence rate of three dIBS states in the AUT and OCT. Results showed that during the AUT, the occurrence rate of States 1 and 2 was significantly higher than during the OCT [see details in **Figure 4A**; State 1: $F_{(1,\ 26)} = 4.90$, $P = 0.036$, $\eta_p{}^2 = 0.16$, $M_{AUT} = 0.08$, $M_{OCT} = 0.06$; State 2: $F_{(1,\ 26)} = 15.71$, $P = 0.001$, $\eta_p{}^2 = 0.38$, $M_{AUT} = 0.33$, $M_{OCT} = 0.19$), and the occurrence rate of State 3 was significantly lower than during the OCT [State 3: $F_{(1,\ 26)} = 19.45$, $P < 0.001$, $\eta_p{}^2 = 0.43$, $M_{AUT} = 0.59$, $M_{OCT} = 0.75$]. In addition, we also measured the number of state transitions during each group communication task and found that the state transitions were significantly higher in the creative communication than in the non-creative communication [see details in **Figure 4B**; $F_{(1,\ 26)} = 13.64$, $P = 0.001$, $\eta_p{}^2 = 0.34$, $M_{AUT} = 9.59$, $M_{OCT} = 5.93$]. These findings suggest that compared to the non-creative communication task, participants exhibited a more efficient and flexible interbrain neural network when performing the creative communication task.

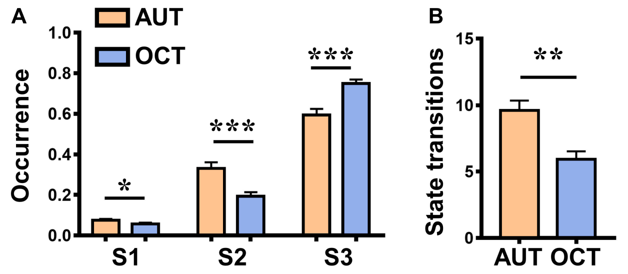

FIGURE 4 | Differences between the alternative uses task (AUT, creative communication) and object characteristic task (OCT, non-creative communication). **(A)** Differences between the occurrence rate of three dIBS states in the AUT and OCT. **(B)** Differences between the state transitions in the AUT and OCT. Error bars indicate standard errors of the mean. $^*P < 0.05$, $^{**}P < 0.01$, and $^{***}P < 0.001$.

Validation Analysis

We conducted a validation test using pseudogroups (i.e., randomly rearranging the participants to form sham dyads). All analyses were applied to the pseudodata in the same manner as for the empirical data. Specifically, we calculated the dIBS matrices of the 27 pseudodyads (the sample size was the same as that of real participants) and obtained 3 representative dIBS states using k-means clustering. Then we calculated graph-based network parameters such as globE of each state in MATLAB using GRETNA (Achard and Bullmore, 2007). Repeated-measures ANOVA was used to assess whether there were significant differences between the globE of these dIBS states. This permutation process was repeated 300 times. Different from real condition, over 95% pseudogroups showed no significant difference between the globE of three dIBS states, and also no significant difference between the occurrence rate of State 1, State 2, and State 3. Moreover, we also examined the observed positive correlation between communication behaviors and the occurrence rate of dIBS states. Considering it was difficult to calculated the IOC scores of pseudodyads, we only examined the correlation between AUT originality and the occurrence rate of dIBS states. The originality score of the pseudodyads were the sum of the two members. Different from real condition, over 95% of pseudogroups showed no significant correlations between AUT originality and the occurrence rate of any dIBS states. This may indicate that our findings are not accidental, but reveal some inherent nature of interpersonal communication.

DISCUSSION

In the present study, we used a fNIRS-based hyperscanning technic and analysis including WTC, sliding windows and k-mean clustering to obtain a set of representative dIBS states during different group communication. By calculating the parameters and temporal occurrence of the inter-brain states, we found that dense efficient interbrain states and sparse inefficient interbrain states appeared alternately and periodically, and the occurrence of efficient interbrain states was positively correlated with collaborative behaviors and group performance. Moreover, compared to the common communication, the occurrence of efficient interbrain states and state transitions were significantly higher during the creative communication, indicating a more active and intertwined neural network. These findings captured the variability and flexibility of inter-brain networks during group communication, and revealed the relationship between distinct dynamic IBS states and specific social behaviors, all of which contributing to our understanding of the multi-brain neural mechanisms involved in social communication.

Specifically, we clustered the dIBS of the AU and OC tasks and found three representative dIBS states. Results showed that State 1 had significantly higher globE and lower Lp than State 2 and State 3, and State 2 had significantly higher globE and lower Lp than State 3 (**Figure 3B**), which means that compared to State 3, State 1 and State 2 may be more beneficial for our interpersonal communication, especially State 1. During State 1, our brains are more aligned, more intertwined, and form a more efficient inter-brain network. The observed positive correlations between the occurrence rate of State 1 and group originality, as well as index of cooperation also support our explanation. Moreover, we found that during both creative and non-creative communication, dense efficient interbrain states and sparse inefficient interbrain states appeared periodically and alternately (**Figure 3C**). This may be related to spontaneous attentional fluctuations. Previous studies found that the electrophysiological activity of antagonistic, attention-relevant brain networks changes at the millisecond level and coordinates with moment-to-moment behavioral variability, which indicates that human attention is inherently dynamic and continuously shifting between external stimuli and internal thoughts (Kucyi et al., 2017, 2020). Therefore, it is difficult to maintain a longish state where we are highly focused and concentrated on the perspectives of others and efficiently absorb others' ideas. In addition, results showed that in both AUT and OCT, State 1 occurs significantly less than State 2 and 3, and State 2 occurs significantly less than State 3. It may indicate the difficulty of entering into a state where group members experience productive interbrain information transmission during both creative and non-creative social communication. These findings uncovered the connections between dIBS states and social behaviors and revealed the dynamic nature of social communication.

To further explore the difference between the creative and non-creative group communication, we compared the occurrence rate of three dIBS states and the number of state transitions between AUT and OCT. AUT requires participants to report as many unusual and original uses as possible for an ordinary item. It is a classical divergent thinking task that is widely used in behavioral and neuroscience studies (Runco and Mraz, 1992; Fink et al., 2009). As for OCT, it requires participants to generate as many relevant characteristics as possible of a common item. In this regard, OCT often serves as a memory-retrieval task and is used as a control task for AUT (Fink et al., 2009; Chen et al., 2020). In the current study, results showed that during the AUT, the occurrence rate of States 1 and 2 was significantly higher than that during the OCT, and the occurrence rate of State 3 was significantly lower than that during the OCT. As mentioned above, States 1 and 2 contributed more to interpersonal communication and were associated with a higher level of mutual understanding as well as collaborative behaviors. Therefore, the higher occurrence rate of State 1 and State 2 during AUT may indicate that compared to the non-creative communication, participants paid more attention to each other, deeply evaluated and incorporated others' ideas, and built more efficient inter-brain networks during the creative communication. Besides, the state transitions were significantly higher in the AUT than in the OCT, which suggests that participants' dynamic inter-brain networks were more flexible, more active during creative communication. In a recent study, Li et al. (2021) clustered participants' dIBS states during a product design task and a common model building task separately, and qualitatively compared these two tasks. They found that compared to the model building task, participants exhibited more complex and stronger IBS during the product design task. Here we expanded their findings into verbal communication tasks and quantitatively compared the properties of the dIBS states between creative and non-creative communication. With more detailed behavioral indices, we also observed a correspondence relationship between dIBS states and specific communication behaviors. During AUT, the group originality and cooperation behaviors were significantly positively correlated with the occurrence of State 1, which suggests that our social behaviors and dynamic inter-brain networks are harmoniously connected. Previous studies which focused on the static IBS networks also found stronger IBS during creative group collaborations (Lu et al., 2019; Mayseless et al., 2019). For instance, researchers found higher IBS in the r-DLPFC and r-TPJ during the creative cooperation tasks than the common cooperation tasks, and the increased IBS in these areas was positively correlated with behavioral indices of cooperation (Lu et al., 2019). Our findings are consistent with previous studies and provide a dynamic perspective to explore the unique inter-brain mechanisms of creative communication.

The sliding window approach is a common and useful method for dynamic FC analysis. It has been used to monitor temporal changes of the brain activity and even to classify and predict brain disorders (Du et al., 2018; Vidaurre et al., 2018). However, there is still a lack of a "gold standard" for determining the optimal window length (Shakil et al., 2016). Therefore, to examine the impact of different window lengths on the dIBS states, we used 5, 8, and 10 s as the length of sliding windows, separately. These window lengths were chosen based on our FOI (0.10–0.19 Hz, corresponding to the period between 5.2 and 10.5 s). As shown in **Supplementary Figure 1**, the dIBS patterns were generally consistent across different window lengths, which validates our findings.

In the present study, we analyzed the temporal variability and flexibility of the dynamic inter-brain networks during both creative communication and non-creative communication and found distinct dIBS states appeared periodically, and the increased efficient dIBS states were positively correlated with group performance, all of which suggest that there is a sophisticated correspondence between dIBS states and social behaviors. Moreover, creative communication has its unique characteristics. During creative communication, participants showed more efficient dIBS states and state transitions, which may indicate a higher level of comprehending and evaluating others' ideas, building shared conceptional model, and collaboratively producing novel products.

There were still several limitations in this study. First, although AUT and OCT are classical cognitive tasks that are widely used in behavioral and neuroscience studies (Guilford, 1967; Fink et al., 2009; Hao et al., 2017), they are not natural social interactions. It should be cautious when generalizing these findings into actual social communication. Future research could use more varied and natural tasks to explore the variability of dynamic inter-brain networks during social communication. Moreover, since we set a time limit for the communication tasks (5 min for each task), participants may not be able to fully express their views during the communication. Future research could use more lenient time settings and explore the elaboration index of creative communication. Besides, we only recorded the activity of several brain areas such as the PFC and r-TPJ in this study. Future research could expand the coverage of the fNIRS optode probe sets so that the underlying inter-brain neural interactions can be fully explored.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the University Committee on Human Research Protection of East China Normal University. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

XW and NH conceived of the project and designed the experiments. XW and YH implemented the experiments and collected the data. XW, YZ, KL, and NH wrote the manuscript. All authors pre-processed the data, performed analyses, and discussed results.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fnhum.2022.907332/full#supplementary-material

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ORIGINAL RESEARCH
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The Groove Enhancement Machine (GEM): A Multi-Person Adaptive Metronome to Manipulate Sensorimotor Synchronization and Subjective Enjoyment

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Synchronization of movement enhances cooperation and trust between people. However, the degree to which individuals can synchronize with each other depends on their ability to perceive the timing of others' actions and produce movements accordingly. Here, we introduce an assistive device—a multi-person adaptive metronome—to facilitate synchronization abilities. The adaptive metronome is implemented on Arduino Uno circuit boards, allowing for negligible temporal latency between tapper input and adaptive sonic output. Across five experiments—two single-tapper, and three group (four tapper) experiments, we analyzed the effects of metronome adaptivity (percent correction based on the immediately preceding tap-metronome asynchrony) and auditory feedback on tapping performance and subjective ratings. In all experiments, tapper synchronization with the metronome was significantly enhanced with 25–50% adaptivity, compared to no adaptation. In group experiments with auditory feedback, synchrony remained enhanced even at 70–100% adaptivity; without feedback, synchrony at these high adaptivity levels returned to near baseline. Subjective ratings of being in the groove, in synchrony with the metronome, in synchrony with others, liking the task, and difficulty all reduced to one latent factor, which we termed enjoyment. This same factor structure replicated across all experiments. In predicting enjoyment, we found an interaction between auditory feedback and metronome adaptivity, with increased enjoyment at optimal levels of adaptivity only with auditory feedback and a severe decrease in enjoyment at higher levels of adaptivity, especially without feedback. Exploratory analyses relating person-level variables to tapping performance showed that musical sophistication and trait sadness contributed to the degree to which an individual differed in tapping stability from the group. Nonetheless, individuals and groups benefitted from adaptivity, regardless of their musical sophistication. Further, individuals who tapped less variably than the group (which only occurred ∼25% of the time) were more likely to feel "in the groove." Overall, this work replicates previous single person adaptive metronome studies and extends them to group contexts, thereby contributing to our understanding of the temporal, auditory, psychological, and personal factors underlying interpersonal synchrony and subjective enjoyment during sensorimotor interaction. Further, it provides an open-source tool for studying such factors in a controlled way.

Keywords: auditory feedback, tapping, social, individual differences, open-source, assistive device

HIGHLIGHTS

- To aid people in synchronizing with each other, we built an assistive device that adapts in real-time to groups of people tapping together.
- By varying the adaptivity of a metronome, we show that we can enhance group synchrony and subjective feelings of enjoyment.
- Both individuals and groups benefit from an optimally adaptive metronome, regardless of their previous musical experience.
- Auditory feedback about one's own and others' taps influences both motor synchrony and subjective experience, and interacts with metronome adaptivity.
- The multi-person adaptive metronome allows to study, in a controlled way, the factors that influence interpersonal synchronization and social bonding.

INTRODUCTION

Sensorimotor synchronization (SMS)—the temporal alignment of motor behavior with a rhythmic sensory stimulus—has been observed in a variety of species and sensory modalities (Greenfield, 2005; Ravignani et al., 2014). Among humans, SMS has been shown to enhance prosocial behavior, social bonding, social cognition, perception, and mood—both within groups and toward outsiders [see Mogan et al. (2017) for review]. While sensorimotor synchronization can occur in a variety of contexts, we focus here specifically on auditory-motor coupling, which has been studied extensively in the music cognition literature as a critical mechanism of musical engagement and prosocial behavior.

When humans interact together in motoric synchrony, they are more likely to subsequently exhibit cooperative behavior, successful joint actions, trust of others, and altruism (Wiltermuth and Heath, 2009; Valdesolo et al., 2010). While such benefits occur during pure motor synchrony—for example, walking in step together—using music to organize movement is a powerful temporal cue and culturally relevant activity. The use of music, or even just a metronome, can enhance cooperative behavior—typically measured via economics games, such as the Public Goods Game (Wiltermuth and Heath, 2009; Kniffen et al., 2017) or Prisoner's Dilemma (Anshel and Kipper, 1988)—and feelings of synchronization or connection with others, typically measured via self-report surveys (Hove and Risen, 2009; Fairhurst et al., 2013, 2014; Zhang et al., 2016; Kirschner and Tomasello, 2010). Interestingly, these prosocial effects are not specific to adults (Kirschner and Tomasello, 2010). Infants as young as 14-months show increased helping behavior toward adults who have bounced together with them synchronously to music (Cirelli et al., 2014a). Such helping behavior even generalizes to positive affiliates of the adults, i.e., adults the infants had seen interact together, though not toward neutral strangers (Cirelli et al., 2014b).

Importantly, however, for music to benefit motoric synchrony and interpersonal coordination, those engaging with it must be able to extract its temporal regularity. Generally, the beat and its (sub)harmonics are the relevant periodicities to which those engaging with music synchronize their movements. Because the perceived beat is typically isochronous (Merker et al., 2009) or quasi-isochronous (Merchant et al., 2015), many studies of sensorimotor synchronization involve asking individual participants to tap to an isochronous auditory pulse or beat (i.e., tap with a metronome), as such a task contains the most basic elements of what occurs during engagement with more complex music. However, the degree to which individuals can perceive and align their action to an auditory pulse varies among individuals and may impede their ability to synchronize well with others.

The most basic version of a sensorimotor synchronization task involves having a single participant synchronize their finger taps with a metronome. These single-person isochronous tapping experiments have revealed much about the motor and cognitive processes underlying sensorimotor synchronization. In terms of motor constraints, the lower inter-onset-interval (IOI) limit for a single finger tapping in 1:1 synchrony with an auditory pulse is around 150–200 ms, though highly trained musicians and/or bimanual tapping may result in slightly lower IOIs of around 100 ms [see Repp (2005) for review]. On the other end of the spectrum, a perceptual constraint prohibits participants from being able to synchronize their taps with IOIs longer than ∼1.8 s. Such durations become too hard to predict accurately; participants' taps become reactive to the metronome tones, rather than anticipatory (Repp, 2005; c.f., Repp and Doggett, 2007). Though these studies of IOI constraints have typically been conducted with adult participants, a growing number of developmental studies (van Noorden and De Bruyn, 2009; Provasi et al., 2014; Thompson et al., 2015) have found that synchronizing with slower tempi becomes less difficult with age. With these limitations in mind, in the following experiments, we have adults stay within a comfortable range of synchronization tempi, using a starting tempo of 120 beats per minute (an IOI of 500 ms).

Complementing tapping tasks using invariant (strict) metronomes set at different tempi, studies seeking to understand the dynamics underlying more realistic joint musical interactions (Repp and Keller, 2008; Fairhurst et al., 2013) have used metronomes that adapt their timing based on the asynchronies between the metronome's tone and the participant's tap. The idea behind an adaptive metronome is that it mimics, in a controlled way, the adaptive behavior another human might adopt during joint tapping. For example, Fairhurst et al. (2013) used a personal computer-based adaptive metronome, implemented in MAX / MSP, that adapted each subsequent metronome tone by some percentage (0, 25, 50, 75, or 100%) of the participant's tap asynchrony relative to the current tone, while they were in a magnetic resonance imagining (MRI) scanner. They found that, across sets of taps (20 taps/trial), adaptive metronome settings of 25% and 50% brought participants into greater synchrony with the metronome, compared to a non-adapting metronome. The opposite was also true; a metronome adapting by 75% or 100% significantly worsened synchronization performance. Functional MRI analyses revealed distinct brain networks differentially activated when participants are in vs. out of synchrony. Greater synchrony resulted in increased motor and "Default Mode Network" activity, possibly related to the social and effortless aspects associated with being "in the groove (Janata et al., 2012)," whereas poor synchrony resulted in increased activity in cognitive control areas of the brain, likely reflecting the increased effort required to align taps with the metronome. Given this ability to enhance or perturb sensorimotor synchronization and subjective experience using an adaptive metronome—coupled with the known group benefits of synchronous motor action outlined previously—we sought, in the current study, to extend the use of an adaptive metronome to a multi-person context.

To our knowledge, the current study is the first to utilize an adaptive metronome in a group-tapping context; however, recent work has explored synchronization among groups of individuals [see Repp and Su (2013), Part 3, for review]. Such studies range from examinations of synchronization in musical ensembles (Rasch, 1979), or duetting pianists (Goebl and Palmer, 2009; Zamm et al., 2015; Demos et al., 2019), to those of how synchrony affects social affiliation between two tappers (adults: Hove and Risen, 2009; Kokal et al., 2011; children+adult: Rabinowitch and Cross, 2018). Additionally, others have explored important factors, such as auditory and visual feedback, that influence tapping synchrony. With respect to auditory feedback, Konvalinka et al. (2010) showed coupling between dyadic tappers changes as a function of auditory feedback and participants are actually worst at keeping the tempo when they can hear each other. More recent evidence suggests such a result might be mediated by musicianship (Schultz and Palmer, 2019); musicians perform well with self and other feedback but non-musicians are worse when receiving feedback from others' taps. In a study of triads with one leader, two followers, and varied conditions of cross-participant feedback, Ogata et al. (2019) show the effect of auditory feedback is dependent on the assigned leader-follower roles. Using visual feedback, Tognoli et al. (2007) observed that seeing the other tapper's finger induced spontaneous synchronization during self-paced finger tapping (without a metronome). Additionally, Timmers et al. (2020) recently showed that visual information reduced synchronization accuracy during dyadic co-performance (one participant live, one participant recorded).

Considering these studies, especially in conjunction with the results of single-person tapping tasks, it is clear that audio and/or visual feedback has an effect on tapping performance. Nonetheless, it remains unclear whether such effects manifest among multiple individuals when the metronome is adaptive. Thus, in the following experiments, we manipulated all versions of auditory feedback (hearing only the metronome, hearing only the metronome and oneself but not others in the group, and hearing the metronome, oneself, and everyone else in the group). So as to avoid visual cues influencing synchronization, we asked participants to look only at their own tapping finger.

The main questions posed in our experiments were: (1) can group synchrony (both objective and subjective) be enhanced using an adaptive metronome? And (2) does auditory feedback influence group synchrony and subjective experience? To address these questions, we introduce a novel hardware/software system for perturbing a metronome and collecting multi-person tapping data in a highly customizable, temporally precise way. This research thus extends the previous adaptive metronome paradigm of Repp and Keller (2008) and Fairhurst et al. (2013) to group contexts.

The Current Study

We created an adaptive device to assist individuals or groups tasked with synchronizing to a pulse. While a variety of hardware and software has been developed for tapping experiments, none fill the exact niche of our device. For example, the E-music Box (Novembre et al., 2015) is a group music-making system giving participants the ability to control the output timing of a musical sequence based on their cyclical rotary control of an electromagnetic music box. Our device, on the other hand, adapts to the measured asynchrony of an individual participant's tap, or to the mean asynchrony of a group of participants tapping together, relative to a defined metronome period. While other systems have been developed to collect and analyze tapping data, such as FTAP (Finney, 2001), MatTAP (Elliott et al., 2009), Tap-It (Kim et al., 2012), Tap Arduino (Schultz and van Vugt, 2016), and TeensyTap (van Vugt, 2020), none of these are currently capable of adaptive, group-tapping experiments.

In building the multi-person adaptive metronome, we sought to keep latencies in the system to a minimum. We were inspired by Tap Arduino (Schultz and van Vugt, 2016), which uses a force-sensitive resistor (FSR) as a tap pad connected to an Arduino microcontroller and PC to collect tapping data. In the validation of Tap Arduino, Schultz and van Vugt (2016) showed that the average latency of the Arduino-based tap pad is less than 3 ms, significantly lower than latencies produced by a standard percussion pad (∼9 ms), FTAP (∼15 ms), and MAX/MSP (∼16 ms) (Cycling'74, 2014). Hence, we decided to build our device using multiple Arduino Uno microcontrollers and FSRs. Please see additional details below in *Apparatus*.

In order to better understand the sensorimotor synchronization of groups in the presence of an adaptive metronome, we conducted five tapping experiments. The goal of the first experiment was to replicate Fairhurst et al. (2013). Therefore, the experiment involved single tappers. The metronome played aloud through a speaker and adapted to participant performance using positive phase correction, as in experiment 1 of Repp and Keller (2008) and Fairhurst et al. (2013), with the following equation:

$$t_{met_{n+1}} = t_{\mathrm{met}_n} + IOI_{met} + (\alpha \times async_n) \tag{1}$$

where the time of the upcoming metronome tone ($t_{\mathrm{met}\ n+1}$) is equal to the time of the current metronome tone, plus the metronome inter-onset-interval (IOI), plus an adaptation based on the human participant's asynchrony. The asynchrony ($\mathrm{async}_\mathrm{n}$) is defined as the participant's tap time minus the metronome tone time ($t_{\mathrm{tap}_\mathrm{n}} - t_{\mathrm{met}_\mathrm{n}}$). Alpha ($\alpha$) represents the adaptivity parameter, and is a fractional multiplier of the asynchrony. Note, if the participant fails to tap, $\mathrm{async}_\mathrm{n} = 0$; the next metronome tone will, therefore, occur at the default IOI. Alpha can be set to any number. When set to $\alpha = 0$, the metronome does not adapt, and is thus considered a control (reference) condition. In Fairhurst et al. (2013), alpha values of 0.25 and 0.5 were found to be optimally adaptive, resulting in a smaller average standard deviation of asynchronies than with a non-adaptive metronome, while values of 0.75 and 1 were overly adaptive, leading to larger SD asynchronies.

Because we were also interested in the effects of auditory feedback on tapping stability, in Experiment 2 we performed an additional version of the single-person experiment outlined above in which participants now heard the sound triggered by their own tap through headphones (the metronome still played aloud through a speaker). We expected the findings from tapping studies with auditory feedback and a standard metronome (e.g., Aschersleben and Prinz, 1995; Aschersleben, 2002) to replicate, such that participants would become more accurate when they received auditory feedback from their taps. We further hypothesized that this greater objective synchrony (tapping accuracy) would correspond to increased ratings of feeling in the groove, liking of the task, etc.

Experiments 3–5 involved groups of four tappers. In these cases, the metronome algorithm was adjusted to adapt based on the average asynchrony of the group (of size I; in our case, 4 tappers):

$$t_{met_{n+1}} = t_{met_n} + IOI_{met} + \left(\alpha \times \frac{1}{I}\sum_{\mathrm{i}=1}^{I} async_{\mathrm{n_i}}\right) \tag{2}$$

with all terms as previously defined. In Experiment 3, participants heard the sound of the metronome through its speaker but not the sound of their own tap. In Experiment 4, participants heard the metronome through its speaker and only the sound of their own tap through headphones. In Experiment 5, participants heard the metronome through its speaker and the sounds of their own and everyone else's taps through speakers attached to each individual Arduino.

Across all experiments, we hypothesized that, compared to no adaptivity or highly adaptive conditions, low levels of metronome adaptivity (i.e., 25–50%) would result in more stable tapping performance, as well as a more positively valanced subjective experience. We further hypothesized that participants' being able to hear their taps more clearly in Experiments 2, 4, and 5 would result in greater temporal accuracy than in Experiments 1 and 3 (in which they could not hear a sound produced by their taps). With regard to Experiment 5, we hypothesized participants would feel more connected to and in synchrony with the group when they could hear each other's taps. A summary of experimental conditions and hypotheses is provided in **Table 1**.

Apparatus

The hardware and software comprising the multi-person adaptive metronome were custom-built using open-source tools. The hardware consists of five Arduino Uno devices[1], five Adafruit Wave Shields (v1.1[2]) for playing sound, and four force sensitive resistors (InterlinkElectronics, 2018) for tapping. The Wave Shields are connected to the Arduinos to enable them to produce sound (i.e., the metronome sound and the sound produced by tapping on the tap pads). For each participant, a single force sensitive resistor (FSR) is used as a tap pad and is connected to a single Arduino which registers the taps, communicates with the metronome Arduino, and plays sounds triggered by the participant's taps. The fifth Arduino is the metronome Arduino. It integrates inputs from the other Arduinos, implements the metronome timing function, generates metronome tones, and transmits event data to a connected computer. All four Arduinos responsible for registering taps are wired into the metronome Arduino (see **Figures 1A,B**). A speaker is connected to the Wave Shield of each Arduino. The Wave Shields have a headphone jack and volume wheel, allowing the experimenter to choose whether participants should hear sounds produced during the experiment *via* a speaker, individually through headphones, or not at all.

Software associated with the multi-person adaptive metronome is freely available for download. All software was custom built in C++, Python 2.7, and Julia 0.6.0 (Bezanson et al., 2012). Separate programs were compiled for the metronome and tapping Arduinos, and downloaded to the respective Arduinos. Because the adaptive metronome code executed directly on the metronome Arduino, the adaptivity calculations were efficient, with minimal delay for registering taps and adjusting subsequent metronome tones. The metronome Arduino was connected to an experiment control computer (ECC)–a MacBook Pro (Apple, Inc., Cupertino, CA, United States)–*via* USB serial port running at 115,200 baud. The PySerial package was used for two-way communication between the metronome Arduino and the ECC. A custom-written Python program running on the ECC handled the randomization of experiment conditions, transmitted alpha values for each trial to the metronome Arduino, received data from the metronome Arduino that was streamed to custom binary files, and displayed relevant information to the experimenter.

We implemented a graphical user interface (GUI) to allow for easily customizable data collection procedures. With a simple Python script, experimenters can set parameters of the

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[1] Arduino.cc

[2] Adafruit.com

TABLE 1 | Summary of experiments, conditions, and hypotheses.

Exp.	# tappers	Tap audio feedback	α levels	Hypothesis
1	1	None	0, 0.25, 0.5, 0.75, 1	Replicate Fairhurst et al. (2013)
2	1	Headphones	0, 0.25, 0.5, 0.75, 1	Reduced async due to audio feedback
3	4	None	0, 0.35, 0.7, 1	Benefits of adaptive metronome extend to group
4	4	Headphones	0, 0.35, 0.7, 1	Reduced async due to audio feedback
5	4	Speakers	0, 0.35, 0.7, 1	Reduced async; increased perceived group sync

Alpha (α) levels correspond to metronome adaptivity conditions; 0 means no adaptivity (control condition, i.e., standard metronome).
Experiment 5 is the only experiment in which participants could hear the taps produced by other tappers.
async, asynchrony; # tappers, the number of participants together in the experiment session; Tap audio feedback, whether or not participants could hear the sound triggered by their tapping on the FSR and how.

metronome (e.g., tempo, adaptivity percentages, number of repetitions for each adaptivity condition, number of tapping Arduinos in the experiment, data output paths, etc.). From the GUI, experimenters can input participant IDs, control the start and stop of runs or practice runs, and monitor the time remaining in the experiment. Please see **Figure 1** for an overview of our hardware, software, and experimental set-up. Also note that all code to create the system is publicly available: https://github.com/janatalab/GEM.

For single person experiments (Exps. 1 and 2), participants always tapped on the same individual tap pad (of the four possible tap pads). At their seat, participants also had an iPad running our experiment web interface, Ensemble (Tomic and Janata, 2007), to answer surveys. All experimental instructions, presentation code, data, and analysis code related to the experiments reported in this paper are available in a separate GitHub respository: https://github.com/janatalab/GEM-Experiments-POC.

Adaptivity Calculations

The calculation of tap asynchronies and subsequent metronome adjustments was defined in relation to the metronome period, or inter-onset-interval (IOI). The fundamental temporal unit for registering taps in relation to a metronome tone was defined as +/− half of the metronome IOI. For example, with a metronome IOI of 500 ms, taps registered in the window spanning −250 ms before to +250 ms after the tone, are ascribed to the current tone. When a tap is registered on the tap pads of any of the tapping Arduinos, an interrupt is triggered on the metronome Arduino. With nanosecond precision, interrupts are a precise way to register the timing of an event.

Once the temporal window of registering taps for the current tone has elapsed (e.g., 250 ms after the metronome tone for an IOI of 500 ms), the times of the taps registered for that tone are used to calculate the timing of the next metronome tone. Upon calculating the time of the next metronome tone, and setting a corresponding timer, the data are sent to the ECC with less than 1 ms delay. The data packet sent to the ECC after every metronome event window is 12 bytes: 4 bytes for the time of the metronome tone onset, and 2 bytes for each tapper's tap time, relative to the metronome (8 bytes total). The ECC streams these data to a custom-formatted binary data file.

Personality and Individual Factors

In each experiment, all participants completed the Goldsmith's Music Sophistication Index (GOLD-MSI; Müllensiefen et al., 2014), the Internality, Powerful Others, and Chance Scales (IPC scales; Levenson, 1981), the Brief form of the Affective Neuroscience Personality Scales (BANPS; Barrett et al., 2013), and a short form assessing basic demographic information. The GOLD-MSI assesses six subcategories of possible musical expertise: *active engagement*, *perceptual abilities*, *musical training*, *singing abilities*, and *emotions*, which, when combined, generate an overall *general musical sophistication* score. We assumed people with higher musical sophistication would exhibit less variable tapping performance. The BANPS is the brief version of Affective Neuroscience Personality Scales (Davis et al., 2003; Davis and Panksepp, 2011) and measures behavioral traits in relation to six primary hypothesized neural affective systems: *play*, *seek*, *care*, *fear*, *anger*, and *sadness*, each of which has hypothesized neural correlates. These scales were included to explore potential relationships between neuromodulatory systems and interpersonal dynamics. The IPC scales (Levenson, 1981) measure the degree to which participants think that: (1) they have control over their own life (*internality*), (2) others control events in their life (*powerful others*), and (3) chance dictates their life (*chance*). Previously, the internality subscale was associated with the degree to which participants were categorized as leaders or follows in a single-person adaptive metronome task (Fairhurst et al., 2014). In the current experiments, we wondered whether those with higher internality score may be more closely synchronized with the metronome and/or the group. Collectively, the above surveys allow for an exploratory analysis of the degree to which person-level factors influence tapping behavior and subjective experience in group settings.

EXPERIMENT 1

Though the multi-person adaptive metronome was built with four tappers in mind, our initial experiments involved only one tapper so we could confirm the system worked as expected in a known scenario. Thus the goal of the first experiment was to replicate the findings of Fairhurst et al. (2013) with our new Arduino-based system.

Methods

Participants

A statistical power analysis was performed for sample size estimation, based on data from Fairhurst et al. (2013)

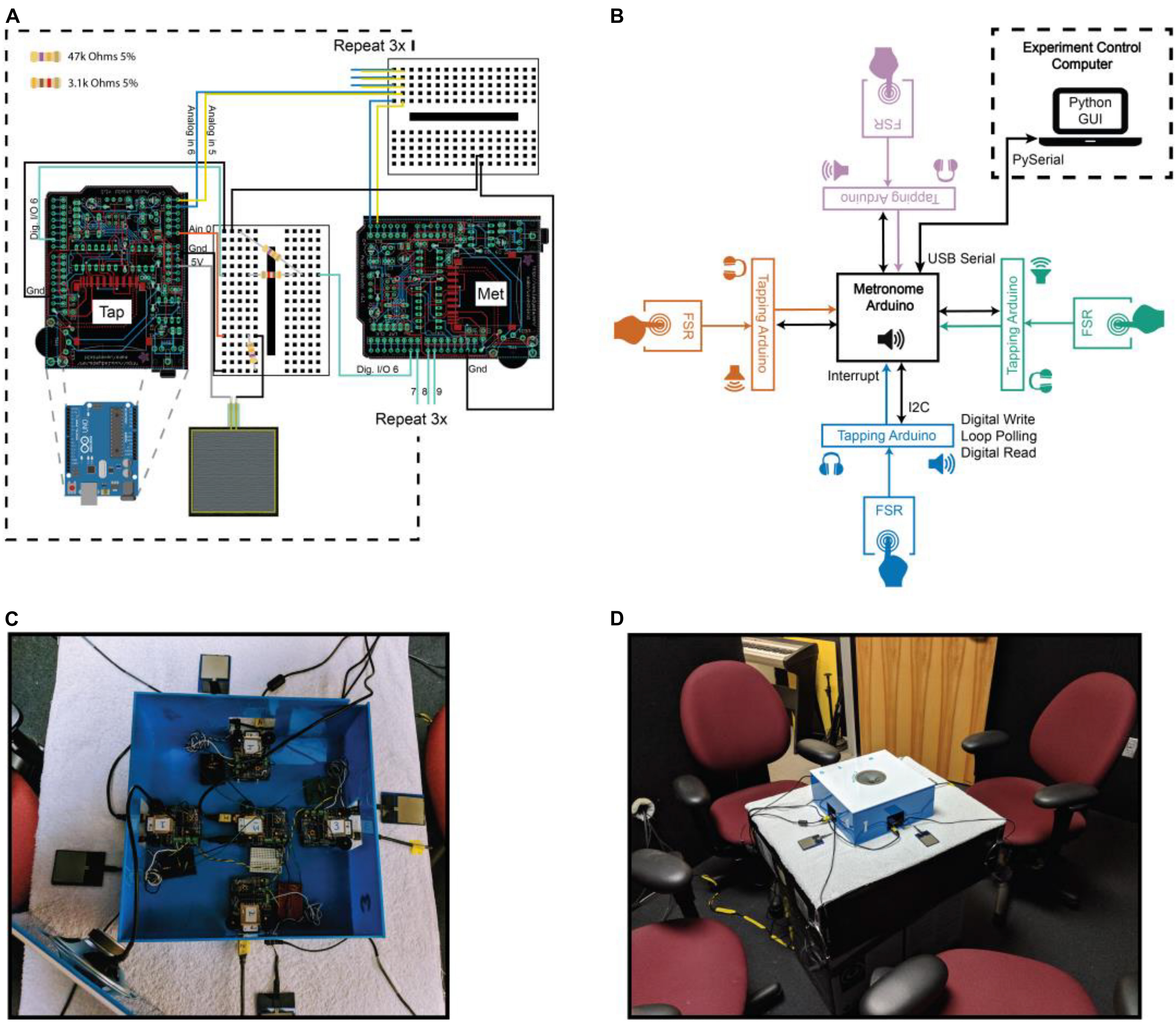

FIGURE 1 | Overview of the GEM system. **(A)** Wiring diagram illustrating the connections between one tapping device (Tap) and the metronome (Met). Note that we repeat these connections three times (indicated by the dotted black box) to arrive at our 4 Tapper + metronome system. Note also that the connections from all Adafruit Wave Shields (v1.1) depicted here in black carry through to the Arduino Uno boards underneath them to which they are attached, indicated by the dotted gray lines connecting the blue Arduino Uno (bottom left) to the Wave Shield. **(B)** Schematic of all devices comprising the multi-person adaptive metronome and their means of communication. The metronome Arduino can be in either an "idle" or "run" state. In the idle state, the Experimental Control Computer (ECC; housed in a separate experiment control room, represented by dotted black box) can set experiment parameters on the metronome Arduino, which in turn sets parameters on the tapping Arduinos. Upon receiving the message from the ECC to start a trial, the metronome Arduino is in a constant loop of producing metronome tones according to our adaptive algorithm, registering participant taps, and sending data packets to the ECC. The tapping Arduinos are constantly polling, reading the value of the FSR input pin. When the FSR pin exceeds a specified threshold (a tap occurs), a digital output pin is pulsed on, resulting in the triggering of an interrupt on the metronome Arduino. Participants can hear the sound of their own tap through headphones, speakers, or not at all. The metronome is always heard through a speaker. **(C)** A photo of the system used in these experiments. **(D)** The view of our multi-person adaptive metronome, from the participants' perspective. The speaker in the top center of the box played the tones from the metronome (all Experiments). During experiments in which participants could hear the sound produced by their own tap, they used headphones, which can be seen hanging from the side of the table. During Experiment 5, when participants could hear everyone in the group, we placed an additional speaker to the left of each tap pad.

(N = 16), comparing metronome adaptivity = 0 to metronome adaptivity = 0.25. The effect size in this original study was −0.95, considered to be large using Cohen's (1988) criteria. With an alpha = 0.05 and power = 0.90, the projected sample size needed with this effect size for the current experiment was approximately N = 12, for this simplest comparison between alpha conditions. We thus sought to collect data from at least 20 participants to allow for attrition. Data collection was set to stop when a maximum of 30 participants had completed the task, or the academic term ended, whichever came first.

Twenty-one undergraduate students from the University of California, Davis, participated in exchange for partial course credit. Data from one participant was discarded because of self-report of abnormal hearing. Data from two participants could not be used due to technical issues with our internet connection during data collection, which resulted in loss of survey data. After the additional data cleaning procedures described below, we had a total of 15 participants, aged 21 +/- 2 years; 8 females. For all experiments reported in this paper, participants provided informed consent in accordance with a protocol approved by the Institutional Review Board of the University of California, Davis.

Stimuli

The only sound heard throughout the experiment was the sound of the metronome. This sound was a marimba sample from GarageBand, with pitch A2 and a 400 ms duration, played through a speaker connected to the metronome Arduino at a comfortable listening volume. All stimuli discussed in this paper are available in the GEM-Experiments-POC repository.

Procedure

The participant was seated in a sound-attenuating room and instructed to synchronize their tapping with the metronome, starting with the third tone. They were told to try to maintain the initial established tempo of the metronome from the first two tones and that the metronome would adapt based on their performance. Following the delivery of instructions, we ensured participants understood the task and showed them how to tap on the force-sensitive-resistors with the index finger of their dominant hand. Participants then completed one practice round of tapping (∼13 s); a maximum of three practice trials was possible, if participants struggled to understand the task. Metronome adaptivity was always at 0 during the practice rounds.

Throughout the experiment, participants completed ten rounds of tapping at each of five adaptivity levels (0, 0.25, 0.5, 0.75, 1), for a total of 50 rounds of tapping. Adaptivity level was randomized across rounds of tapping. Each round consisted of 25 metronome tones and lasted approximately 13 s. The initial metronome tone inter-onset-interval for all rounds was set to 500 ms (120 beats per minute). Following each round of tapping, participants answered a short questionnaire which assessed, on a set of 5-point scales, the degree to which they felt: (1) synchronized with the metronome, (2) in the groove, (3) they had influence over the metronome pulse, (4) the task was difficult, and (5) they would have liked to continue with the task. We defined synchronization as the degree to which participants thought their taps were aligned with the tones of the metronome (from an objective perspective) and "being in the groove" as an effortless, pleasurable feeling of oneness with the metronome (a subjective experience; see Janata et al., 2012). This distinction was explained to participants during the instruction period (for full instructions text, please visit our GEM-Experiments-POC repository wiki). In total, all rounds of tapping, including post-tapping surveys, typically lasted 30–40 min. Participants then completed the personality-related and demographic surveys, which typically took 15–20 min. The entire experiment lasted approximately 1 h.

Data Analysis

Binary tapping data files were converted to .csv using a custom file parser in Julia (available in the GEM repository). All data were then preprocessed and concatenated using custom scripts in MATLAB (Mathworks, Natick, MA, United States). Note that while all hardware and software used to build and run the adaptive metronome is open source, MATLAB is not. We used MATLAB purely due to its convenient interface with our web-based data collection tool, Ensemble (Tomic and Janata, 2007). After concatenating all cleaned tapping and survey data into tables in MATLAB, the remaining analyses were conducted in Python. The anonymized data tables for each experiment and the analysis code are available in the GEM-Experiments-POC repository. All statistical analyses can be recreated using the provided data tables and Jupyter notebooks.

Tapping Data

Participants who missed 30% or more of the required number of taps were eliminated from further analysis. Of the data remaining, any rounds missing > 30% of the taps were discarded. If these data cleaning procedures resulted in a participant not having any observations for any of the adaptivity conditions, that participant was removed from further analyses (3 participants). All tapping data were analyzed with respect to metronome adaptivity condition. The dependent measure of interest was the standard deviation of tap asynchronies, which serves as a measure of synchronization stability, as in Repp and Keller (2008) and Fairhurst et al. (2013).

Survey Data

All questionnaires were analyzed *via* a custom MATLAB implementation of the original instrument authors' scoring metrics. For the post-tapping survey, data were z-score normalized within each rating scale for each participant. Correlations among surveyed variables were checked and an exploratory factor analysis was conducted.

Statistical Analyses

All statistical analyses were conducted in Python using the *pingouin* (Vallat, 2018), *statmodels* (Seabold and Perktold, 2010) and *factor-analyzer* (Biggs, 2020) packages. All code is available in the associated Jupyter notebooks.

Results

The tapping results for Experiment 1 are plotted in **Figure 2**, left panel (solid line), as a function of metronome adaptivity condition (α). A repeated measures analysis of variance (ANOVA) revealed a main effect of α condition on tapping SD asynchrony, $F(4, 56) = 8.16$, $p = 0.002$, $\eta^2 = 0.26$. Paired t-tests were calculated one-sided, based on a level of alpha = 0.05. The t-tests revealed significant differences in SD asynchrony between the baseline condition ($\alpha = 0$) and what we might call optimally adaptive conditions: $\alpha = 0.25$, $t(14) = 2.81$, $p = 0.007$, $d = 0.48$, Δ async = −8.10 ms, and $\alpha = 0.5$, $t(14) = 2.92$, $p = 0.006$, $d = 0.39$, Δ async = −6.64 ms. There were no significant differences from the baseline condition when $\alpha = 0.75$ or 1, both $t < 1$.

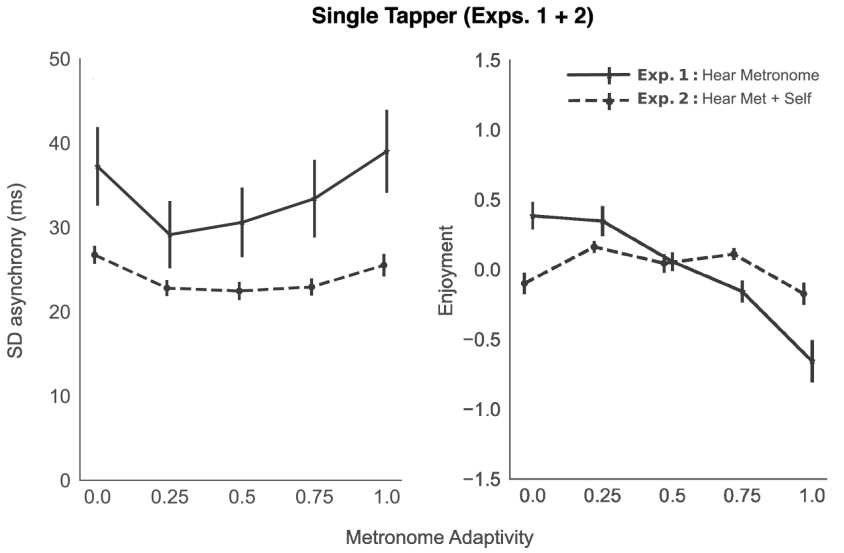

FIGURE 2 | Tapping performance (standard deviation of tap—metronome asynchrony), left panel, and subjective enjoyment, right panel, averaged across participants, as a function of metronome adaptivity, in the two single tapper experiments. Solid black lines represent experiments in which participants could only hear the sound produced by the metronome; dashed lines, experiments in which participants could hear the metronome and the sound of their own tap. Error bars represent standard error of the mean.

Turning to subjective ratings, we found participants' perceived synchrony with the metronome was significantly negatively correlated with their tapping SD asynchrony [$r_{rm}(603) = -0.40$, 95% CI (-0.47, -0.33), $p < 0.001$]. Reduced asynchronies (better synchrony with metronome) led to a greater sense of subjective synchrony, suggesting participants have at least a moderately accurate assessment of their own tapping performance. Before analyzing subjective ratings in relation to metronome adaptivity, we checked for correlations among the individual items and found all showed significant correlations with each other (see **Supplementary Appendix 1**). Thus, we performed an exploratory factor analysis to identify one or more latent variables. Two preliminary tests confirmed the suitability of applying a factor analysis to these data (Bartlett's test of sphericity = 810.04, $p < 0.001$; Kaiser-Meyer-Olkin measure of sampling adequacy = 0.738, $p < 0.001$). Eigenvalues and a scree plot indicated a 1-factor solution. We therefore ran the factor analysis again, specifying a one factor solution, using the maximum likelihood method, and no rotation (rotation is not possible with one factor). Factor loadings and communalities are shown in **Table 2**. Groove, synchrony, and liking all loaded strongly and positively onto this factor, while difficulty had a high negative loading. With a loading less than 0.3, participants' felt influence over the pulse played only a small role in this overall factor and was therefore excluded from the overall factor score. We hereafter refer to this factor as "Enjoyment."

Participants' enjoyment factor scores are plotted as a function of metronome adaptivity in **Figure 2**, right panel (solid line). A repeated measures ANOVA revealed a main effect of α condition on enjoyment, F(4, 56) = 13.65, $p < 0.001$, $\eta^2 = 0.49$. There was no significant difference between baseline ($\alpha = 0$) and $\alpha = 0.25$. However, a significant decrease in enjoyment was observed between baseline and $\alpha = 0.5$, 0.75, and 1. Detailed statistics for all pairwise comparisons can be viewed in the associated Jupyter Notebook.

Discussion

The tapping results of Experiment 1 replicate those of Fairhurst et al. (2013), using our new Arduino-based adaptive metronome. The Arduino-based system functions as expected: it brought participants into greater synchrony with the metronome at adaptivity levels of 25–50% (compared to baseline), as in Fairhurst et al. (2013). At higher levels of adaptivity (75% or 100%) participants' tapping performance returned to baseline or worse. We can, therefore, conclude, like Fairhurst et al. (2013), that it is possible for the metronome to be in "optimal" vs. "overly" adaptive states, as could be the case with a real person with whom one might interact. By simulating such states in a controlled way, we can assess the degree to which optimal vs. extreme adaptivity influence participants' experience.

With respect to subjective experience during the task, we firstly found participants' perceived synchrony with the metronome was correlated with their objective (measured) tapping synchrony.

TABLE 2 | Item loadings for the Enjoyment factor (Exp. 1).

Item	Enjoyment	Communality
Groove	0.663	0.450
Synchrony	0.836	0.699
Liking	0.460	0.212
Difficulty	−0.772	0.596

Cumulatively, the single factor enjoyment had a sum of squared loadings of 2.01, explaining a proportional and cumulative 49% of variance.

We also found their synchrony rating is highly correlated with their groove, liking, and difficulty ratings. An exploratory factor analysis showed all of these ratings could be reduced to one collective factor which we labeled Enjoyment. These correlations between our rating items echo previous studies that have also often found associations between groove, liking, and difficulty (e.g., Janata et al., 2012; Hurley et al., 2014; Witek et al., 2014).

In examining participants' enjoyment scores in relation to metronome adaptivity, we did not see any increase in enjoyment with optimal adaptivity, though we did find significant decreases in enjoyment when the metronome adapted by 50% or more. It is hard to directly compare these subjective findings with those of Fairhurst et al. (2013), as they used only difficulty, influence, and synchrony ratings on a visual analog scale, ranging from 0 to 10, whereas we included additional items, all on 5 pt. scales. Nonetheless, our results follow their overall pattern of subjective rating findings (see their Supplementary Table 1), with about the same ratings observed in baseline and 25% adaptivity conditions, followed by an increased difficulty (in our case, decreased enjoyment), at adaptivity levels 50% and higher, compared to baseline. Whether the overall patterns in tapping synchrony and subjective experience reported here will remain the same when participants receive auditory feedback about their taps is the topic of Experiment 2.

EXPERIMENT 2

Before applying our adaptive metronome to group contexts, we first wanted to more clearly characterize its functioning in the single-person use case. To this end, we repeated Experiment 1, but additionally provided participants auditory feedback from their taps. We hypothesized such feedback would lead to better synchronization with the metronome and increased enjoyment of the task.

Methods

All methods were identical to those of Experiment 1, with the following exception: participants could hear the sound produced by their own tap, through headphones. This sound was a woodblock sample from the Proteus 2000 sound module. Participants could still hear the metronome through its speaker. Therefore, before the experiment started, we had participants calibrate their headphone volume such that the volume of their tap was perceptually matched to that of the metronome. Twenty-eight participants took part in the study. Two were removed according to the data cleaning procedures outlined in Exp. 1, for a total of 26 remaining participants, mean age 20 +/− 2 years; 24 were female. No participant participated in more than one experiment reported in this paper.

Results

The tapping data for Exp. 2 are plotted in **Figure 2**, left panel (dashed line). A repeated measures analysis of variance again showed a main effect of α condition on tapping SD asynchrony Exp. 2: $F(4, 100) = 8.69$, $p < 0.001$, $\eta^2 = 0.26$. Comparing means, we not only found significant differences between baseline and $\alpha = 0.25$, $t(25) = 5.33$, $p < 0.001$, $d = 0.77$, Δ async $= -3.94$ ms, and $\alpha = 0.5$, $t(25) = 4.39$, $p < 0.001$, $d = 0.78$, Δ async $= -4.28$ ms, but also between baseline and $\alpha = 0.75$, $t(25) = 4.51$, $p < 0.001$, $d = 0.72$, Δ async $= -3.81$ ms.

To assess the effect of auditory feedback on tapping SD asynchrony, we conducted a mixed ANOVA with auditory feedback as a between subjects predictor, adaptivity condition as a within subjects predictor, and their interaction. Compared to Exp. 1, we found tapping performance improved significantly when participants receive auditory feedback from their taps [main effect of auditory feedback, $F(1,39) = 8.57$, $p < 0.001$, $\eta^2 = 0.18$]; on average, participants' SD async decreased by 9.79 ms (i.e., became more stable). The main effect of adaptivity was also significant [$F(4,156) = 10.86$, $p < 0.001$, $\eta^2 = 0.22$], as was the interaction between adaptivity and auditory feedback [$F(4,156) = 2.59$, $p < 0.001$, $\eta^2 = 0.06$]—at higher levels of adaptivity, the effect of auditory feedback on tapping performance was more pronounced.

With regard to subjective experience, participants' perceived synchrony with the metronome was significantly negatively correlated with their tapping SD asynchrony [$r_{rm}(1{,}085) = -0.30$, 95% CI $(-0.36, -0.25)$, $p < 0.001$], suggesting accurate assessment of their own tapping capabilities. As in Experiment 1, we again found significant correlations between subjective rating scales (see **Supplementary Appendix 1**), and, therefore, conducted a confirmatory factor analysis, in line with the exploratory results of Exp. 1. Two preliminary tests confirmed the suitability of this approach (Bartlett $\chi^2 = 1{,}307.07$, $p < 0.001$; KMO $= 0.727$, $p < 0.001$). Our 1 factor solution showed all loadings in the same directions and relative magnitudes as in Exp. 1, **Table 2** (see **Supplementary Appendix 2** for the loadings of this experiment). We therefore continued with the labeling of this factor as Enjoyment.

Participants' Enjoyment factor scores are plotted in **Figure 2**, right panel (dashed line). A repeated measures ANOVA revealed a main effect of α condition on enjoyment score, $F(4, 100) = 4.04$, $p = 0.015$, $\eta^2 = 0.14$. All paired, t-tests were calculated one-sided, based on a level of alpha = 0.05. Compared to baseline ($\alpha = 0$), there was a significant increase in enjoyment at $\alpha = 0.25$ [$t(25) = -3.30$, $p = 0.014$] and $\alpha = 0.75$ ($t = -2.03$, $p = 0.03$).

To assess the effect of auditory feedback on enjoyment, we conducted a mixed ANOVA with auditory feedback as a between subjects predictor, adaptivity condition as a within subjects predictor, and their interaction. While the main effect of auditory feedback was not significant, the interaction between auditory feedback and adaptivity condition was [$F(4,156) = 8.84$, $p < 0.001$]. With no adaptivity (baseline condition), having auditory feedback was significantly less enjoyable [$t(30) = 3.91$, $p = 0.001$], whereas at higher levels of adaptivity ($\alpha = 0.75$ and 1), auditory feedback resulted in greater enjoyment. All comparisons of means can be found in the associated Jupyter Notebook.

Discussion

When participants received auditory feedback from their taps, they achieved greater synchrony with the metronome (in all conditions). In terms of metronome adaptivity, performance was improved, even at higher levels of adaptivity (75%), but returned to near baseline with 100% adaptivity. Auditory feedback resulted in a significant overall decrease in SD asynchrony, compared to no feedback (overall difference in means between Exp. 1 and 2 was ∼10 ms). Though there was no overall difference in enjoyment scores between Exps. 1 and 2, in Experiment 2, we did find a significant improvement in participants' enjoyment at 25% and 75% adaptivity, compared to no adaptivity baseline, as well as an interaction between auditory feedback and alpha condition. Whereas in Experiment 1, enjoyment plummeted at higher levels of adaptivity, in Experiment 2, when participants received auditory feedback, enjoyment remained high. These results speak to the relevance of auditory feedback in influencing both tapping accuracy and subjective enjoyment in an adaptive metronome context. We thus continued to explore the effect of auditory feedback in group tapping contexts, reported below.

EXPERIMENT 3

After replicating and extending single-person adaptive metronome studies using our Arduino-based system, we next sought to validate the use of an adaptive metronome in multi-person contexts.

Methods

Participants

Because the power analysis detailed in Experiment 1 was based on individuals rather than groups, and no previous adaptive metronome group-tapping experiment existed to use for an effect size calculation, we erred on the side of more groups, with data collection set to stop when a maximum of 35 groups had completed the task, or the academic term ended, whichever came first. Participants were not systematically assigned into specific groups. They could register for a timeslot in the experiment *via* UC Davis's online recruitment system. Hence, the four people who had signed up (for, e.g., the 9 am–10 am timeslot) were all grouped together. One hundred twenty-four undergraduate students (31 groups of 4) from the University of California, Davis, participated in exchange for partial course credit. Four groups had to be removed due to technical difficulties (Wi-Fi issues during survey completion). The remaining 108 participants (27 groups) had a mean age of 21 +/- 3 years; 83 were female.

Stimuli

Same as in Experiment 1. Participants only heard the metronome (marimba sample) and did not hear any sound produced by their own or others' taps. As in Experiment 1, the initial metronome tone inter-onset-interval for all rounds was set to 500 ms (120 beats per minute).

Procedure

The procedure was largely the same as in Experiment 1, with the following exceptions. Participants were instructed to keep their gaze on their own finger as they tapped and not to speak with the other participants during the experiment. Surveys, such as the IPC scales, were taken before the tapping experiment started, rather than at the end, so as not to be influenced by any perceived social dynamics during the experiment. The post-tapping survey presented after each round asked an additional question about how in synchrony participants felt with the others. Participants completed six rounds of tapping at each of four adaptivity levels (0, 0.35, 0.7, 1), for a total of 24 rounds of tapping. Each round lasted approximately 30 s (as opposed to 13 s in Experiments 1 and 2). As previously, adaptivity level was randomized across rounds of tapping. Instructions remained the same; we acknowledge that there is perhaps an ambiguity in how participants could now interpret the phrase "based on your performance" (either as an individual or as a group)—both would be acceptable and accurate interpretations.

Data Analysis

All data concatenation, cleaning, and analysis procedures were identical to those for Exps. 1 and 2, with the following exceptions.

Tapping Data

Groups in which 30% or more of the required number of taps were missed (across the entire group) were eliminated from further analysis.

The main dependent measure of interest was the standard deviation of the mean asynchrony of the group, relative to the metronome tones (referred to below as SD async). An additional metric of interest was the relative performance of the individuals with respect to the group, which we calculated as the individual's SD asynchrony with respect to the metronome minus the group's SD asynchrony with respect to the metronome, as defined in the following sequence of equations. Equation 3 represents the tapping asynchrony of the individual (*i*) with respect to the metronome (*met*) for each metronome window (*w*),

$$async_{\mathrm{w_i}} = t_{tap_{w_i}} - t_{met\,w} \tag{3}$$

Equation 4 the asynchrony of the group (*G*) with respect to the metronome for each metronome window,

$$async_{wG} = \frac{1}{I}\sum_{\mathrm{i}=1}^{I} t_{tap_{wi}} - t_{met\,w} \tag{4}$$

and Equation 5 the difference in standard deviation of tapping asynchrony between the individual and the group.

$$SDasync_{difference_i} = \sqrt{\frac{\sum\left(async_{wi} - \mu_{\mathrm{async}_i}\right)^2}{w}} - \sqrt{\frac{\sum\left(async_{wG} - \mu_{\mathrm{async}_G}\right)^2}{w}} \tag{5}$$

We were also interested in the stability of the group members' tapping relative to each other and calculated this by first taking the standard deviation of the four participants' asynchronies for each metronome window:

$$SD_{Gw} = \sqrt{\frac{\sum\left(async_{wGi} - \mu_{\mathrm{async}_{wG}}\right)^2}{I}} \tag{6}$$

Then taking the standard deviation of those standard deviations over time:

$$SD_{SD_G} = \sqrt{\frac{\sum \left(SD_{G_W} - \mu_{SD\,G}\right)^2}{W}} \tag{7}$$

These different metrics are illustrated in **Figure 3** and detailed in its caption.

Survey Data

All questionnaires were analyzed *via* a custom MATLAB implementation of the original instrument authors' scoring metrics. For the post-tapping survey, data were z-score normalized within each participant, each rating scale, then averaged across participants within each group.

Results

A repeated measures ANOVA showed a main effect of α condition on the average group tapping SD asynchrony [F(3, 78) = 11.33, $p < 0.001$, $\eta^2 = 0.30$]; see **Figure 4**, left panel, solid line. Comparisons between all means showed significant improvements in tapping performance at α = 0.35 [t(26) = 3.02, $p < 0.001$, $d = 0.54$, Δ async = −6.22 ms], and α = 0.7 [t(26) = 2.09, $p < 0.001$, $d = 0.33$, Δ async = −4.19 ms], but not at α = 1, compared to baseline. The group's tapping SD asynchrony was negatively correlated with both the average (across the group) of each individuals' perceived synchrony with the metronome [r_{rm} (605) = −0.42, 95% CI (−0.48, −0.35), $p < 0.001$] and the average (across the group) of each individuals' perceived synchrony with the group [r_{rm} (605) = −0.37, 95% CI (−0.44, −0.30), $p < 0.001$]. Collectively, these correlations indicate groups can accurately judge their own tapping stability. Similarly, the group's tapping variability with respect to each other (i.e., SD of SD async, **Figure 3**, right panel, black error bars) was significantly correlated with the average perceived synchrony of the group [r_{rm} (605) = −0.32, 95% CI (−0.39, −0.24), $p < 0.001$]; see **Figure 5**.

As in the previous experiments, we again found significant correlations between the subjective rating scales (see **Supplementary Appendix 1**), and, therefore, conducted a confirmatory factor analysis, in line with the exploratory and confirmatory results of Exps. 1 and 2, respectively. Two preliminary tests confirmed the suitability of this approach (Bartlett χ^2 = 2,129.74, $p < 0.001$; KMO = 0.865, $p < 0.001$). Our 1 factor solution showed all loadings in the same directions and relative magnitudes as in Exps. 1 and 2. The additional item present in the group experiments ("To what extent did you feel in synchrony with the other players in the group?") had a high positive loading, similar to the rated synchrony of the self with the metronome. Factor loadings are shown in **Table 3**. The Enjoyment factor explains 65% of the variance in the ratings data.

The group's average Enjoyment factor scores are plotted in **Figure 4**, right panel (solid line). A repeated measures ANOVA revealed a main effect of α condition on enjoyment score, F(3, 78) = 78.03, $p < 0.001$, $\eta^2 = 0.75$. All paired t-tests were calculated one-sided, based on a level of alpha = 0.05. Compared to baseline (α = 0), there was no change in Enjoyment at α = 0.35; however, there was a significant decrease in enjoyment at higher adaptivity levels: α = 0.7 [t(26) = 6.38, $p < 0.001$] and α = 1 (t = 10.16, $p < 0.001$).

Discussion

With this experiment, we show that an adaptive metronome can be employed successfully in a group context. By adapting to the average asynchrony of the group, we find groups of tappers can be brought into greater synchrony (compared to baseline). Alternatively, too much adaptivity results in performance at or worse than baseline. Thus, the tapping stability of groups can be manipulated using our multi-person adaptive metronome in a manner analogous to the results observed in single tapper contexts without auditory feedback (Exp. 1).

In terms of subjective experience, we replicate the factor structure of our previous experiments, with the addition of feeling in synchrony with the group also loading onto the Enjoyment factor. We found enjoyment significantly decreased at higher levels of adaptivity but not at optimal adaptivity (35%), mimicking the effects observed in Exp. 1. We also found that groups are generally able to accurately assess the stability of their own tapping performance, as indicated by the significant correlation between their ratings of synchrony and their measured tapping SD asynchrony, on the trial level. In the following experiments, we explore the effect of auditory feedback on group tapping stability and enjoyment.

EXPERIMENT 4

Methods

Participants

One hundred and four undergraduate students (26 groups of 4) participated. One group had to be removed due to technical difficulties during data collection. In total there were 25 groups, 100 participants, with a mean age of 20 +/− 2 years, 79 female.

Stimuli

Participants heard the metronome (marimba sample) through its speaker and their own tap sound through headphones. All participants' taps produced the same sound (the woodblock sample from Experiment 2). Before the experiment started, we had participants calibrate their headphone volume such that the volume of their tap was perceptually matched to that of the metronome.

Procedure

Same as Exp. 3.

Results

A repeated measures ANOVA showed a main effect of α condition on the average group tapping SD asynchrony [F(3, 72) = 22.09, $p < 0.001$, $\eta^2 = 0.48$]. Comparisons between all means showed significant differences between α = 0 and all other conditions. Tapping performance significantly improved at α 0.35 [t(24) = 5.17, $p < 0.001$, $d = 1.10$, Δ async = −5.70 ms], α 0.7 [t(24) = 7.71, $p < 0.001$, $d = 1.43$, Δ async = −6.51 ms],

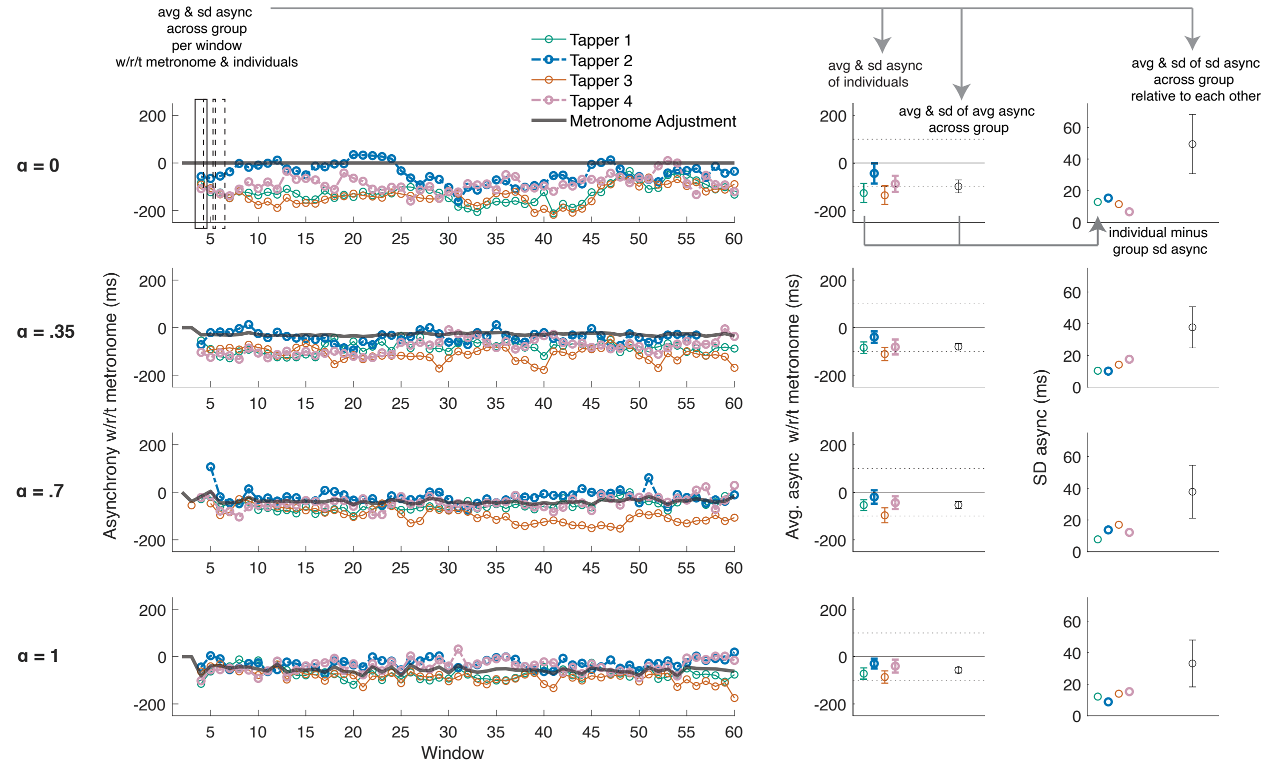

FIGURE 3 | An example run (left panels) at each adaptivity condition (rows) during the group tapping experiments. The metrics illustrated in this figure are applicable to all group tapping experiments, though this particular example comes from Exp. 5 (when all participants could hear each other and the metronome). The individual, colored lines and dots represent the individual tappers in the group. The solid gray line represents the adjustments of the metronome. Note that there are no adjustments in the top left panel when **α** = 0 (i.e., the control condition that mimics a standard metronome). In the middle panels, the average asynchrony (dots) and SD of the average asynchrony (error bars) of all individuals (colored dots) and the group (black dot), with respect to the metronome, are plotted. A solid line at 0 and dotted lines +/– 100 ms are plotted for reference. The group SD asynchrony (error bars of black dot) was our main metric of interest (see **Figure 4**). In the right-most panels, the colored dots show the difference between each individual's SD asynchrony and the group SD asynchrony. This metric indexes how variable the individual is vs. the group as a whole, with respect to the metronome, and is used in our models assessing individual differences. The black dot represents the average of the SD asynchrony of the individuals, across all windows; the error bar is the SD of this average SD asynchrony, which we consider an index of how variable individuals' taps are with respect to each other (rather than the metronome).

and α 1 [t(24) = 4.51, $p < 0.001$, $d = 1.10$, Δ async = −5.28 ms]. In brief, tapping performance remained significantly improved, no matter how adaptive the metronome was (see **Figure 4**, left panel, dashed line).

As in Experiment 3, the group's tapping SD asynchrony was negatively correlated with the average perceived synchrony with the metronome [r_{rm} (541) = −0.24, 95% CI (−0.32, −0.16), $p < 0.001$] and the average perceived synchrony with the group [r_{rm} (541) = −0.22, 95% CI (−0.30, −0.14), $p < 0.001$]. Similarly, the group's tapping variability with respect to each other was significantly negatively correlated with the average perceived synchrony of the group [r_{rm} (541) = −0.33, 95% CI (−0.4, −0.25), $p < 0.001$].

Ratings data were again subject to a confirmatory factor analysis (see Factor Loadings in **Supplementary Appendix 2**). The group's average Enjoyment factor scores are plotted in **Figure 4**, right panel (dashed line). A repeated measures ANOVA showed no main effect of α condition on enjoyment score, F(3, 72) = 1.53, $p = 0.213$, $\eta^2 = 0.06$.

Discussion

We successfully replicated the effect observed in Experiment 3: The multi-person adaptive metronome can be used to bring groups of tappers into greater synchrony, compared to their baseline. In contrast to Exp. 3, in the current experiment with self-related auditory feedback, we found groups were able to maintain enhanced synchrony, even at higher levels of adaptivity. These results are interesting as they suggest 1) groups are able to more flexibly adapt to a greater degree of difficulty when they have additional information (auditory feedback), and/or 2) individuals in groups are able to synchronize better with the metronome and thereby each other when they receive feedback, so as to negate the potentially disruptive effects of a highly adaptive metronome. Pushing the group into a difficult and unpleasant state may, therefore, require using adaptivity levels greater than 100%. Future experiments should explore this possibility. In Exp. 5, we continued, for consistency, with the same levels of adaptivity as we added auditory feedback about the other tappers in the group.

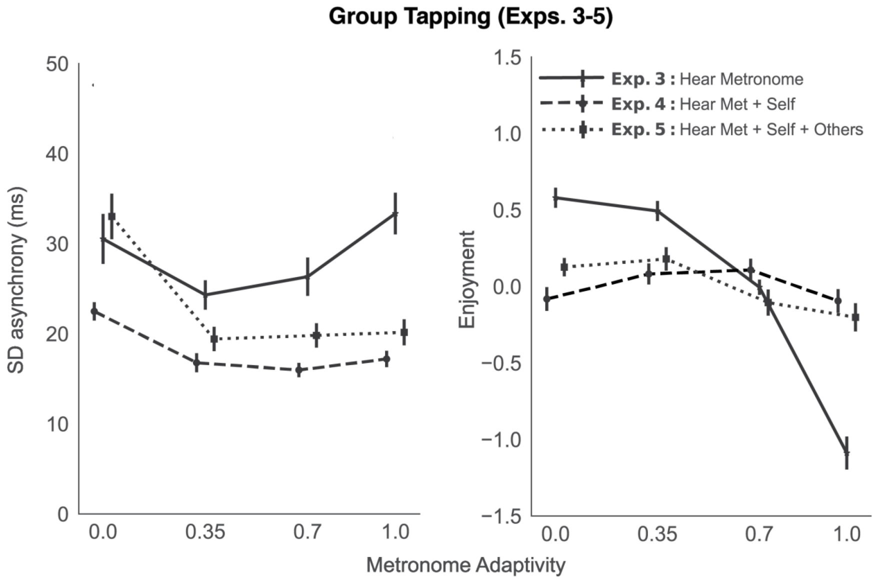

FIGURE 4 | Tapping performance and subjective enjoyment, averaged across participants, as a function of metronome adaptivity, in the three group tapping experiments. Solid black lines represent experiments in which participants could only hear the sound produced by the metronome; dashed lines, experiments in which participants could hear the metronome and the sound of their own tap; dotted lines, experiments in which participants could hear the metronome, themselves, and all others in the group. Error bars represent standard error of the mean.

EXPERIMENT 5

Methods

Participants

One hundred and four undergraduate students (26 groups of 4) participated. Three groups were removed due to technical issues. An additional, three groups were removed during data cleaning (outlined below). In total there were 20 groups, or 80 participants, with a mean age of 21 +/- 4 years, 57 female.

Stimuli

Participants heard the metronome (marimba sample) through its speaker and their own taps (woodblock sample) through their own individual speakers. In other words, all participants' taps produced the same sound, and all participants could hear the tap sounds produced by all others.

Procedure

Same as Exp. 3.

Results

A repeated measures ANOVA showed a main effect of α condition on the group tapping SD asynchrony [F(3, 54) = 33.73, $p < 0.001$, $\eta^2 = 0.65$]; see **Figure 4** (left panel, dotted line). As in Experiment 4, tapping performance improved significantly in all adaptivity conditions, compared to baseline [α 0.35 : t(18) = 7.29, $p < 0.001$, $d = 1.61$, Δ async = −13.61 ms; α 0.7 : t(18) = 6.19, $p < 0.001$, $d = 1.56$, Δ async = −13.21 ms; α 1 : t(18) = 6.23, $p < 0.001$, $d = 1.49$, Δ async = −12.86 ms].

As in Experiments 3 and 4, the group's tapping SD asynchrony was negatively correlated with the average perceived synchrony with the metronome [r_{rm} (407) = −0.16, 95% CI (−0.26, −0.07), $p < 0.001$] and the average perceived synchrony with the group [r_{rm} (407) = −0.25, 95% CI (−0.33, −0.15), $p < 0.001$]. The group's tapping variability with respect to each other was significantly negatively correlated with the average perceived

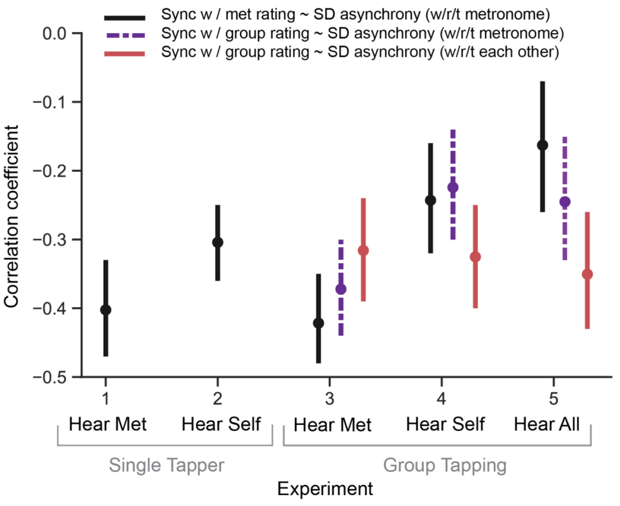

FIGURE 5 | Correlations between motor tapping asynchrony and subjectively rated synchrony with the metronome in all experiments. Note that in group tapping experiments, we have additional data about how in synchrony participants felt with the group. We analyzed that data separately as a function of synchrony with respect to the metronome (dotted purple line) and synchrony with respect to everyone in the group (red line). Error bars represent confidence intervals of the correlation coefficients.

synchrony of the group [r_{rm} (407) = −0.35, 95% CI (−0.43, −0.26), $p < 0.001$].

A comparison of the correlation coefficients among experiments is shown in **Figure 5**. Across all experiments, it is interesting that the strongest correlations between subjective feelings of synchrony and actual measured SD synchrony occur with no auditory feedback (i.e., participants most accurately judge their tapping performance when they do not have auditory feedback, despite their being worse at the task). It is also interesting that the SD asynchrony of group members with respect to each other does not seem to change as a function of auditory feedback, meaning in all group experiments participants can equally tell how in sync they are with each other, regardless of auditory feedback (even though their ability to judge their group synchrony with the metronome is best with less auditory feedback).

To examine the effect of auditory feedback on SD asynchrony (across Exps. 3, 4, and 5), we ran a mixed ANOVA, with auditory feedback as a between-subjects factor, adaptivity condition as a within-subjects factor, and their interaction. There was a main effect of auditory feedback in predicting tapping performance [F(2, 281) = 32.29, $p < 0.001$, $\eta^2 = 0.19$]. Compared to no feedback, tapping SD asynchrony decreased on average by 10.52 ms with self-feedback [t(149.96) = 8.23, $p < 0.001$, $d = 1.11$] and by 5.53 with self + other feedback: t(179.97) = 3.46, $p < 0.001$, $d = 0.5$). Transitively, tapping performance was better, on average, in Experiment 4 compared to 5, by 4.99 ms [t(111.19) = 4.14, $p < 0.001$, $d = 0.68$]. In other words, tapping performance is best in Exp. 4, when participants hear the metronome and only themselves, followed by Exp. 5 when all participants can hear each other. Group tapping performance is worst when participants receive no auditory feedback (Exp. 3). There was also a main effect of adaptivity condition [F(3,204) = 38.12, $p < 0.001$, $\eta^2 = 0.36$], as well as an interaction between auditory feedback and adaptivity condition [F(6,204) = 10.75, $p < 0.001$, $\eta^2 = 0.24$]. As is visible in **Figure 4**, at higher levels of adaptivity, having no auditory feedback significantly worsens performance.

With respect to subjective experience, ratings data affirmed the same factor structure as previous experiments (see Factor Loadings in **Supplementary Appendix 2**). The group's average Enjoyment factor scores are plotted in **Figure 4** (right panel, dotted line). A repeated measures ANOVA showed a main effect of α condition on enjoyment score, F(3, 54) = 3.96, $p = 0.013$, $\eta^2 = 0.18$. Enjoyment showed no significant difference between baseline and α = 0.35, but did significantly decrease at higher levels of adaptivity (α = 0.7 and 1). In comparing Enjoyment scores across all three group tapping experiments, *via* mixed ANOVA with auditory feedback as a between-subjects factor, adaptivity condition as a within subjects factor, and their interaction, we find a main effect of adaptivity condition [F(6,204) = 21.58, $p < 0.001$, $\eta^2 = 0.39$] but no main effect of auditory feedback. However, we do find a significant interaction between adaptivity and auditory feedback [F(3,204) = 47.55, $p < 0.001$, $\eta^2 = 0.41$]. At baseline (no adaptivity), enjoyment is highest when participants receive no auditory feedback. This effect is reversed at higher levels of adaptivity, where hearing the metronome is significantly more enjoyable than no feedback. Statistics for all t-tests can be found in the associated Jupyter notebook.

TABLE 3 | Item loadings for the Enjoyment factor (Exp. 3).

Item	Enjoyment	Communality
Groove	0.893	0.798
Synchrony (w/ metronome)	0.937	0.877
Synchrony (w/ group)	0.823	0.677
Liking	0.517	0.268
Difficulty	−0.792	0.628

Cumulatively, the single factor enjoyment had a sum of squared loadings of 3.25, explaining a proportional and cumulative 65% of variance.

Discussion

With this experiment, we again successfully replicated our ability to enhance group synchrony with the metronome by adapting its timing. Contrary to our hypothesis that groups would be even better at tapping when they received auditory feedback about everyone in the group, we found, though hearing everyone resulted in better performance than hearing only the metronome, groups were best in Exp. 4 when they could hear only themselves. Similarly, their enjoyment did not change as much as it did in Exp. 4. In fact, in this experiment, enjoyment did not increase (as in Exp. 4 at optimal levels of adaptivity), but rather decreased at higher levels of adaptivity (70 and 100%), a result more similar to Exp. 3. Implications of these results will be elaborated further in the General Discussion. First, we explore the role of individual differences in shaping tapping performance and subjective experience.

INDIVIDUAL DIFFERENCES

Musical Sophistication

Across all experiments, we were interested in whether participants' benefit from metronome adaptivity (in terms of improved tapping performance) could be predicted by their musical sophistication. We defined adaptivity benefit as the difference in tapping performance between the baseline and optimally adaptive condition (α = 0.25 and 0.35 for individual and group experiments, respectively). Thus, a positive value corresponds to improved tapping synchrony or enjoyment, while a negative value indicates decreased synchrony or enjoyment. As we found the subscales of the Gold-MSI were all significantly highly correlated with each other, we used only the overall general sophistication index. We felt this general index was better than choosing one subscale, as the musical training, perceptual abilities, and even singing abilities subscales all contain items that would have a direct bearing on tapping abilities.

To test whether musical sophistication mattered in terms of how much people, or groups, benefitted from metronome adaptivity, we split both the single tapper and group tapping data into two musicianship groups *via* median split (single tapper: low musicianship: $n = 19$, sophistication mean = 57+/− 8; high musicianship: $n = 18$, soph mean = 89 +/− 10; group tapping: low musicianship: $n = 39$, soph mean = 66 +/− 5; high musicianship: $n = 32$, soph mean = 77 +/− 5. The adaptivity benefit of each of the musicianship groups in the single and group tapping contexts was compared against zero, using paired, one-sample, one-tailed t-tests. All musicianship groups showed a significant benefit from metronome adaptivity [single / low: t(18) = 5.33, $p < 0.001$, $d = 1.12$, mean benefit = 5.93 ms; single / high: t(17) = 2.05, $p = 0.028$, $d = 0.48$, benefit = 4.89 ms; group / low: t(38) = 6.68, $p < 0.001$, $d = 1.07$, benefit = 6.49 ms; group / high: t(31) = 4.85, $p < 0.001$, $d = 0.86$, benefit = 9.87 ms]; see **Figure 6**. These results indicate people of all musical levels benefit from an adaptive metronome. There were no significant differences between the means of low vs. high musicianship individuals, or groups, both $t < 1.5$.

Personality Factors and Individual-Group Asynchronies

While we had no *a priori* hypotheses about which individual traits, besides musical sophistication, and perhaps internality (Fairhurst et al., 2014), might be relevant in the context of group tapping, we were nonetheless interested in exploring predictors of participants' SD asynchrony with respect to the group, as well as participants' subjective ratings, with respect to their individual asynchronies.

To start, we asked which person-level variables predict participants' individual SD asynchrony difference with respect to the group (i.e., the individual minus group SD async; see colored dots in **Figure 3**, rightmost panels). We ran a linear mixed effects model (*lme4* package in R, Bates et al., 2015; *sjPlot* package, Lüdecke, 2021) with the individual minus group SD asynchrony difference as the dependent variable; all person-level variables were included as fixed effects, while a term specifying adaptivity condition nested within participant, nested in group, nested in experiment was included as a random effect. Note that, as opposed to earlier analyses in which we were interested in adaptivity as a predictor of synchrony, here we wanted to understand the role of person-level features over all conditions. The variance inflation factor for all fixed effects was checked and all were found to be safely < 2.

All model output is presented in **Table 4**. We found musical sophistication was a significant predictor of individuals' difference scores. Interestingly, we also found a significant effect for the *sadness* scale of the BANPS (Barrett et al., 2013). Overall, the variance explained by the fixed effects, though significant, is nonetheless small (∼3%), while the random effects (adaptivity, participants, groups, experiment) account for much more variance (∼48%) in the tapping data.

The sadness scale is known to be related to *neuroticism* from the five-factor model, as well as the *behavioral inhibition system* from reinforcement sensitivity theory (Barrett et al., 2013).

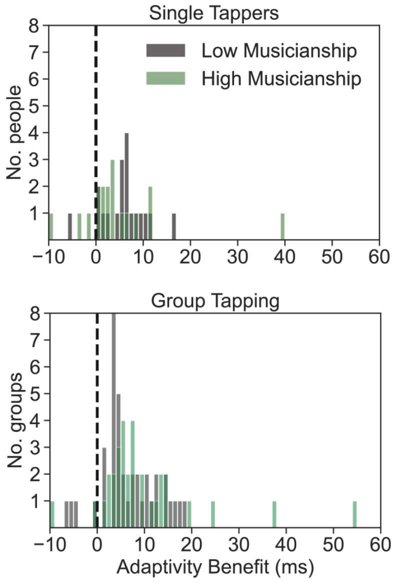

FIGURE 6 | The enhanced tapping accuracy (in ms) that participants experienced during optimally adaptive metronome conditions, as a function of their musical sophistication, in single and group tapping experiments. Participants (top panel) or groups (bottom panel) scoring in the top half of musical sophistication (Gold-MSI) are plotted in green, while those in the bottom half (low musical sophistication) are plotted in gray. Positive values indicate the extent to which participants' SD asynchrony improved. Negative values indicate the opposite (that participants or group became worse at optimal adaptivity).

TABLE 4 | Person-level predictors of individuals' SD asynchrony differences from the group.

Predictors	Estimates	CI	*p*
(Intercept)	25.50	15.35–35.64	< 0.001
General sophistication (Gold-MSI)	−0.19	−0.24–−0.14	< 0.001
Internality (IPC)	0.14	−0.02–0.31	0.085
Powerful Others (IPC)	−0.01	−0.14–0.12	0.882
Chance (IPC)	0.07	−0.06–0.19	0.309
Play (BANPS)	−0.39	−2.05–1.27	0.644
Seek (BANPS)	−0.39	−1.90–1.11	0.610
Care (BANPS)	−0.07	−1.37–1.22	0.911
Fear (BANPS)	−0.77	−2.11–0.58	0.263
Anger (BANPS)	−0.35	−1.46–0.75	0.533
Sadness (BANPS)	2.22	0.90–3.53	0.001
Random effects			
σ^2	184.74		
$\tau_{00\ alpha:subID:group:exp}$	158.22		
ICC	0.46		
N_{alpha}	4		
N_{subID}	284		
N_{group}	71		
N_{exp}	3		
Observations	6508		
Marginal R^2 / Conditional R^2	0.031 / 0.478		

The survey instrument from which each predictor comes is indicated next to each item in parentheses.

Behaviors associated with the *sadness* system are often related to loss and grieving, separation distress, or breaking of social bonds; these behaviors are in a somewhat antagonist relationship with the *play* system and its related behaviors. More concretely, higher *sadness* scores are associated with social phobia and negative affect, and show a negative relationship with self-esteem (Barrett et al., 2013). Electrical brain stimulation studies have implicated areas from dorsal periaqueductal gray to anterior cingulate, and the role of neurotransmitters associated with social bonding (i.e., endogenous opioids, oxytocin, and prolactin), in the *sadness* system, which evolved over a hundred million years ago (e.g., in birds); see Panksepp (2010). The fact that *sadness* scores in the current study predicted an individuals' distance from the group, even when accounting for other factors (musicianship, adaptivity, etc.), is perhaps indicative of the way physiological / affective states related to *sadness* affect one's overall ability to connect with others—a situation with both psychological and neurochemical underpinnings. Indeed, oxytocin has recently been suggested to improve predictive sensorimotor abilities in dyadic tapping contexts (Gebauer et al., 2016). In general, high sadness might involve low overall arousal which may translate to less attention, motivation, or motoric responsivity in trying to align with a beat. Future studies should more directly investigate the possible links between person-level variables and tapping performance in social contexts.

A second exploratory analysis aimed to predict participants' individual groove ratings from their SD asynchrony difference from the group. Note that we used groove ratings because groove was the scale we were most interested in and because we were on the single participant level (i.e., the factor analysis to obtain enjoyment scores reported earlier had been done on the group average level; obtaining factor scores for individuals would require re-running the factor analysis in a multi-level way, which is beyond the scope of these exploratory analyses). Groove rating was the dependent variable, individual-group SD asynchrony the independent variable, and all random effects were as specified in the previous model (adaptivity nested in participant, group, experiment). The full model is reported in **Table 5**.

TABLE 5 | Individual groove ratings as a function of SD asynchrony difference from group.

Predictors	Estimates	CI	*p*
(Intercept)	0.09	0.05–0.13	< 0.001
Individual-Group SD async	−0.01	−0.01–−0.00	< 0.001
Random effects			
σ^2	0.87		
$\tau_{00\ \text{alpha:subID:group:exp}}$	0.07		
ICC	0.07		
N_{alpha}	4		
N_{subID}	284		
N_{group}	71		
N_{exp}	3		
Observations	6,508		
Marginal R^2 / Conditional R^2	0.009 / 0.080		

Individual differences in SD asynchrony from the group significantly predicted individual groove ratings, though this effect was quite small (explaining 0.9% of variance). With random effects included, the variance explained by the model increased to ∼8%. This low percentage of variance explained perhaps indicates that while individual performance in a group context is a predictor of individual subjective experience, complex subjective states, like being in the groove, are also much more than a function of individual performance when in a group context.

We also wish to note the asymmetry with respect to individual SD async differences: Having a negative asynchrony difference is predicted to be more groove-inducing than the opposite (positive value = less groove); see **Figure 7**. At first this finding may seem confusing, as one may think a difference from the group is just that, and the sign should not necessarily matter. To explore the underlying source of this important asymmetry further, we asked whether tappers with negative SD asynchronies with respect to the group tended to be the better tappers in the group. We assigned a tapper rank for each run, by sorting the tappers in the group by the absolute value of their individual minus group asynchronies. For example, if, on a given run, a group's four tappers had the following SD asynchrony differences [10.9, −7.8, 6.5, 15.4], their ranks would be [3, 2, 1, 4]. We then compared this ranking (based on absolute value) with the signed differences. Out of the 1,627 runs across all groups for this analysis, only 424 runs (26%) had tappers exhibiting negative SD async differences. Of those 424 runs, 269 (63%) were from a tapper who ranked 1 (144/424) or 2 (125/424) for that run, suggesting there was an asymmetry in the type of tapper that tends to have a negative SD asynchrony difference to the group (N.B. there were 149 unique tappers in this pool). To further confirm the relationship between rank and signed SD asynchrony difference, we ran a linear mixed model with signed individual minus group SD async difference as the dependent variable and rank as the predictor (with all random effects as before). The overall model is significant; with rank 1 as

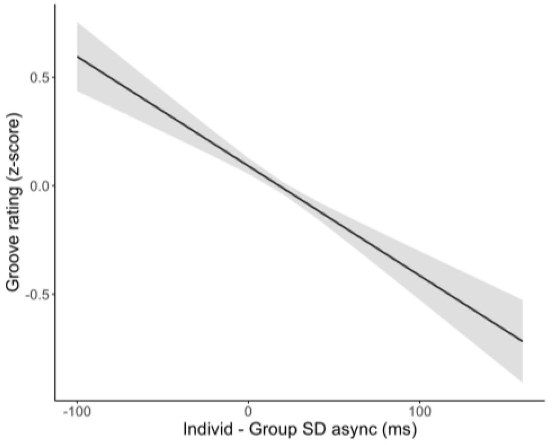

FIGURE 7 | Predicted groove ratings as a function of individuals' SD async differences from the group, adjusted for random effects of adaptivity, participant, group, and experiment (see model reported in **Table 5**).

TABLE 6 | Tapper rank as a predictor of their SD async difference.

Predictors	Estimates	CI	*p*
(Intercept)	15.67	14.63–16.71	< 0.001
Rank [2]	0.37	−0.69–1.44	0.491
Rank [3]	3.44	2.34–4.53	< 0.001
Rank [4]	5.58	4.51–6.65	< 0.001
Random effects			
σ^2	181.82		
$\tau_{00\ \text{alpha:subID:group:exp}}$	159.71		
ICC	0.47		
N_{alpha}	4		
N_{subID}	284		
N_{group}	71		
N_{exp}	3		
Observations	6508		
Marginal R^2 / Conditional R^2	0.015 / 0.476		

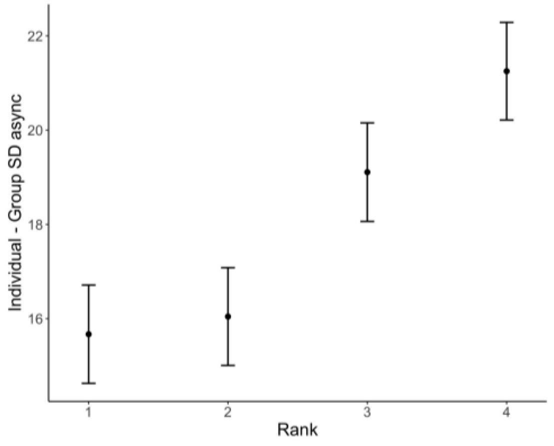

FIGURE 8 | Predicted individual minus group SD asynchrony as a function of individual rank in the group, adjusted for random effects of adaptivity, participant, group, and experiment (see **Table 6**).

the referent, tappers of ranks 3 and 4 have significantly higher SD asynchrony differences (see **Table 6** and **Figure 8**).

Upon further reflection, an interpretation for this asymmetric finding begins to come into focus: Tappers whose individual minus group SD asynchrony is negative are more stable tappers than the group. While it was often the case that the group was more stable than any individual (all individuals with positive SD async differences), over a quarter of the time, there were some individuals who outperformed the group—such performance was associated with higher groove ratings. Future studies might more directly explore these relations, as well as the way individual vs. group performance might change as a function of group size.

GENERAL DISCUSSION

To probe the psychological effects of motor synchronization among individuals and groups of tappers, we developed an open-source, multi-person adaptive metronome. Across five experiments, individuals and groups tapped along with our adaptive metronome, while we manipulated both metronome adaptivity and auditory feedback. In an initial proof-of-concept experiment, we replicated the findings of Fairhurst et al. (2013) using our new device. Specifically, we showed that at optimal levels of adaptivity (25–50%), individuals achieve improved motor synchrony with the metronome, compared to non-adaptive conditions, and that subjective enjoyment can be manipulated as a function of metronome adaptivity. In a second experiment, we extended these single person tapping findings by showing synchrony with the metronome is further enhanced with the use of auditory feedback (participants hearing a sound produced by their own tap). In this experiment, asynchronies were lower in all conditions, compared to Experiment 1. Hence, depriving a person of self-auditory feedback induces a significant synchronization cost. However, auditory feedback evokes mixed effects in terms of subjective experience: no feedback results in higher subjective enjoyment when the metronome does not adapt (adaptivity = 0%); however, participants report much less enjoyment at higher levels of adaptivity, when they have no feedback. Conversely, with auditory feedback, subjective enjoyment can be enhanced *via* use of optimally adaptive metronome conditions.

In experiments 3–5, we tested synchronization abilities among groups of four people tapping together. We showed that the synchronization abilities of the group improve with both optimal levels of adaptivity and auditory feedback. Hearing oneself and/or the others in the group led to greater stability in tapping performance, compared to no feedback, especially at higher levels of adaptivity. The role of auditory feedback in improving tapping performance is in line with previous results (Goebl and Palmer, 2009; Konvalinka et al., 2010; Schultz and Palmer, 2019; N.B. these studies involve tapping continuation paradigms and do not use an adaptive metronome). Interestingly, though, while hearing everyone in the group is most similar to an actual music-making situation, and perhaps most ideal in terms of social engagement, tapping performance was best when participants could only hear themselves (not all others in the group). This finding makes sense when considering the likely perceptual interference caused by hearing others' taps. This logic is in line with the results of a previous dyadic tapping study which showed poorer synchronization performance when tappers could hear each other (Konvalinka et al., 2010), as well as Versaci and Laje's (2021) findings that auditory feedback decreases re-synchronization accuracy after period perturbation. While having information about others' taps would be relevant for synchronizing appropriately with the metronome in the adaptive conditions, it is possible hearing all taps was distracting for overall performance and/or that masking occurred because all participants produced the same tap sound (Meyer, 2009). Future studies should explore whether assigning each participant a different instrument timbre affects these results. Overall, these findings point to the importance of considering the type of auditory feedback participants receive when designing future tapping studies.

With regard to subjective experience, we found that the factor structure we identified in the single person experiments replicated in the group experiments. Namely, feeling in the groove, feeling in synchrony with the metronome, feeling in synchrony with the group, and wanting to continue the task all loaded positively onto a one-factor solution, while experiencing the task as difficult loaded negatively. We termed this factor Enjoyment and found that, while Enjoyment was easy to push around in the individual tapper experiments, in group experiments, it was only with no auditory feedback and at higher levels of adaptivity that we were able to reduce subjective enjoyment. With auditory feedback, enjoyment stayed relatively flat, not moving significantly from baseline, though trending up or down with respect to optimally adaptive conditions or not. However, those enjoyment scores were averaged across the whole group.

In exploratory analyses, we related an individual's groove ratings on any given trial to their personal SD asynchrony distance from the group on that trial. We found the lower the SD asynchrony difference, the more in the groove participants felt. We also found their SD asynchrony difference from the group was predicted by their Gold-MSI score and the *sadness* scale of the BANPS. Such exploratory findings relating individual differences to group performance and subjective experience should be more systematically explored in future studies by, for example, comparing groups of people matched/opposed in musical ability and/or some specific personality feature of interest, or, by assigning people with certain personality traits to certain musical roles. Importantly, although musical sophistication was relevant in predicting an individual's performance, we showed individuals or groups benefited from optimal metronome adaptivity regardless of their musical abilities.

Future Directions

We have shown that the multi-person adaptive metronome helps to bring groups of people into greater synchrony and we know from previous studies that such alignment increases social bonding and cooperative behavior. Future studies should directly investigate this connection using the adaptive metronome. For example, to further study the social utility of interacting with a multi-person adaptive metronome, one could have participants complete tasks such as the public goods game (e.g., Fischbacher and Gachter, 2010) or facial emotion recognition task (Passarelli et al., 2018) after rounds of tapping. Such experiments could additionally manipulate person-level variables to study group affiliation, for example, to study whether the adaptive metronome can enhance cohesion between people with conflicting viewpoints, identities, and/or milieus.

Others might also consider studying the effects of group size on synchronization dynamics. For example, in a previous tapping continuation task, Okano et al. (2017) showed that dyadic vs. solo tappers tend to show a greater increase in speed over time. These dynamics could now be explored in an adaptive context, with more tappers. Such medium-size group research has been suggested to be particularly fruitful for uniting large and small-scale theories of coordination dynamics, under a framework combining the Kuramoto and Haken–Kelso–Bunz equations (Kelso, 2021), or to study coordination at local vs. global timescales (Okano et al., 2019). However, we wish to note, at present, the group size with our current system is limited to four tappers because the Arduino Uno has only four input/output pins. While this hardware allows the study of group sizes from 2 to 4 people, those interested in exploring dynamics of larger groups should implement the adaptive metronome code on microcontrollers with a greater number of I/O pins.

Future studies should also experiment with different real-time adaptive algorithms. For example, it would be possible to differentially favor the best or worst participants *via* a weighted average of participant asynchrony, or, to adjust the volume of the metronome based on participant performance. Additionally, others might consider using more interesting repeating patterns for the metronome, such as the *clave son* pattern, and asking participants to tap along. It is likely more interesting rhythms will lead to even greater engagement with the task and feelings of group affiliation, as previous studies have shown rhythmic music has greater effects on prosocial behavior than a purely isochronous metronome (Stupacher et al., 2017a,b) and that rhythmic complexity modulates synchronization abilities (Mathias et al., 2020). It would also be possible to have participants freeform tap and have the metronome come in as an additional player, based on the rhythmic characteristics of the participants' tapping, though this would require significant additional programming and perhaps a micro-controller with more random-access memory than the Arduino.

Without developing new metronome algorithms, researchers might still experiment with sonic and group dynamics, using the existing system as is. For instance, one could use different timbral or registral qualities of the metronome and tapping sounds to influence participant dynamics [see Keller and Repp (2008) for single person example]. Likewise, the attack, duration, and frequency of a sound are known to affect the perception of the center of the beat and tapping synchronization with the beat (see e.g., Hove et al., 2007; Danielsen et al., 2019); such dynamics could now be explored in a multi-person context, with sounds varying in these different features assigned to different participants and/or the metronome. Similarly, one could assign certain tappers certain roles and investigate leader-follower dynamics in dyads, triads, and quartets. As visual information has been shown to influence synchronization dynamics and groove ratings (see e.g., Tognoli et al., 2007; Dotov et al., 2021), participants' visual information with respect to each other could also be manipulated. Single finger or bimanual tapping could be used, different metronome tempi could be investigated, and so on. Further, the effects of the multi-person adaptive metronome could be explored in groups of individuals sharing (or not) similar preferred endogenous tempi and/or musical expertise, as previous work points to the importance of both of these factors in influencing synchronization abilities (Zamm et al., 2016; Schultz and Palmer, 2019; Scheurich et al., 2020). Additionally, recent work reveals systematic differences in tapping synchronization abilities in neurodevelopmental (Vishne et al., 2021) and neurodegenerative (Janzen et al., 2019; Curzel et al., 2021) disorders; the adaptive metronome may, therefore, be a useful therapeutic device in clinical contexts.

In summary, this low-latency, low-cost, adaptive metronome system holds promise in bringing groups of people into greater motoric and psychological alignment in a variety of contexts. For example, it could be used in an assistive context, so those with difficulty perceiving and tapping to a beat, or little musical training, can easily come together to have a musical experience and feel connected, or a pedagogical context, such that those just starting out in music might experience less frustration when learning to accurately keep time and might more quickly come to experience the feeling of being in synchrony with a metronome or in the groove with others. Most importantly, the multi-person person adaptive metronome, which we internally refer to as GEM: the Groove Enhancement Machine, allows for studying, in a controlled way, the variables which may impact motor synchronization, subjective experience, and social bonding in a group context. In making the code and wiring diagram for GEM publicly available (see GitHub repository), we hope others will join us in building out the capabilities of the metronome system, and in carrying out future experiments probing the psychological and neural underpinnings of inter-personal synchronization.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. All code required to program the Arduinos and create the GEM system is available at: https://github.com/janatalab/GEM/releases/tag/v1.0.0. All code required to run the experiments reported in this paper and to recreate the statistical analyses is available at: https://github.com/janatalab/GEM-Experiments-POC.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by University of California, Davis, Institutional Review Board. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

LF: methodology, software, validation, data curation, investigation, formal analysis, visualization, and writing—original draft. PA: methodology, software, validation, data curation, formal analysis, and writing—review and editing. PJ: conceptualization, methodology, software, validation, data curation, formal analysis, visualization, writing—review and editing, supervision, resources, project administration, and funding acquisition. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fnhum.2022.916551/full#supplementary-material

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Interpersonal Physiological Synchrony Predicts Group Cohesion

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A key emergent property of group social dynamic is synchrony–the coordination of actions, emotions, or physiological processes between group members. Despite this fact and the inherent nested structure of groups, little research has assessed physiological synchronization between group members from a multi-level perspective, thus limiting a full understanding of the dynamics between members. To address this gap of knowledge we re-analyzed a large dataset (*N* = 261) comprising physiological and psychological data that were collected in two laboratory studies that involved two different social group tasks. In both studies, following the group task, members reported their experience of group cohesion via questionnaires. We utilized a non-linear analysis method-multidimensional recurrence quantification analysis that allowed us to represent physiological synchronization in cardiological interbeat intervals between group members at the individual-level and at the group-level. We found that across studies and their conditions, the change in physiological synchrony from baseline to group interaction predicted a psychological sense of group cohesion. This result was evident both at the individual and the group levels and was not modified by the context of the interaction. The individual- and group-level effects were highly correlated. These results indicate that the relationship between synchrony and cohesion is a multilayered construct. We re-affirm the role of physiological synchrony for cohesion in groups. Future studies are needed to crystallize our understanding of the differences and similarities between synchrony at the individual-level and synchrony at the group level to illuminate under which conditions one of these levels has primacy, or how they interact.

Keywords: physiological synchrony, cohesion, group-level synchrony, individual-level-synchrony, recurrence quantification analysis

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INTRODUCTION

Social interactions entail the coordination of different biobehavioral processes between individuals, and a prominent pattern of coordination that has been increasingly researched in the past decades is that of interpersonal synchrony. Interpersonal synchrony is defined as "the spontaneous rhythmic and temporal coordination of actions, emotions, thoughts and physiological processes" between individuals (Mayo and Gordon, 2020, p. 1) which is a meaningful aspect of various categories of human interactions. Initiated early on developmentally, biological and behavioral synchrony during parent-infant interactions is considered one of the building blocks of attachment and social development (Feldman, 2007). Moreover, coupling in language, emotion, movement, and autonomic physiological processes is manifested both in close relationships but also during first-time interactions between strangers (Koole and Tschacher, 2016; Azhari et al., 2020).

Synchrony in different modalities is considered to be dependent on a common neural mechanism pertaining to social herding and has been related to several prosocial outcomes (Kokal et al., 2011; Rennung and Göritz, 2016; Shamay-Tsoory et al., 2019; Gordon et al., 2020a). Among these, cohesion has been a major topic in group studies due to its contribution to the group's performance, connectivity, and effectiveness (Evans and Dion, 1991; Burlingame et al., 2001; Beal et al., 2003). Furthermore, group cohesion was found to be vastly connected to coordinated behavior, whilst there is sparse evidence regarding its association with physiological synchrony (Conradt and Roper, 2000; Wiltermuth and Heath, 2009; Valdesolo et al., 2010; Jackson et al., 2018).

A large body of research focused on physiological synchrony, the temporal coordination in physiological processes between two individuals or more, and how it is linked to relationship characteristics or social outcome (Palumbo et al., 2017; Mayo et al., 2021). Due to their high accessibility, cardiovascular measures are widely used in interpersonal synchrony research. Specifically, coupling in heart rate (HR) or cardiological interbeat intervals (IBIs) were found to be positively associated with beneficial relationship elements, although there is heterogeneity in reported results regarding the effects of this type of physiological synchronization (Järvelä et al., 2013, 2016; Prochazkova et al., 2019; Mayo et al., 2021).

In the present study, we focus on assessing physiological synchronization by calculating the continuous covariation of cardiological IBIs between group members. IBI represents the time between consecutive heartbeats, and it is regulated dynamically by both branches of the autonomic nervous system (ANS): The parasympathetic branch and the sympathetic branch. Synchrony in IBIs has been shown to support social bonding between mother and infant (Feldman et al., 2011), and has also been shown to emerge as a consequence of shared psychological states (Golland et al., 2015, 2019) or active cooperation (Mønster et al., 2016) between adults. In a previous study, we found IBI synchrony was related to a sense of group cohesion and predicted behavioral coordination in group members (Gordon et al., 2020b). A recent meta-analysis of the outcomes of physiological synchrony (Mayo et al., 2021) pointed to an overall positive effect of IBI synchrony on group outcomes such as cohesion, commitment, and performance.

Notwithstanding, social synchrony dynamics are complex and there are continuous shifts in and out of synchrony throughout social interactions. The flow of social interactions relies on a flexible system allowing a transition between synchronous and asynchronous interactions patterns (Mayo and Gordon, 2020). As such, context is an important determinant of the meaning of physiological synchrony (Danyluck and Page-Gould, 2019) since it poses different demands on the balance between the need for synchronization and the need for segregation (Mayo and Gordon, 2020). Will synchrony during an argument indeed lead to a sense of cohesion between partners, or should brainstorming involve more synchrony between partners? These questions highlight how context adds another layer of complexity to physiological coupling as different environments and different tasks yield different correlations between physiological synchrony and relationship outcomes (Mayo et al., 2021). For instance, Danyluck and Page-Gould (2019) found that both verbal communication and social framework changed the meaning of physiological synchrony (in parasympathetic nervous system activity)–specifically, its relationship with friendship interest.

While there has been much progress in terms of uncovering coordination patterns in various domains, as we have summarized above, several questions remain unanswered. Among these are questions pertaining to how physiological synchrony is shaped by contextual aspects of the situation and task, and at what level in the group such coordination is organized. Regarding the latter aspect, a key challenge remains when conceptualizing the interaction of two or more individuals. Is it mainly an interaction of otherwise separate individuals, or do these individuals behave more like a superorganism (Emerson, 1939)? The individualistic (or intra-personal) account has probably been the most clearly spelled-out by investigations of linguistic alignment during conversations (Pickering and Garrod, 2004, 2013), where a specific linguistic mechanism is proposed that controls the interaction of two otherwise separate actors (Fusaroli and Tylén, 2016). On the other hand, dyads or groups that interact have been proposed to function in terms of synergetic relationships (Fusaroli et al., 2014), where the individual actors are bound together by their interactions in a more intricate way, so to act as a superorganism.

For dyadic interactions, this distinction is more of a conceptual nature, as analyzing synchrony in such interactions from the perspective of two separate but interacting entities vs. a synergetic whole is relatively immaterial when it comes to the concrete analysis approach taken. However, multi-level consideration becomes tangible and pertinent when addressing the behavior of groups bigger than two. The complication of investigating coupling in groups is related to the fact that interaction dynamics (Arrow et al., 2000; Moreland, 2010; Williams, 2010; Jones, 2014; Kenny and Kashy, 2014), for example in terms of synchrony, can in principle be situated at the level of the individual, among certain or all dyads of that group, or at higher group levels–the latter would strongly favor the interpretation of group coordination as synergetic (Riley et al., 2011; Wallot et al., 2016b).

Hence, when studying relationships among triads, it is favorable to be attentive to various levels of synchrony within the group–individual tendency to synchronize, as well as dyadic and triadic connections (Gordon et al., 2021). With sparse literature regarding physiological synchrony in groups of more than two people, the current study focuses on studying the role of cardiovascular coupling in determining triadic relationships during collaborative small-group interactions. Specifically, building on initial results indicating an association between group cohesion and physiological synchrony in HR or IBIs (Mønster et al., 2016; Gordon et al., 2020b), we were interested in exploring how this relationship changes at different levels of synchrony within a group and in various contexts.

The investigation of the contextual factor is important because different contexts have the power to shape interactions in different ways, specifically in groups. While free interaction among a group of people might allow for the emergence of higher group-level dynamics, where the group behaves as a synergetic superorganism, we can imagine that other contexts that heavily restrict interaction among members of the group prevent such kind of coordination. For example, groups of people working at an assembly line act in an environment where each member only provides input to the next member in the line, and the mechanized pace and structure of the interaction likely delimits bidirectional interpersonal coordination, making the group behave as the sum of individual behaviors or the sum its dyadic interactions.

From these considerations follow the concrete aims of the present study. First, we aimed to assess if physiological synchrony in IBI between group members predicts cohesion. Our second aim was to investigate the modulatory role of context on the relationship between synchrony and cohesion by comparing two different experimental social tasks with two conditions each. In the current study, we thus present a re-analysis of data sets from two studies that examined the outcomes of physiological synchrony in groups (See Gordon et al., 2020a,b). The first study involved a social drumming task, and the second study involved a group decision-making task. In both studies, triads of participants interacted under different contextual conditions: In one task, participants drummed together in a structured manner without verbal communication, and in another study, they reached a unanimous group decision in ranking the order of several items that would aid their survival if they were stranded on a deserted island. As mentioned above, previous studies, including the drumming study from our own lab (Miles et al., 2011; Tarr et al., 2016; Gordon et al., 2020b) have shown initial evidence that group cohesion, as measured with a self-report questionnaire after the group interaction phase, was related to interpersonal synchronization.

The investigation of data from two different studies with different tasks is of importance, because they differ in important aspects in their structure: The decision-making task is relatively unstructured, allowing for free social interaction between group members, while the drumming task is more structured and aimed at prompting a more direct, stimulus-driven interaction between group members, which relies more on the individual contribution of group members. We set out to assess if the different task characteristics will lead to a different relationship between physiological synchrony and cohesion.

Our final aim was to assess at which level these effects (the link between physiological synchrony and cohesion) occur–individual- or group-level, or whether both of these levels contribute. Particularly if we were to find a contribution of group-level synchrony to perceived cohesion by group members, this could be taken as evidence for synergetic group interactions, where the group behavior acts as a superorganism of sorts.

In order to investigate group-level processes, we employed multidimensional recurrence quantification analysis (MdRQA) (Wallot et al., 2016b). While many analysis techniques exist that allow computation of synchrony measures for dyads, such as cross-correlation (e.g., Konvalinka et al., 2010), relative-phase analysis (e.g., Lumsden et al., 2012), or cross-recurrence analysis (e.g., Shockley et al., 2003), the simultaneous integration of more than two time series, such as data from triads or even bigger groups is more difficult. However, MdRQA allows to compute measures of coupling and synchrony at different group levels–for dyadic, triadic, or greater groups–and thus makes it possible to look at emergent coordination at the group level. Furthermore, it is possible to use MdRQA to compute measures of individual-level (Gordon et al., 2021), or more precisely, the degree to which individual participants are involved in the synchronous interactions with other group members. Accordingly, MdRQA is well suited to investigate effects at individual, as well as group-level effects of synchrony.

As noted above, based on previous work (Gordon et al., 2021), we expect to see a positive effect of IBI synchrony on cohesion, as this physiological synchrony construct may indicate positive joint arousal during a shared task (Konvalinka et al., 2011) linked to closeness between individuals comprising the group. Whether group cohesion is linked to physiological interactions which are based on local interactions between individuals or are situated on the simultaneous interaction among members at the group level is currently an open question, and most likely also a function of context and task. This question can be tested by comparing synchrony measures representing different group levels, as we will do in the following study by using MdRQA: This analysis allows us to compute group-level interactions, that do not only consider dyadic interactions, but also interactions that emerge among more than two members simultaneously. Finding effects of IBI synchrony at this group-level may be considered as evidence for synergetic group processes, where the group behaves more like a superorganism of sorts (Emerson, 1939), rather than the sum of the individuals (or dyads) comprising a group. Conversely, finding that such effects are located at the lower levels of interaction may indicate that a group is quite well described by assessing individual's participation in all dyadic interactions.

In line with the above, we sum the aims of the current study: (1) To examine if physiological synchrony in IBIs relates positively to group cohesion in a large dataset across multiple social tasks. (2) To assess at which level do these effects occur–individual or group or an interaction of the two. (3) To understand the meaning of an individual-level vs. group-level effect of physiological synchrony on cohesion.

MATERIALS AND METHODS

Participants and Procedure

This study was a re-analysis of data from a total of 261 participants (72.4% female, mean age = 23.32, SD = 3.1) who participated in one of two experiments (from here on labeled as "drumming" and "decision-making") conducted in our lab during 2017 and 2018. Most participants were Psychology undergraduate students and were compensated with course credits, while others received payment. The study was approved by Bar Ilan University Department of Psychology Ethics Committee, and every participant provided informed consent.

Both experiments aimed to investigate the relationship between interpersonal coordination of physiological markers and group outcomes such as cohesion and efficacy. Both were conducted with groups of three persons, which were connected to MindWare Mobile Record (MindWare Technologies Ltd., Gahanna, OH, United States) for electrocardiogram monitoring. Out of 101 groups, we analyzed data from 87 triads ("Drumming"–45, "Decision-making"–42) due to incomplete or corrupted physiological data.

In the current study, we focus on the first two stages of each experiment–a baseline phase and a group social interaction phase (see **Figure 1**). The baseline phase in both studies entailed participants sitting quietly together, not talking or doing anything for 5 min. They were instructed to either focus on the wall or a certain object in the room or to close their eyes and relax. After the baseline, a social interaction phase commenced. During the "drumming" experiment (Gordon et al., 2020a), participants took part in a drumming task where they were asked to tap on their electronic drumming pad (Roland V-Drum) to a specific tempo that was broadcast in the room via a speaker. During the "decision-making" experiment, participants completed a well-known task in which they ranked, individually and as a group, 15 items based on their relevance to the group's survival after an airplane crash–a version of the Desert Survival Task (DST) (Lafferty et al., 1974). Both the drumming study and the decision-making study included two task condition. For the drumming task–half of the groups heard a predictable tempo and half of the groups heard a non-predictable tempo. For the decision-making task half of the group were led by a polite experimenter and half were led by an impolite experimenter. In both studies, after the group social interaction, participants filled questionnaires regarding their sense of group cohesion. Our analyses of physiological data are based on cardiological IBIs data that was recorded continuously throughout the experiments from all group members (at baseline and during the interaction) as well as on the self-reported group cohesion score (Podsakoff and MacKenzie, 1995).

Cohesion Questionnaire

Group cohesion was measured using four items of the widely used questionnaire by Podsakoff and MacKenzie (1995). Each participant responded how well he or she can relate to the following statements on a 1–6 Likert scale: "If possible, I would be happy to participate in another group experiment with the members of my current work group"; "My group worked together as a team"; "We were cooperative with each other"; and "We knew that we could rely on one another" and "We were supportive." Individual's experience of group cohesion was calculated as the average of the above scores.

Collection and Pre-processing of Physiological Data

Electrocardiograms were obtained from group members using a modified lead-II configuration. Respiratory data were derived from the standard tetrapolar electrode procedure for the impedance cardiogram described elsewhere (Sherwood et al., 1990). Electrodes were transmitting synchronously and wirelessly to the control room at a sampling rate of 500 Hz. Electrocardiograms were analyzed in MindWare Technology's HRV 3.1.4 application and amplified by a gain of 1,000 and filtered with a hamming windowing function. Trained coders in the lab reviewed data manually and visually inspected all data to ensure the removal of artifacts and ectopic beats (Berntson et al., 1997). Inter-beat-intervals (IBI) were extracted from the continuous ECG data. Note that IBI time series differed in length across individuals. Hence, for the purpose of correlating IBI data between members of dyads or groups, we had to trim the longer time series to the shortest time series length for each particular dyad or group. This was done by removing the excess data points at the end of the longer series.

Calculating Physiological Synchrony

To quantify physiological synchrony, we conducted MdRQA (Wallot et al., 2016b) on the IBI time series using a software implementation in MATLAB version 2021b (The MathWorks, Inc.). This method is suitable for physiological data primarily due to its ability to capture the correlations among multivariate signals. Furthermore, we analyzed our data on both the individual and triadic levels (Gordon et al., 2021).

Similar to other recurrence-based methods (Webber and Zbilut, 1994; Marwan and Kurths, 2002), MdRQA begins with a matrix of distances between pairs of data points in the time series (the IBI data obtained from each participant). For example, if we have three time-series with four data points each $x_1 = [1, 1, 2, 25]$, $x_2 = [1, 1, 3, 40]$ and $x_3 = [1, 1, 1, 99]$, then these three time series provide us with four coordinates in their joint phase-space: $c1 = [1, 1, 1]$, $c2 = [1, 1, 1]$, $c3 = [2, 3, 1]$, and $c4 = [25, 40, 99]$. **Table 1** charts the distance matrix between these coordinates.

If we look at the distances in **Table 1**, we see that coordinates c1 and c2 are identical–their distance is zero, Hence, the first and second coordinate based on the first and second data point of the three time series are recurrent. The distance to the third

FIGURE 1 | The common phases of the two experiments – "drumming" and "decision making".

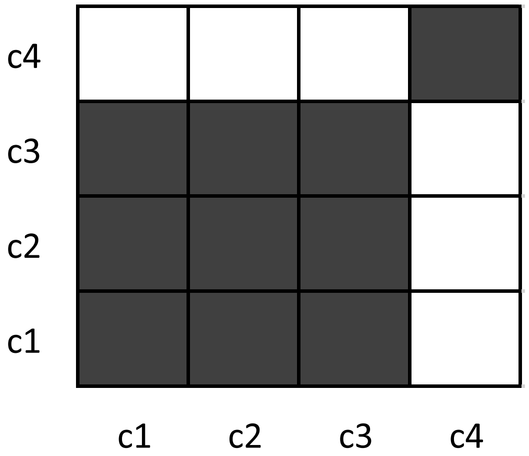

FIGURE 2 | Example recurrence plot for toy data. The dark squares in the plot indicate recurrence (identical/similar coordinates), while the white points indicate the absence of recurrence. Note that the recurrence plot (RP) is, by convention, rotated by 90° compared to the conventional display of a matrix, so that time runs from the lower-left to the upper-right of the plot. Recurrence measures for this plot are: %REC = 62.5%; %LAM = 90%; meanV = 3; maxV = 3. See text for how these values are computed.

data point is bigger than zero–so c1 and c2 are not identical to c3, but similar. Finally, the distance to c4 is comparatively big. c1, c2, and c3 are not very similar to c4. For continuous data that might also include measurement noise as a source of variability, we cannot simply count only identical coordinates as recurrent, but we need to define some range within which two coordinates are counted as recurrent, albeit not being identical. Hence, we determine two points as recurrent (i.e., similar) if their distance is under a preset threshold; otherwise, they would count as non-recurrent (different). Applying such a threshold results in a binary recurrence plot (RP) (**Figure 2**) of recurrent and non-recurrent data points. If we apply a threshold value of $r = \pm 3$, the distance matrix in **Table 1** yields a recurrence plot as portrayed in **Figure 2**.

There are multiple RQA outcome measures that evaluate different aspects of the RP (Marwan et al., 2007). The simplest measures is percent recurrence (%REC), which quantifies the raw amount of individual instances (coordinates) that recur with each other. It is the sum of all recurrences divided by the size of the plot. Further measures are percent laminarity (%LAM), which quantifies the degree to which recurrences appear in larger patterns. It is calculated as the sum of all recurrence points having at least a single vertical neighbor divided by the number of all recurrence points. Further, there is the average vertical line length, which captures the average duration of such patterns (meanV), calculated as the average length of vertical lines of recurrences on the plot, and there is the maximum vertical line length (maxV), which captures the longest period over which the time-series form such a pattern, and is captured by the maximum number of vertically adjacent recurrence points. There are further measures (e.g., Marwan et al., 2007).

TABLE 1 | Distances between the four coordinates.

	c1	c2	c3	c4
c1	0	–	–	–
c2	0	0	–	–
c3	2.2	2.2	0	–
c4	108.2	108.2	107.3	0

Here, we focused on recurrence rate (REC%), laminarity (LAM%, percentage of recurrence points with vertical neighbor), and both the maximum and average lengths of the vertical lines (meanV and maxV). We did so, because recurrences of signals that have a substantial stochastic component or a of noise-type show up in terms of squares and patches of recurrences, which are better captured by the vertical lines on a recurrence plot, as can be seen in the plot presented in **Figure 3**.

To conduct recurrence quantification analysis, further parameters must be set, such as the delay and embedding dimension parameters. These parameters are used to recover higher-order dynamics from the (potentially) lower-order number of time series which have been recorded from a system (Takens, 1981). The delay parameter is estimated by the first local minimum of the average mutual information function of the time series to be subjected to MdRQA. The embedding dimension parameter is estimated by the false-nearest-neighbor function, at the point where this function bottoms out. For a detailed introduction to multivariate recurrent analysis, and the parameter estimation procedure, see Wallot and Leonardi (2018).

For MdRQA, the delay parameter (d), as well as the embedding parameter (m), were approximated using a multivariate mutual information and false-nearest neighbor functions for parameter estimation applied through MATLAB (Wallot and Mønster, 2018). Here, the embedding parameters are estimated for each triad or dyad. Then, these estimates are averaged over the whole sample and rounded to the nearest high integer. Then, these values are used for each data set, which allows to compare data sets with the sample based on the same embedding parameters (see Wallot and Leonardi, 2018). Furthermore, the threshold parameter (r) was fixed across data sets so that each data set entered the analysis with the same value for *r* and the value for r was chosen to provide an average of REC% between 1 and 5% (Webber and Zbilut, 2005) across all data sets by calculating the recurrence rate for a series of optional *r*-values until an appropriate REC% was found.

As stated above, we aimed to capture both individual contributions to the group's physiological synchrony, as well as the group's physiological synchrony as a single entity. To pursue these goals, we conducted MdRQA according to guidelines described by Gordon et al. (2021) on two distinct levels–individual and triadic. That is, to investigate group-level dynamics, which contain the interactions between all group members over time (Wallot et al., 2016b), the time-series for all members of the group were subjected simultaneously to MdRQA (as in our toy example above) and recurrence measures were then computed.

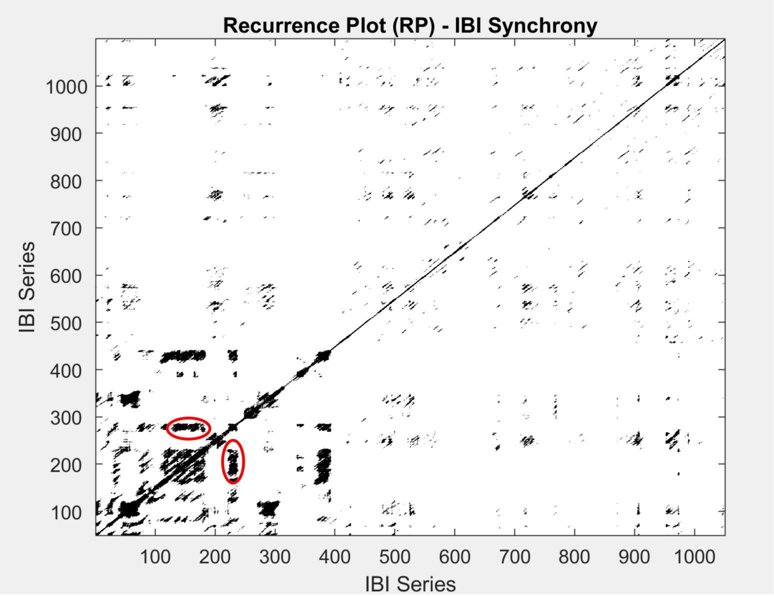

FIGURE 3 | An example of a multidimensional recurrence plot for one group participating in this study. Both the *x*-axis and *y*-axis represent the IBI time series. Blackened areas are recurrent points, and vertical lines are circled in red. To quantify the recurrence rate (REC%), we calculate the percentage of recurrent points across the matrix. Further, to identify recurrence patterns in time, we use LAM%, the rate of recurrence points with a vertical neighbor, and the length of the vertical lines (meanV and maxV).

In order to capture each individual's participation in the group dynamics (a so-called individual-level synchrony), we computed all possible dyadic recurrence plots and recurrence measures for every individual in a group and then averaged these for each individual. For instance, participant A's scores were computed as the average recurrence measures of data from participants A and B (Dyad I) and data from participants A and C (Dyad II). Similarly, participant B's scores were computed as the average recurrence measures of data from participants B and A (Dyad I) and data from participants B and C (Dyad III), and so forth.

Note that different parameters were assigned for dyads and triads (**Table 2**), while parameters were kept constant across the set of triads and dyads, respectively. This was done to facilitate the comparability of the MdRQA results across data sets. Furthermore, we generated false-pair surrogates by randomly partnering participants' time-series with others from different groups (Richardson and Dale, 2005). The same analysis (with the same sets of parameters) was applied on the fabricated groups to indicate random recurrence levels.

TABLE 2 | Multidimensional recurrence quantification analysis (MdRQA) parameters assigned for dyads and triads.

Parameters	Delay	Embedding dimension	Threshold	Norm
Dyad	2	7	0.457	Euclidean distance norm
Triad	2	7	0.51	Euclidean distance norm

The IBIs data was not normalized prior to the analysis.

Due to the strong correlation [Partial and Semi-Partial Correlation R package by Kim (2015)] between the last three parameters (**Table 3**), we created a primary vertical measure (Vertical Synchrony) which addresses the intermittency in time-series by averaging the z-scores of LAM%, meanV and maxV. While REC% stands for general repetition of values between time series, high vertical synchrony better represents a stronger coupling (Richardson et al., 2008; Wallot et al., 2016a; Proksch et al., 2022).

RESULTS

First, to test our hypothesis that physiological coupling occurs within groups while interacting, we compared the recurrence

TABLE 3 | Correlation matrix, laminarity, mean and maximum vertical line length on the triad level during group interaction.

Partial correlation

		IBI LAM%	IBI meanV	IBI maxV
IBI LAM%	Pearson's r	–		
	p-value	–		
IBI meanV	Pearson's r	0.655	–	
	p-value	<0.001	–	
IBI maxV	Pearson's r	0.593	0.915	–
	p-value	<0.001	<0.001	–

Results presented here control for the effects of the experiment ("drumming" and "decision-making" ranked 1 and 2).

rates of IBI, calculated at the triadic level of the MdRQA, to recurrence rates of IBI in false-pair surrogates. Applying Wilcoxon signed-rank test in Jamovi 1.2 (The Jamovi Project, 2021), we discovered that actual groups were more in-sync, as represented by higher REC%, than pseudo-groups (Wilcoxon $T = 1686$, $p = 0.033$), see **Figure 4**.

Next, a Wilcoxon rank signed test revealed that the degree of physiological synchrony during the task was higher than the degree of synchrony found at baseline (Wilcoxon $T = 1018$, $p < 0.001$), see **Figure 5**. However, we did not find significant differences in recurrence rates at baseline compared to those found among surrogate groups (Wilcoxon $T = 1619$, $p = 0.55$). Thus, it appears that IBIs synchrony between group members, which is significantly above chance level, develops when participants act together rather than when they merely sit in the same room together. In so far as IBI-activity captures arousal, it is also plausible that IBI-synchrony is observed in the mere presence of others, without tangible joint activities–such as in a baseline phase where all participants are present in the same room and can see each other, but do not interact in a specific task. However, the results indicate that synchrony during baseline was not significantly higher than what would be expected due to the chance-level of false-pairs.

To test whether synchrony in IBI during social interaction predicts group cohesion, we applied a mixed model in Jamovi using GAMLj module (Gallucci, 2019). As independent predictors, we deployed a combined recurrence measure (Vertical Sync, see Section "Materials and Methods"), and condition while the group (drumming or decision making) acted as a random factor (**Table 4**). No significant results for cohesion were found for the groups' synchrony during the task stage of the experiment; in contrast, the effect of baseline synchrony on cohesion was negative (**Table 5**). Hence, refining the on-task synchrony measure, we created a delta measure (ΔSync) by subtracting the baseline levels of synchrony from the interaction levels.

While most studies investigating interpersonal synchrony analyzed the degree of synchrony during social interaction, it has also been proposed that a physiological coupling occurs among individuals who share the same space without engaging in an interaction (Golland et al., 2015). The mentioned mere co-presence setting resembles the baseline stage in our experiments in which participants were asked to sit quietly in the same room. Therefore, to account for the outcomes of the collaborative task, we investigated the formation of synchrony by subtracting each group's degree of synchrony at baseline from its interaction synchrony score. This measure, ΔSync, constitutes the change in joint physiological activity from the first inactive 5 min (i.e., the baseline) to interaction during the shared task. **Figure 6** shows the data at baseline in comparison to the interaction minus baseline model.

Our findings indicate that ΔSync was positively related to a participants' sense of group cohesion when synchrony was calculated at the group level (**Table 6**) and that experimental condition was associated with cohesion. To test the robustness of this relationship between physiological synchrony and cohesion, we ran a second mixed model predicting cohesion from ΔSync calculated separately for each participant, holding group as a random coefficient (**Table 7**). Similarly, both experimental condition and individual ΔSync yielded a significant effect on group cohesion. Interestingly, the positive relationship between ΔSync and cohesion was consistent across experimental

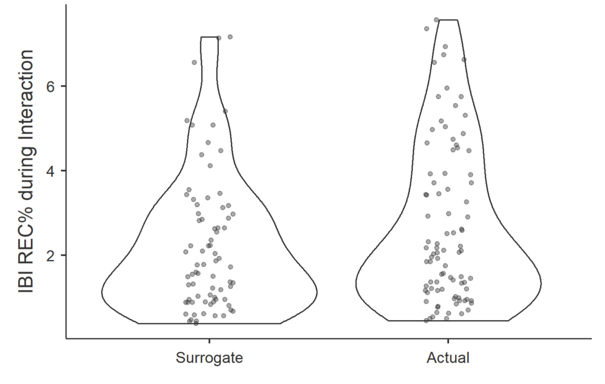

FIGURE 4 | Violin plots show the distribution of REC% of actual and pseudo triads during a group interaction.

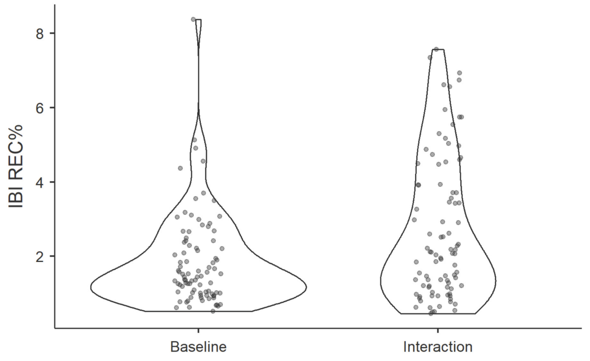

FIGURE 5 | Violin plots show the distribution of REC% of triads at baseline and during the group interaction.

TABLE 4 | A mixed model predicting cohesion from IBI synchrony at the interaction.

Group Level IBI sync at interaction model–Fixed effect on cohesion

	F	Numerator df	Denominator df	*p*
Condition	3.12	3	2	0.252
IBI Sync at Interaction	1.75	1	85	0.190

TABLE 5 | A mixed model predicting cohesion from IBI synchrony at baseline.

Group Level IBI sync at baseline model–Fixed effect on cohesion

	F	Numerator df	Denominator df	*p*
Condition	3.31	3	2	0.240
IBI Sync at Baseline	4.38	1	83	0.039

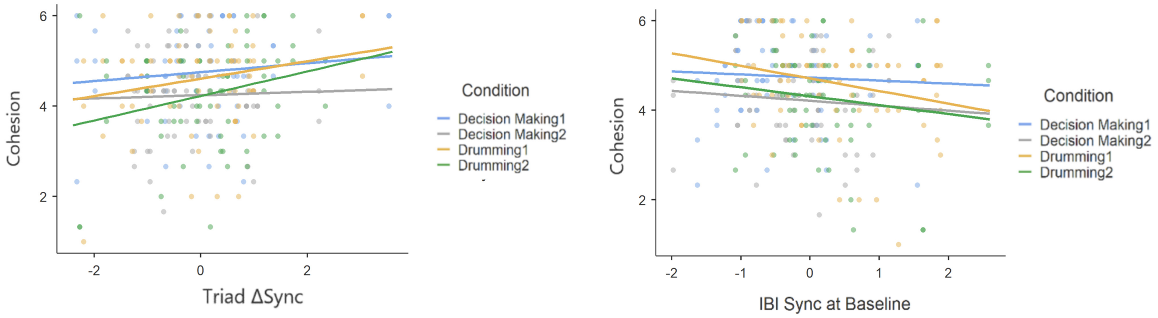

FIGURE 6 | Scatter plots and slopes for the IBI data during task minus baseline (triadic ΔSync) and the baseline data (IBI Sync at Baseline).

conditions in both experiments as no interaction effect was found between ΔSync and condition (**Figure 7A** and **Figure 7B**).

However, model comparisons between a model containing only the individual-level predictors and a model containing both, the individual-level and the group-level predictors suggested that the triadic level of ΔSync does not contribute to the prediction of cohesion beyond the individual-level effects (X^2 = 0.0014, $p = 0.97$).

$$Cohesion_{ij} = \gamma_{00} + u_{0j} + \gamma_{10} \cdot \Delta Sync$$
$$+\gamma_{20} \cdot Condition + \gamma_{12} \cdot Int\left(\Delta Sync * Condition\right) + \varepsilon_{ij}$$

TABLE 6 | A mixed model (see equation above) predicting participant's cohesion from ΔSync (γ_{10}), task condition (γ_{20}), and their interaction (γ_{12}) at the triad level.

Group level ΔSync model–Fixed effect on cohesion

	F	Numerator df	Denominator df	*p*
Condition	3.443	3	114.7	0.019
Triad ΔSync	5.204	1	79.0	0.025
Condition × Triad ΔSync	0.581	3	79.0	0.629

Group cohesion serves as a random effect (u_{0j}) and is added to the general cohesion average (γ_{00}). Marginal R^2 = 0.074.

DISCUSSION

In the present study, we analyzed group interaction data from two different studies–one from a joint drumming and the second from a joint decision-making task. Specifically, we examined how synchronous IBI dynamics at the individual- and triadic-level were related to self-reported group cohesion. Across all conditions, we found a positive effect of physiological synchrony on cohesion. This effect was observed at the individual-level and at the triadic-level. While the reported level of cohesion differed between different study conditions, the effect of IBI synchrony on cohesion was stable across conditions, as no significant interaction between synchrony and condition emerged.

Considering the role of synchronization in social tasks, our results highlight the centrality of physiological synchronization mechanisms as potentially facilitating the formation of groups and their members' sense of group cohesion. These results are pivotal as experiencing the group as cohesive has been demonstrated to have a strong effect on the group's objective performance outcomes (Evans and Dion, 1991; Beal et al., 2003). These findings also provide a much called for extension of previous work on the prosocial implications of synchrony from the dyad-level to the much less examined group context (Bernieri and Rosenthal, 1991; Hove and Risen, 2009). More specifically, we provide further evidence for the role of physiological synchrony in IBIs for prosocial effects in groups (Palumbo et al., 2017; Mayo et al., 2021) while utilizing a non-linear analytical approach on two datasets that involve two different types of social tasks–one verbal and the other rhythmic-motor, one very structured and the other only relatively unstructured.

Regarding the question of emergent synchronization at the group-level (i.e., the group-as-superorganism), we found a significant synchronization beyond what would be expected at chance-level. This suggests that IBI synchronization in the groups across the different conditions indeed represents a group behaving to some extent as a superorganism, and that such group-level coordination needs to be taken into account when modeling data in groups bigger than two. However, effects on the individual-level (i.e., how much each member of the group synchronized with the other two members), occurred as well. On the one hand, these results seem to point to multilevel synchronization emerging in the groups, suggesting that the analysis of both, the individual- and the group-level effects of synchrony illuminates a potential multilayered aspect of cohesion as a group phenomenon. As cohesion is evaluated through self-report questionnaires at the individual-level (Evans and Jarvis, 1980; Dion, 2000; Salas et al., 2015), it is intriguing that both individual-level and group-level physiological synchrony contributed to predicting cohesion. While group-level synchrony may reflect the group's unification and cooperation, the individual-level synchrony emphasizes one's attraction to the group members and his\her willingness to continue collaborating with the other members. These dual aspects that impact cohesion are important to consider in future research.

However, the results of model comparisons indicated that the group-level dynamics did not substantially contribute to model fit of cohesion values beyond what could be inferred from the

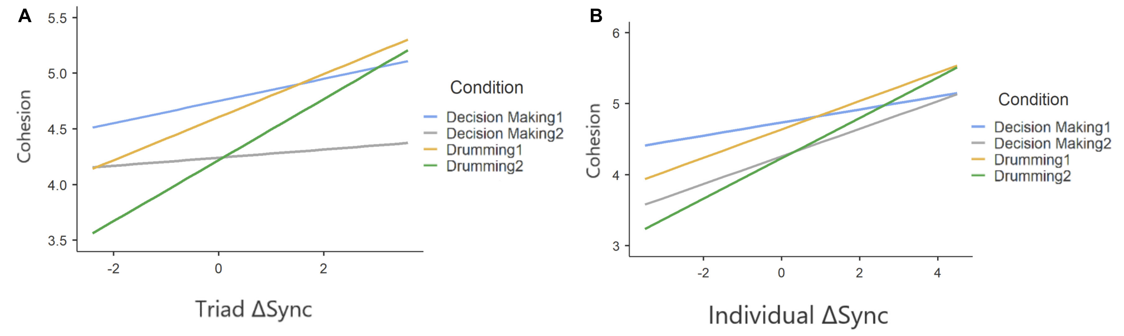

FIGURE 7 | Two-way interaction plot, based on a random slopes and random intercept mixed model, predicting cohesion from ΔSync on triad level **(A)** and individual level **(B)** and on under different conditions (plotted as different colors). The positive correlations indicate that a positive change in IBI synchrony, from baseline to engagement in a group activity, predicts a stronger sense of cohesion among group members.

individual-level predictors alone. Obviously, in the current datasets, both sets of predictors where highly correlated. This did not allow us to tell specific sources of contribution on these different levels apart. Accordingly, the results do not yield substantial evidence for emergent coordination among the group members regarding the superorganism hypothesis. However, these results illustrate the importance of measuring group dynamics and coordination on different levels, because sometimes such effects are only present on some or none of the levels (Wallot et al., 2016a; Gordon et al., 2021). Moreover, pitting these effects against each other allows for a more accurate test of the importance of the different levels. If we had only considered group-level dynamics and tested them against surrogate data as well as in terms of their predictive value for cohesion ratings, we might have taken these results as strong evidence of emergent group-level synchronization, while the comparison to the individual-level data calls such a strong conclusion into question.

Our study lays out an innovative perspective on the development of synchrony as a key factor in understanding social group dynamics. By investigating the change in the degrees of synchrony (ΔSync), rather than its absolute value during social interaction, we put more weight on the initial stages of the formation of social bonds. A similar point of view was presented regarding cohesion (Marks et al., 2001), defining it as an emergent state, a dynamic temporal component, that is altered with team experiences. Still, our approach might be more suitable to investigate in newly formed groups of relative strangers that, according to our findings, do not tend to synchronize with each other at baseline prior to the interaction.

TABLE 7 | A mixed model predicting cohesion from ΔSync, task condition and their interaction at an individual level.

Individual level ΔSync model–Fixed effect on cohesion

	F	Numerator df	Denominator df	*p*
Condition	3.385	3	80.9	0.022
Triad ΔSync	8.557	1	113.0	0.004
Condition × Triad ΔSync	0.431	3	112.4	0.731

Marginal R^2 *= 0.08.*

It is interesting to note here that in the original drumming study, when we utilized a linear approach to quantifying synchrony during the group task (Gordon et al., 2020a), we found a relationship with cohesion without considering the baseline period. Perhaps this fact has to do with the methodology, in which the linear cross-correlation function as we used it, considered only the strongest correlation close to lag0 to assess synchrony. Conversely, MdRQA looked only at strict lag0 recurrence, but incorporated autocorrelation (i.e., auto-recurrence) information from other lags as well (Marwan et al., 2007). Another explanation for the "baseline" effect, is that the antecedents of meaningful synchronization between group members already exists in the very initial stages of social grouping–what may be termed as a "first impression" effect. This explanation is intriguing but requires further examination in future studies.

It should be noted that we did not find any differences regarding the effect of physiological synchronization on cohesion across tasks or experimental conditions. Even though the two tasks appear to differ in terms of how they implement group coordination, they did not moderate effects of synchrony on cohesion. On the one hand, this suggests that the effects of IBI synchrony on cohesion are very stable across a certain range of tasks and interaction types. On the other hand, it remains unclear what exactly drives differential effects of synchrony in different group settings (Palumbo et al., 2017; Mayo et al., 2021). Future studies should test if negative contexts or competitive ones would yield similar results to the ones we found here.

This is also one of the limitations of the present analyses: The two studies seem to differ in their tasks demands, but they were not specifically designed to manipulate factors that may change the role or meaning of synchronization during interaction (Danyluck and Page-Gould, 2019). Further limitations are a lack of control for gender as well as a homogenous sample mainly consisting of undergraduate students. As a result, we could not account for background differences and in-group or out-group effects, which carry relevance for synchrony's prosocial effects (Tunçgenç and Cohen, 2016; Cirelli, 2018).

To expand the knowledge on the role of physiological synchrony for group processes, future studies should aim to implement experimental manipulations that are likely to change the meaning or role of synchronization for the group (from a positive to a negative context for instance or from cooperation to competition). Moreover, additional longitudinal research should trail newly formed groups' development and bond formation alongside the development of physiological synchrony over time. Nonetheless, our results represent an important step in reaching a more crystallized understanding of group processes via objective non-biased measurements of the dynamics of group interactions. We further emphasize the importance of incorporating multilevel representations of synchrony within groups when analyzing the effects of synchronization on cohesion.

DATA AVAILABILITY STATEMENT

The original contributions presented in this study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

ETHICS STATEMENT

The study was approved by Bar-Ilan University Department of Psychology Ethics Committee. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

AT analyzed the data. All authors discussed and interpreted the results and wrote the manuscript.

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Exploring how healthcare teams balance the neurodynamics of autonomous and collaborative behaviors: a proof of concept

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Team members co-regulate their activities and move together at the collective level of behavior while coordinating their actions toward shared goals. In parallel with team processes, team members need to resolve uncertainties arising from the changing task and environment. In this exploratory study we have measured the differential neurodynamics of seven two-person healthcare teams across time and brain regions during autonomous (taskwork) and collaborative (teamwork) segments of simulation training. The questions posed were: (1) whether these abstract and mostly integrated constructs could be separated neurodynamically; and, (2) what could be learned about taskwork and teamwork by trying to do so? The taskwork and teamwork frameworks used were Neurodynamic Information (*NI*), an electroencephalography (EEG) derived measure shown to be a neurodynamic proxy for the pauses and hesitations associated with individual uncertainty, and inter-brain EEG coherence (*IBC*) which is a required component of social interactions. No interdependency was observed between NI and IBC, and second-by-second dynamic comparisons suggested mutual exclusivity. These studies show that proxies for fundamental properties of teamwork and taskwork can be separated neurodynamically during team performances of ecologically valid tasks. The persistent expression of *NI* and *IBC* were not simultaneous suggesting that it may be difficult for team members to maintain inter-brain coherence while simultaneously reducing their individual uncertainties. Lastly, these separate dynamics occur over time frames of 15–30 s providing time for real-time detection and mitigation of individual and collaborative complications during training or live patient encounters.

KEYWORDS:

teamwork, taskwork, EEG, hyperscanning, uncertainty, representation design, team neurodynamics, information theory

Introduction

Teams are a social response to recurring and required tasks that are too difficult for one person to accomplish. The dual complexities of teams and tasks result in evolutionary systems, with teams varying their behaviors in response to external perturbations and changing task requirements while also using their behaviors to constrain and shape the task (Ashby, 1956). As expected from the changing complexities of the task and the environment, teams are different from the natural flow of most human activities by being constrained by time, resources, and ability. In these dynamic decision-making moments, the changing individual and collaborative elements contributing to the success or failure of teams are difficult to identify, challenging our ability to predict future dynamics either by humans or machines (Stevens and Galloway, 2021a).

Historically the dynamics of teams have been observed through many lenses. These include intentions from the perspective of agents (Cohen and Levesque, 1990) or humans (Knoblich and Sebanz, 2008), shared plans and planning (Grosz and Kraus, 1996), joint actions (Sebanz et al., 2006) shared cognition (Gorman and Cooke, 2011), team mental models (Mohammed et al., 2010), team coordination (Gorman et al., 2010), and macrocognition (Klein et al., 2003). What these ideas share is an increased understanding of how well individuals can recognize and act appropriately on the intentions of others. While intention provides a social cognitive background for the shared actions of a team, the interdependencies of the joint actions provide the organizational structure within; and with that, teams perform joint tasks and realize common goals (Wageman, 2001; Kozlowski and Bell, 2020).

Team functioning

When people collaborate on a task at least two simultaneous processes are thought to occur, taskwork and teamwork (Salas et al., 2004; Driskell et al., 2018). The taskwork of individuals is where their expertise and experience are used to develop information relevant to the team goals and convey it efficiently and effectively to others (Paris et al., 2000). The skills of taskwork are defined by the task domain, i.e., being a sonar operator or surgeon. Task skills are easier to define, observe, describe, and assess than team skills and can be measured using standard psychometric techniques (Von Davier and Halpin, 2013).

The skills of teamwork include those that help establish and support effective communication, problem-solving, management of resources, and managing conflict (Salas et al., 2007). These skills are usually taught by working together on-the-job, or through simulation-based training and are measured by expert observations (Baker et al., 2011) and the use of vetted rubrics (Jones et al., 2011); this is likely to change.

While our understanding of individual skill development is improving, our understanding of how to develop team skills often results in unanswered questions (Stevens et al., 2017): Are teams more (or less) than the sum of their parts? Can teamwork be separated from taskwork? What distinguishes the temporal and spatial dynamics of teamwork and taskwork, and are the boundaries between them discrete or continuous? Are the dynamics of these constructs independent, interdependent, or mutually exclusive at time scales (i.e., the hierarchical depth of cognition) that would have immediate relevance for planning and training? Answering such questions would have implications for: training (Fisher, 2014), assembling and enabling task vs. collaboration enhanced robots (Kamika, 2019) and for training artificial intelligence to forecast possible team outcomes based on their neurodynamics (Stevens and Galloway, 2021a).

The expanded repertoire and analytic capabilities of physiologic sensors are shifting the research lens once again, providing increasingly rich data and quantitative tools for describing the brain during increasingly complex situations (Kazi et al., 2021). This re-focusing of teamwork research emphasizes a shift toward more implicit (automatic, fast, subconscious) interactions (as opposed to observations) of team members during dynamic social interactions in ecologically valid, uncontrolled, and prolonged real-world tasks (Wiese et al., 2018; Abubshait et al., 2021). These capabilities and shifts toward ecologically valid settings are also causing researchers to re-think experimental designs and analyses, shifting toward representative design as a principled basis for ecological generalizability, taking complex phenomena and deconstructing them into manageable components (Nastase et al., 2020; De Sanctis et al., 2021; Gramann et al., 2021), where theoretical assumptions are relaxed at the stage of experimental design and data collection, and later imposed during different stages of analysis.

Looking forward, we are now at a point where the practical insertion of these technologies into improving teamwork and learning will benefit from knowing how the dynamics of these measures interrelate with one another in the context of evolving tasks and team behaviors.

In this representative design study, we ask whether elements of teamwork and taskwork can be neurodynamically separated? For this we draw from two EEG-derived neurodynamic frameworks, neurodynamic organizations and inter-brain coupling. Neurodynamic organizations are information-based abstractions, expressed in bits, of the structure of long-duration EEG amplitude levels. Neurodynamic information (*NI*, the variable of neurodynamic organization) is felt to continually accumulate as EEG amplitudes cycle through periods of persistent activation and deactivation in response to the activities and uncertainties of teamwork. The level of inter-brain EEG coupling during social interactions is estimated by wavelet transform coherence (*WCoh*) measures, based on the phase and amplitude of the EEG signals (Czeszumski et al., 2020).

Inter-brain coupling

Simultaneous multi-brain recordings (hyperscanning) have often used the lower limits of neuroimaging technologies to document synchronized millisecond to seconds-long shifts in the EEG phase or amplitude (Lindenberger et al., 2009; Dumas et al., 2010; Hasson et al., 2012; Filho et al., 2016; Muller et al., 2021). Such inter-brain coordination during social interaction reflects temporal adjustments to brain network dynamics based on perceptions resulting from social interaction, or more recently from external modulation (Muller et al., 2021).

Outside the range of a few seconds, the ideas of interdependence among team members are mostly unexplored. There are indications that brain hyper-connections can occur independently in different people as intrinsic and extrinsic information become integrated over longer time scales (minutes or more; Hasson et al., 2008; Tranquillo and Stecker, 2016; Silva et al., 2019). These scrolling windows of cognition playing out well-practiced sequences of events are beginning to be described in individuals as temporal receptive windows (TRW), with elements of the Default Mode Network playing a role in integrating internal predictions of the future with the continuous updation of sensory information (Lerner et al., 2011; Yeshurun et al., 2021).

Examples include different individuals viewing the same movie segments or listening to the same narratives or music (Lerner et al., 2011; Clayton et al., 2020). Here the only dependency among people is the time the data stream starts, and again when different cognitive elements are sequentially activated internally by the unfolding sequence of sounds and events. Under these conditions the brainwaves being externally entrained could be coherent, but not necessarily coordinated (Burgess, 2013).

Such sequence entrainment/synchrony in real-world settings was shown to occur with submarine navigation teams (Stevens and Galloway, 2014, 2019, 2021b). The submarine navigation team consists of one group responsible for keeping the ship on course and they do so by checking and reporting the position every 3 min through a timed sequence of activities called Rounds. Meanwhile, another group is responsible for avoiding collisions and it does so by establishing possible collision targets using the course and direction of other ships. Prolonged periods (30–40 s) of time-ordered neurodynamic organization have repeatedly been observed with the submarine navigation group in parallel with time-ordered, recurring sequence of activities. Similar significant correlations among team members have been shown with healthcare teams as illustrated below. What has been lacking from these studies is information regarding the *IBC* among team members during these periods of neurodynamic organization. In fact, it is unknown whether prolonged periods of *IBC* are even produced during continuous simulation training.

Neurodynamic organization and uncertainty

Uncertainty is a fundamental property of neural computation used by the brain to estimate the (perceived) state of the world. The brain draws from this uncertainty to access memories (the past) to imagine future possibilities and the actions needed to give the best outcomes. In this way, uncertainty serves as a trigger for adaptation (Knill and Pouget, 2004). While it is generally accepted that uncertainty should be avoided, it is also becoming apparent that uncertainty drives learning by triggering a switch from strategies exploiting past experiences to strategies exploring novel approaches (O'Rielly, 2013; Soltani and Izquierdo, 2019; Domenech et al., 2020; Gillon et al., 2021).

During teamwork, this exploratory uncertainty, and the pauses and hesitations it generates, are often early indicators of deteriorating performance (O'Riordan et al., 2011; Kaufman et al., 2015; Ott et al., 2018). Uncertainty is an intrinsic condition within healthcare that affects individual clinicians and teams during training and practice. Defined by Han et al.'s (2011) as, "a subjective perception of ignorance" uncertainty is messy and non-linear, and adds complexity to patient care that may result in patient harm since it is often a precursor state to error (Farnan et al., 2008). This fundamental perception of not knowing gives rise in conventional terms to doubts, hesitations, and lack of reliability in patient care (Han et al.'s, 2011). It likewise elicits a variety of behavioral and cognitive responses among clinicians (Lally and Cantillon, 2014; Nevalainen et al., 2014), and increases healthcare costs on a national and global scale (Dine et al., 2015). While hesitations represent a concern for the individual experiencing it, they also serve as an interruption to the team. Here, hesitation on the part of one team member interferes with work continuity and causes a resumption lag before the recommencement of the primary task. Most studies have shown that interruptions lead to a decline in performance (Zikerick et al., 2021).

Despite uncertainty's ubiquitous presence, there has been little discussion about how to develop quantitative measures for detecting and modeling the dynamics of aggregated levels of uncertainty in teams. We have identified, and trained machines to recognize, neurodynamic correlates of uncertainty based on the pauses, hesitations, and verbalizations of teams (Stevens and Galloway, 2017, 2019, 2021a). These neurodynamic correlates are based on persistent information structures or neurodynamic organizations in EEG data streams.

EEG analyses are dictated by the physical units of amplitude, frequency, and phase of brain waveforms. Understandings of team behavior, however, are constructed around organizations, whether they be: production, personnel, distribution, or other variant structures (Mathieu et al., 2014). A useful transformation would be one that input physical units of EEG amplitude (μ-volts) and the output measures of organization (in bits), the rationale being that information-organization representation would better align with the organization-based measures of teamwork behaviors.

As detailed under "Methods" Section, the symbolic modeling generates a normative framework organization with 0, the information of a single symbol being the lower bound and the upper bound is the maximum information of a data stream containing a randomized set of the system symbols (i.e., 1.585 bits for a 3-symbol system, 3.17 for a 9-symbol system, etc.). The values between these bounds can be quantitatively compared across performances, or across brain regions or across the frequencies of the 1–40 Hz EEG spectrum (Stevens and Galloway, 2017).

Within this normative framework a measure termed Neurodynamic Information (*NI*), is generated which temporally bridges the gap between low level neural processes associated with everyday activities, and the hesitations and pauses associated with team member uncertainty (Stevens et al., 2018a; Stevens and Galloway, 2019, 2021b). The emerging picture from these studies is that as simulations and real-world events evolve, the accumulated *NI* of each individual becomes a measure of the frequency, magnitude, and duration of periods of uncertainty that have been experienced (Stevens et al., 2019).

In this way, a neurodynamic organization is a useful intermediate abstraction (Flack J. C., 2017) that contributes properties not always possessed by the amplitude or phase of brainwaves such as linking with the organization of team activities (Stevens and Galloway, 2017), or speech (Gorman et al., 2016), or the expertise of submarine or healthcare team proficiency (Stevens et al., 2018b; Stevens and Galloway, 2021b). In the spirit of representative design (Dhami et al., 2004; Nastase et al., 2020), and quantitative collectivity (Daniels et al., 2021) they also serve as the starting point for macro-scale to micro-scale cognitive deconstructions across temporal and spatial scales of brain dynamics where environmental properties are preserved.

Methods

Subjects and tasks

Medical flight teams

Five two-person medical flight teams performed a required pediatric patient simulation (acute bronchiolitis) within the interior of an emergency helicopter while wearing 19-sensor (Cognionics, Inc.) EEG headsets (112 min containing briefings and scenarios was recorded). All participants were experienced practitioners with 5 years or more in ICU-CCU settings who were participating in required training sessions. The sequence of events in each of the performances was an introduction to the task, an examination of the equipment and supplies available, a presentation of the patient's history, and a short Q&A while on the tarmac. The team then entered the helicopter, assembled themselves with one person at the head of the patient (TM-1) and one at the side (TM-2). The team then managed the patient during the simulated trip to the hospital. The distribution of time in each segment varied for each team.

Medical student team

A second team with three 4th-year medical students managed a patient with a benzodiazepine overdose. This team performed simulations in a high-fidelity operating-room environment. The neurodynamics of this team and performance were previously studied in the context of speech to clarify the relationship between team communication and resolving uncertainty (Stevens et al., 2016).

Ethics statement

Informed consent protocols were approved by the Biomedical IRB, San Diego, CA (Protocol EEG01), and the Order of Saint Francis Healthcare Institutional Review Board. Participating subjects consented (including images and speech for additional analysis) per approved applicable protocols. To maintain confidentiality, each subject was assigned a unique number known only to the investigators of the study, and subject identities were not shared. This design complies with DHHS: protected human subject 45 CFR 46; FDA: informed consent 21 CFR 50.

Neurodynamic measures

EEG collection and pre-processing

Currently, the most common methods for removing artifacts in movement studies are methods based on independent component analysis (ICA) which transforms a set of vectors into a maximally independent set. EEG artifacts can be broadly divided into two classes: non-stereotyped artifacts due to multiple factors like the subject's movements or external sources of interference, and stereotyped artifacts due, for example, to ocular eye movements, blinks, heartbeats (Onton et al., 2006). Artifacts from the second class are likely to be captured by some ICA components because they have a highly reproducible spatial distribution and temporal profiles. ICA decomposes the observed signals into independent components and after removing the unwanted components, the clean signal is reconstructed from the remaining independent components (Makeig et al., 1996). Artifacts from the first class are problematic for ICA because since their spatial distribution is extremely variable, they introduce a large number of unique scalp maps, leaving few ICs available for capturing brain sources. The data streams were therefore processed with a combination of ICA and artifact subspace reconstruction (ASR) which has several advantages including the automated removal of artifact components, its usability for online applications, and the ability to remove transient or large-amplitude artifacts that the ICA method struggles with (Kothe and Jung, 2014; Chang et al., 2018; Gorjan et al., 2022).

The 19 quick dry-electrode system sensors (CGX Cognionics Inc., San Diego) were designed with noise reduction into the hardware, with active electrodes, active shielding, and extremely low-noise electronics, and were fitted on each subject and then adjusted for good contact. When impedance was low ($<10\Omega$) and the subject was ready, EEG data were continuously recorded with a sampling frequency of 500 samples/s from sensors positioned over the scalp according to the international 10/20 system, and all subject's data streams were monitored throughout the session.

Although wireless systems enable mobility, accurate timing is difficult due to the inherent latency and jitter in wireless communications. The EEG data streams of team members, as well as audio and video recorders, were synchronized before and after each data acquisition with the Cognionics Trigger electronic time synch markers. The trigger system is created to accurately broadcast time markers with millisecond precision, resolving the issues of latency and jitter. The electronic time markers were also inserted during acquisition at task segment events like the end of the briefing, the beginning of a debriefing, or the start and finish of specific procedures like intubation. Because the timing accuracy is guaranteed in hardware, there is no need for software or algorithmic timing compensation (CGX Cognionics Inc., San Diego).

The time-synchronized EEG data were visually inspected to identify bad electrodes; these were not present in any of the study teams. Next, to remove linear trends and to obtain good quality ICA decompositions (Klug and Gramann, 2021), we high pass filtered the data at 1 Hz. To remove the 60 hz line noise, we applied the CleanLine EEGLAB (Mullen, 2012) plugin that adaptively estimated and removed sinusoidal noise coupling multi-tapering and a Thompson F-statistic. To aggressively remove transient and high amplitude medium to large artifacts that the ICA method struggles with, we applied ASR (EEGLAB Clean Rawdata) with the recommended cut-off parameter of $k = 20$, retaining approximately 20–40 percent of unmodified data. For stable decomposition, we applied the InfoMax independent component analysis (ICA) algorithm (runica) to detect and remove additional electrode drifts, eye movements, electromyographic and electrocardiographic interference (Delorme et al., 2007, 2011). All data sets were average referenced (Nunez and Srinivasan, 2006; Ludwig et al., 2009).

Team neurodynamic modeling

The modeling goal was to develop a multi-modal, multi-level system that would provide neurodynamic measures from each team member at a 1 Hz resolution that could be quantitatively compared across sensor sites (i.e., the occipital lobe vs. the motor cortex) and the individual 1–40 Hz frequency bins from each person.

Detecting structure in data streams involves first deconstructing continuous EEG data into discrete symbols which requires choosing the number of partitions. Some EEG rhythms, like alpha waves (∼10 Hz), show either enhancing or suppressive neurodynamic properties depending on whether they are in a high or low power state (Klimesch, 2012) and so at its simplest, EEG amplitudes of a team member could be assigned any three symbols such that the states are easy to visualize and understand. In our studies, activated states are assigned "3", deactivated states are assigned "-1" and neutral states are assigned "1". The result is a data stream of 3's, 1's, and -1's.

Figure 1 shows a team of two persons where the EEG amplitudes were separated into three states each second (**Figure 1A**), six states (**Figure 1B**), or nine states (**Figure 1C**). Since there are two persons and three symbols in each person's data stream in **Figure 1A**, the team data stream would have nine symbols. The temporal structure (not power) in this data stream can be estimated each second by measuring the mix (i.e., entropy) of the nine symbols in a 60 s segment that slides over the data and is updated each second. If only one of the nine symbols was expressed in this 60 s segment the entropy would be 0 bits; if there was an equal mix of the nine symbols, then the entropy would be 3.17 bits which is the maximum. So the fewer the symbols expressed in a window of 60 s the more organized the team was and the lower the entropy.

Neurodynamic Information (*NI*) is the information that remains when the experimental entropy values are subtracted from the maximum entropy for the number of unique system symbols. The *NI* profile for the team in **Figure 1A** is shown to the right and the average *NI* of the team's performance was 0.16 bits. Similar calculations were made when the amplitude was separated into six or nine states (**Figures 1B,C**). Although the *NI* values increased with additional symbols in each group, the *NI* profiles were similar indicating that adding additional symbols had a negligible effect on the dynamical structure of the data; for most studies, the EEG data of each team member is separated into three categories.

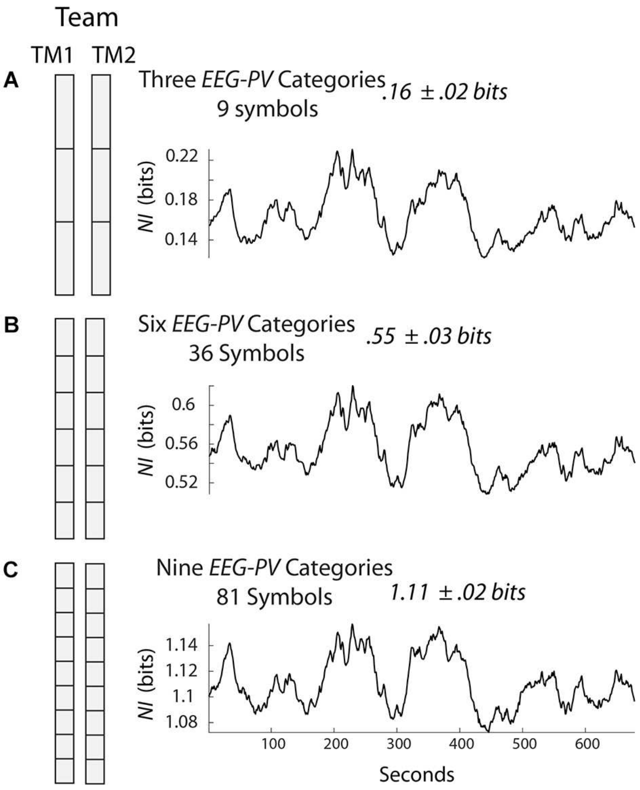

FIGURE 1
Symbolic modeling of neurodynamic data. The electroencephalography (EEG) was collected from two team members (TM1 and TM2) and each second the scalp averaged EEG amplitude values of each team member was separated into three **(A)**, six **(B)**, or nine **(C)** equal divisions. The *NI* was calculated for the three models using a 60 s moving window that was updated each second. NI, neurodynamic information.

Symbolically analyzing the structure of EEG amplitude creates a normative scale of EEG organizations ranging from 0 to the maximum *NI* of the number of symbols being used. A data stream with no organization would have an *NI* of 0. If the EEG were maximally organized the *NI* would be the maximum for the number of symbols in the system, i.e., 4.75 bits for a 27-symbol three-person team, 3.17 bits for a 9-symbol dyad, or 1.59 bits for a 3-symbol individual (i.e., high, average, low).

These mathematical limits have implications for creating quantitative performance measures. In other words, the *NI* of any two-person team performing a task where the EEG is separated into three PSD levels will have *NI* levels between 0 and 3.17 bits. The average value of 0.16 bits for the team in **Figure 1A** is one that can be quantitatively compared with other teams. If a team member's average *NI* is calculated, this value can be quantitatively compared with that of other team members. Similarly, the neurodynamic organization of one brain region can be compared with that of another brain region and across the 1–40 Hz EEG frequency spectrum. The same reasoning applies if the team *NI* is compared during the simulation scenario vs. the debriefing, or during a critical healthcare event like intubation.

Wavelet coherence

Methods for estimating inter-brain neural coordination are based on covariance in amplitude (Yun et al., 2012), or phase synchronization (Lindenberger et al., 2009). Wavelet transform coherence (*WCoh*) has also been used as an analytic tool, providing information on the level of coupling across brain regions of individuals or during social interactions (Czeszumski et al., 2020). Wavelet coherence is useful for analyzing nonstationary signals and considers both the phase and amplitude of the signals.

For deriving wavelet coherence coefficients the EEG data streams were down sampled to 1 Hz to parallel the dynamics of the EEG power spectrum density (PSD) estimates used for determining neurodynamic information.

The *IBC* between the two team members was made at the sensor level using the Matlab® function *wcoherence.m*. This function returns the magnitude-squared wavelet coherence,

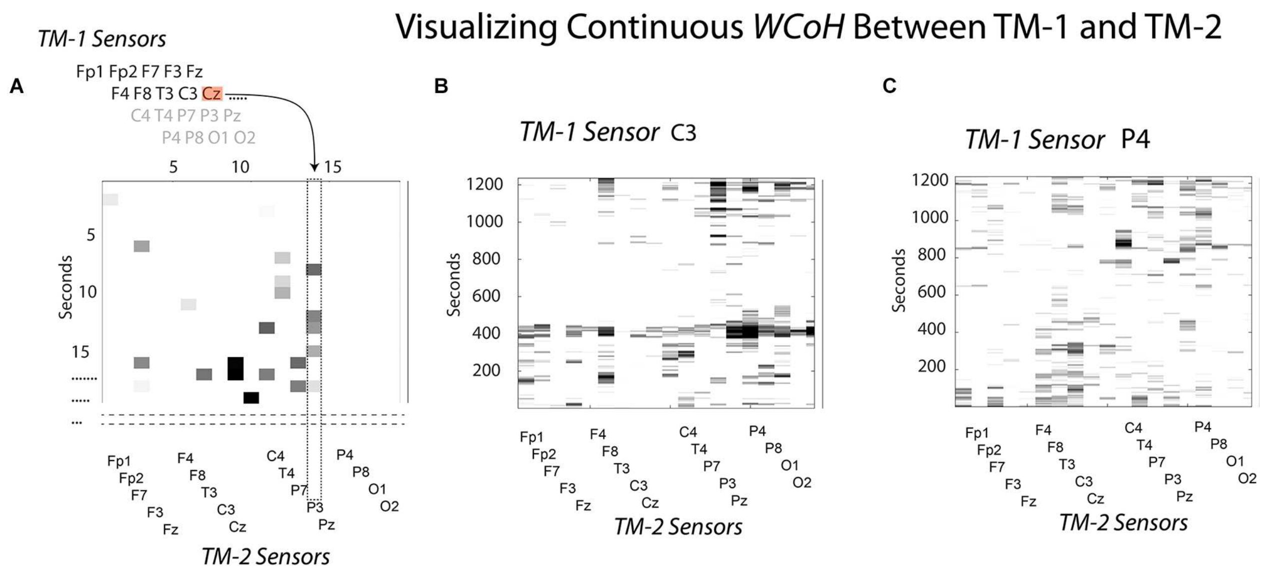

FIGURE 2
This figure illustrates how *WCoh* and *MI* were calculated across sensors for a dyad. **(A)** The neurodynamic measures at the sensors of TM-1 were sequentially modeled with those of TM-2 at each second to calculate the *IBC*; refer to the text for details. **(B)** The *WCoh* pattern after the neurodynamics of TM1's C3 sensor were passed over the 19-sensors of TM-2. **(C)** The *WCoh* pattern after the neurodynamics of TM1's P4 sensor were passed over the 19-sensors of TM-2.

which is a measure of the correlation between signals x and y in the time-frequency plane. A similar analysis was performed for data streams that had been randomized three times and these values were subtracted from the performance values.

Wavelet coherence is most useful for measuring how similar the power and phase are at each frequency of the two signals, and are robust for non-directed functional connectivity studies like ours (Bastos and Schoffelen, 2016). Other source information measures of connectivity like the Source Information Flow Toolbox (SIFT; Delorme et al., 2011) are more appropriate if directional, causal connectivity analyses are being considered as they are less sensitive to volume conduction effects.

To visualize the sensor × time *WCoh* dynamics, the EEG data stream of the first sensor (Fp1) of TM-1 were sequentially used to make wavelet coherence coefficients in combination for each of the remaining 18 sensors of TM-1, resulting in a 19-sensor wavelet coefficient map of the performance for the Fp1 sensor. This would be repeated with the second sensor of TM-1 to create another 19-sensor performance map, and so on until the 19 × 19 × time maps were completed. The diagram in **Figure 2A** illustrates the point in the modeling where the Cz sensor of TM-1 is being used in conjunction with the P3 sensor of TM-2, the previous 13 sensors of this map having been completed.

Two of the 19 *WCoh* sensor × performance maps are shown in **Figures 2B,C**, the first where the EEG data of the C3 sensor of TM-1 had been passed over the 19 sensors of TM-2, and the second map after the P4 sensor of TM-1 had been modeled. These two maps were selected to show the variability across *WCoh* maps. The first illustrates strong coherence around 400 s where the activity in the C3 sensor of TM-1 shows coherence with most of the sensors of TM-2 (i.e., a global form of coherence). This activity was missing when the P4 EEG of TM-1 was used instead of the C3 sensor. While the different *WCoh* maps show large temporal variability, the peaks within each map were sparse and discrete. These findings are representative of the remaining 17 *WCoh* maps which are not shown.

The *MI*-determined couplings across brain regions were visualized as described above for *WCoh*.

Results

Scalp-wide averages of *NI*, *MI*, and *WCoh*

The scalp-wide *NI*, *MI*, and *WCoh* levels were calculated using EEG-frequency and sensor averaged values for seven healthcare dyads. The average *NI* level was 0.09 bits, and the *MI* was 0.007 bits, or 7.7% of the dyad's average *NI* levels. The *NI* and *MI* values were both similar to previously published averages for a mix of 49 healthcare, military, and undergraduate dyads (Stevens et al., 2018a). *WCoh* levels are measured in terms of percent coherence and cannot be quantitatively compared with *NI* or *MI* (**Figure 3**).

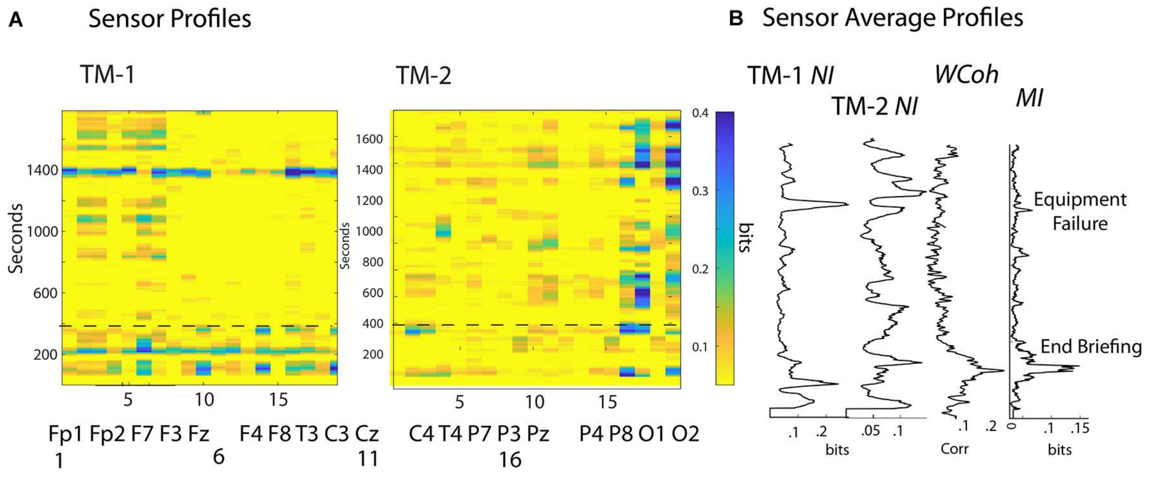

FIGURE 3
(A) The frequency-averaged *NI* values are plotted for each sensor every second for TM-1 at the Head position, and TM-2 at the Side position. The dotted line separates the Briefing and Scenario portions of the performance. **(B)** Profiles are shown for the sensor-averaged values of *NI* of TM-1 and TM-2; and the *WCoh* and *MI* of the dyad. The labels beside the *MI* plot indicate when the Briefing ended and when the ventilator failed to initialize (~1,400 s). There was a positive *MI*-*WCoh* correlation in **(B)** ($r = 0.68$, $p < 0.05$).

The *NI* correlations between the members of each dyad were variable, averaging $r = 0\ 0.37$, $p = 0.02$ with a range of r = -0.02–0.54. There were no correlations between the *NI* of the team members and the *WCoh* ($r = 0.08$), or the *MI* (r = -0.06) of their dyads. There was a weak but non-significant ($r = 0.27$, $p = 0.26$) positive correlation between *MI* and *WCoh* levels.

Temporal and spatial profiles of *NI*, *MI*, and *WCoh*—example 1

Overall dynamics

The analyses first explored the temporal (across the time of the performance) and spatial (sensors across the scalp) neurodynamics of *NI*, *MI*, and *WCoh* (**Figure 3**). The measure dynamics are displayed each second as frequency-averaged values for each of the 19 sensors in (**Figure 3A**) or as the sensor-averaged profiles of the performance (**Figure 3B**).

The surface maps sequence the sensors from the frontal scalp positions on the left of the maps, towards the rear of the scalp on the right. The frontal region sensors were those numbered 1–7, the central region sensors were in columns 8–12, the parietal region sensors were in columns 13–17, and the occipital region sensors were in columns 18 and 19.

The *NI* activity of both TM-1 and TM-2 was sparsely distributed at both the temporal and spatial levels with most peaks discrete and lasting 20–40 s. At any time, the elevated *NI* could be limited to a few sensors or be more globally distributed. During much of the Scenario, the elevated *NI* of TM-1 was in the frontal region (sensors 2–3, 5–7), while elevated *NI* of TM-2 was mainly in the parietal (sensors 16–17) and the occipital (O2) regions.

The sensor-averaged profiles (**Figure 3B**) of *MI* and *WCoh* indicate that much of this activity was during the Briefing when the instructor presented the patient's history and flight direction plan. There was a parallel, more discrete *MI* peak that aligned with the center of the *WCoh* peak. These peaks coincided with a period of low team *NI* levels when both team members were silent, still, and attentive.

Briefing dynamics

An expansion of the 1–500 s Briefing segment (**Figures 4A,B**) shows the majority of the *NI* of TM-1 occurred at sensor positions Fz, T4, P8, and O2 (# 5, 12, 17, 19), while those of TM-2 *NI* were simultaneously elevated in the C4 and O1 sensors.

The *WCoh* activity was broadly distributed from ∼150 s until ∼450 s with a multi-sensor prominent peak at ∼325 s when the *NI* levels of TM-1 and TM-2 were low (<0.05 bits). The elevated *WCoh* activity was globally distributed across the scalp being present in all sensors except at F7 and F8 (sensors 3, 7) in the frontal region, and P3, P4, T4, and O1 (sensors 14, 16, 12, and 18) in the parietal/occipital regions (**Figure 4C**).

The *MI* was more restricted over a 45 s period with the highest levels in the Fp1, F3, Fz, Cz, C4, T4, and Pz sensors (1, 4, 5, 10, 11, and 15; **Figure 4D**). The correlation between scalp-averaged *MI* and *WCoh* was $r = 0.68$ for the performance,

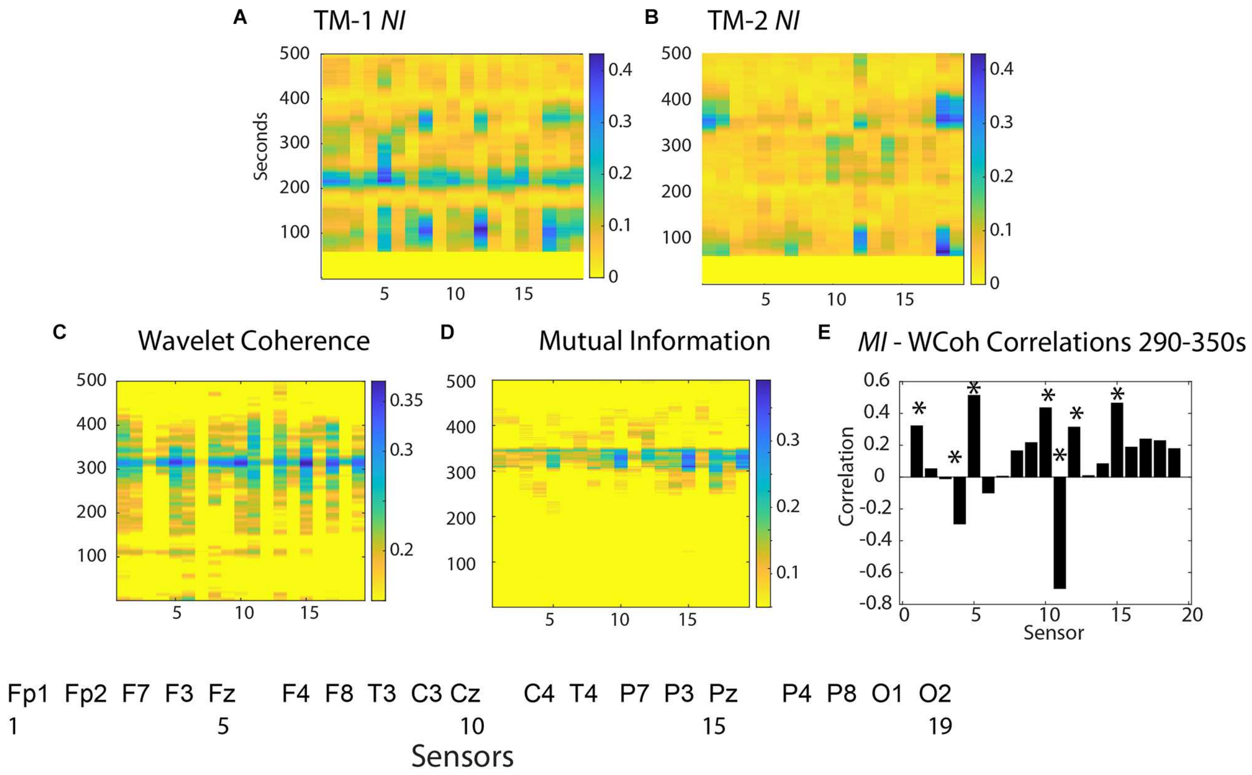

FIGURE 4
Neurodynamics of the Briefing Segment (1–500 s). The *NI* values are plotted at each sensor for **(A)** TM-1 and **(B)** TM-2. The bottom row shows surface plots for **(C)** *WCoh* and **(D)** *MI* values. **(E)** This figure plots the *WCoh-MI* correlation at each sensor for 1,290–1,350 s; correlation *p*-values < 0.01 are indicated by asterisks (∗).

and a channel-by-channel analysis showed that the highest (positive) correlations were at sensors Fz (5), Cz (10), Pz (15), and (negative) at C4 (11) (**Figure 4E**).

These results suggest that when present, the *WCoh* and *MI* levels were elevated outside the times of elevated *NI* and that they were more globally expressed than the peaks of *NI* in the Briefing.

Equipment failure

The rhythm of the team was perturbed between 1,300–1,500 s when the ventilator machine failed to initialize properly for the size and weight of the infant. During this period, the *NI* levels of both TM-1 and TM-2 increased, although not in parallel (r = -0.49, p = 0.05). The elevated levels of *NI* with peaks >0.4 bits indicated high levels of uncertainty, confirmed by statements like. "How come I can't. . . and It's not coming up like usual for non-invasive." There was also a small peak of *MI* in the profile in **Figure 5A**.

The sequence of events during this period began at 1,280 s with TM-2 focusing on arranging the breathing hoses prior to attaching them to the ventilator and the baby. These activities were associated with elevated *NI* at the P4 and O2 sensors (16, 19) (**Figures 5A,C**). When TM-2 changed tasks and began assisting TM-1, her *NI* activity rapidly decreased, and at the time when both team members' *NI* was low (∼1,340 s), the *MI* rose while they co-entered settings into the ventilator (**Figures 5A,B,D**). When the team realized the machine was not initializing properly, the *NI* of TM-1 elevated in the frontal regions and decreased in the sensorimotor regions for ∼45 s as she worked unsuccessfully to reset the machine. Around 1,370 s, the *NI* activity in the Pz and O2 sensors of TM-2 rose as she assumed control in adjusting the settings. At 1,420 s the instructors intervened to help reset the machine and by 1,500 s the Scenario continued.

Estimating the frequency, magnitude, and duration of *NI* and *MI* peaks

Scalp-averaged *NI* levels, representing periods of uncertainty vary based on their frequency, magnitudes, and durations of neurodynamic organization, while for *MI* and *WCoh*, these characteristics would apply to periods of *IBC*. The frequency and magnitude of *NI* peaks can be estimated

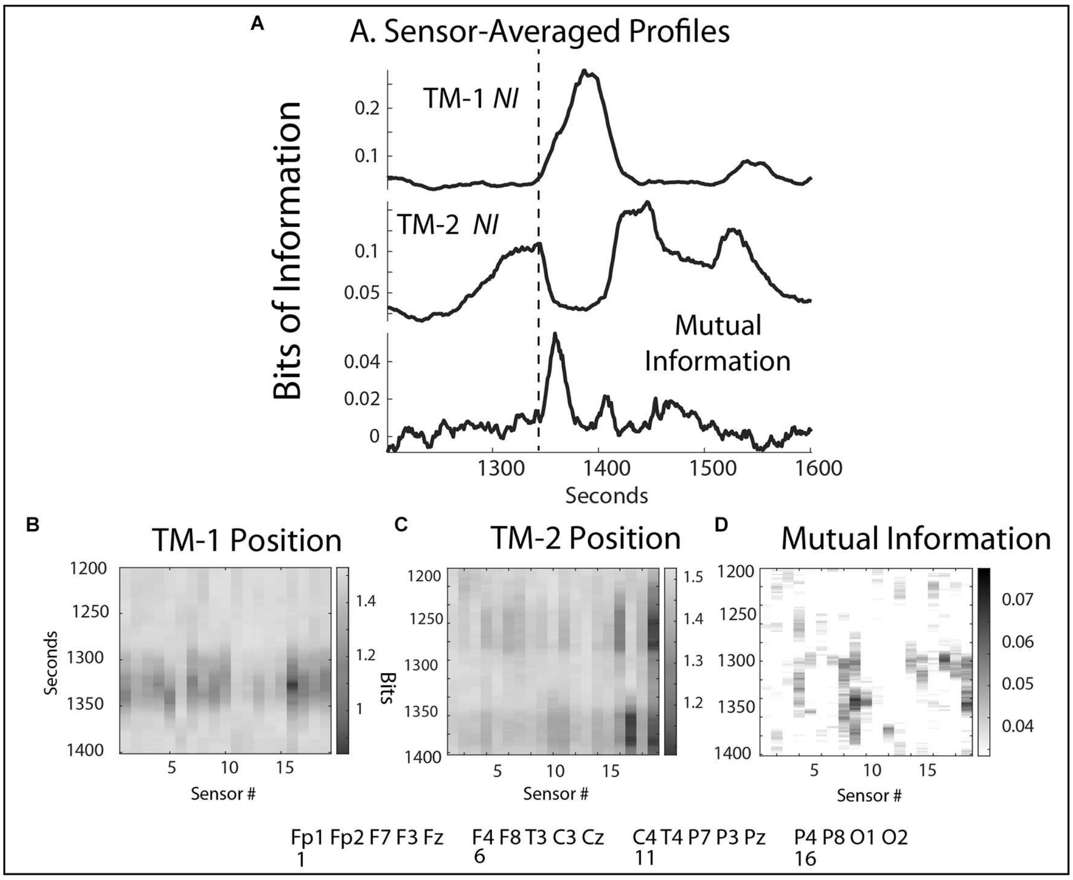

FIGURE 5
(A) Sensor-averaged profiles of the *NI* from TM-1 and TM-2, and the *MI* during the same episode. The dotted line indicates the start of the *MI* elevation. **(B,C)** The *NI* sensor profiles during the 1,300–1,500 s interval. **(D)** The average *MI* sensor profile over the same interval.

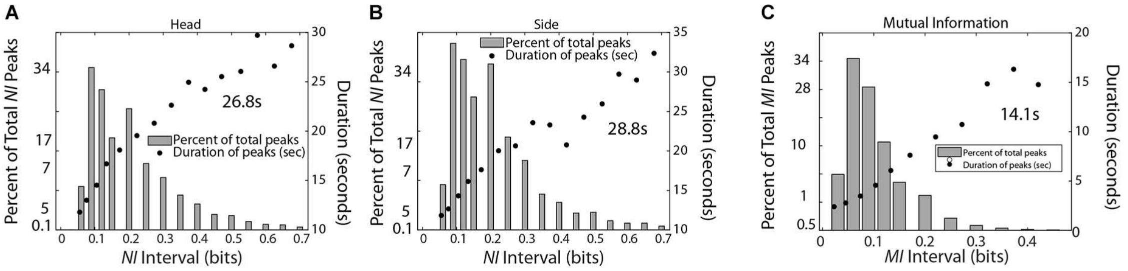

FIGURE 6
This figure shows the relationship between the magnitude and duration of the *NI* peaks for TM-1 **(A)** and TM-2 **(B)**, and the *MI* of the dyad **(C)**. The mean duration was calculated for each panel from the top five data points for **(A,B)** and the top four data points for **(C)**.

by peak-finding routines that identify peaks based on the magnitude and the relationships with their neighbors. One function is Matlab® *findpeaks.m* which identifies a peak as being a data sample that is larger than its neighbors and has a specified prominence (magnitude). In addition, the function calculates the extent (duration) of the peak at half prominence. For the data in **Figure 6**, the data was considered a peak if it was at least 0.05 bits larger than neighboring peaks. Subsequently, the peak measures were selected based on them being within the intervals ranging from 0.005 to 0.7 bits for **Figures 6A,B** or 0.005 to 0.4 for **Figure 6C**.

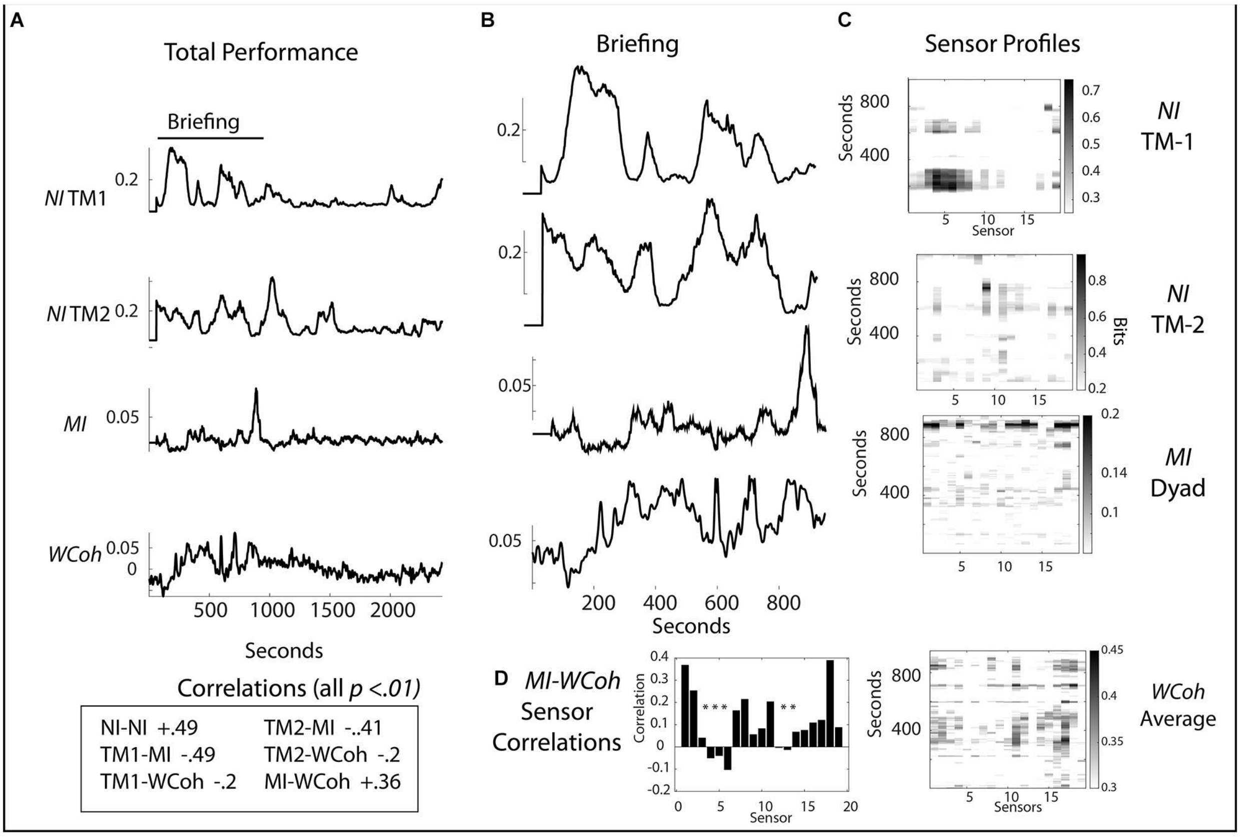

FIGURE 7
(A) Scalp averaged profiles of the *NI* and *MI* of TM-1 and TM-2 are shown for the entire performance. **(B)** Scalp-averaged profiles for the Briefing segment of the performance. **(C)** Sensor profiles are shown for the *NI* of TM-1 and TM-2, as well as for the *MI* and *WCoh* during the Briefing segment. **(D)** Correlation between *MI* and *WCoh* for the Briefing Segment; the asterisks indicate $p < 0.01$.

The data stream for TM-1 was a concatenation of the 1–40 Hz frequency bins for each sensor for both team members (total epochs = 1,288,770). The occurrence of *NI* peaks was 0.074 for both TM-1 and TM-2 while the occurrence of *MI* peaks was 0.016 for the dyad. The *MI* was chosen for this comparison as the peaks were more discrete than those of *WCoh*. The peak durations for the *NI* of TM-1 and TM-2 were 26.8 s and 28.8 s, respectively while those of *MI* were 14.5 s.

Medical flight team neurodynamics—example 2

The neurodynamic profiles of a second medical flight team are shown in **Figure 7**. In this performance the team members' *NI*-*NI* correlation was ($r = 0.49$, $p < 0.01$) and there were negative correlations between *MI* and the team member's *NI* ($r = -0.49$, $p < 0.01$ and $r = -0.41$, $p < 0.01$) for TM1 and TM2 and between *WCoh* and *NI* for the team members ($r = -0.20$, $p < 0.01$ and $r = -0.30$, $p < 0.01$). The correlation between the team's *MI* and *WCoh* values was $r = 0.36$, $p < 0.01$.

Like the first team performance, there was greater *NI*, *MI*, and *WCoh* activity in the Briefing for this team. The first *NI* segment for TM-1 (120–318 s) occurred when the dyad was developing its management plan for the infant. Then TM-1 entered the helicopter (474–800 s) to initialize the onboard medical equipment (**Figures 7A,B**). The major *NI* peak for TM-2 occurred between 955 and 1,160 s inside the helicopter after the Briefing and when patient management began. There were also minor peaks ∼732 and 793 s (**Figures 7B,C**) when TM-2 was watching TM-1 initialize the machines; this *NI* activity was centrally (C3 and C4 sensors) located (**Figure 7C**).

The major *MI* profile between 830 and 952 s occurred while the *NI* of both team members was low. This peak was more uniform than the parallel peak of *WCoh*. The broad region of *WCoh* activity from ∼200 to 600 s was visible in the *MI* profile but at a low rate. The highest *WCoh* levels were in sensors C4 (11) and P4 (16). These were also present in the major *MI*

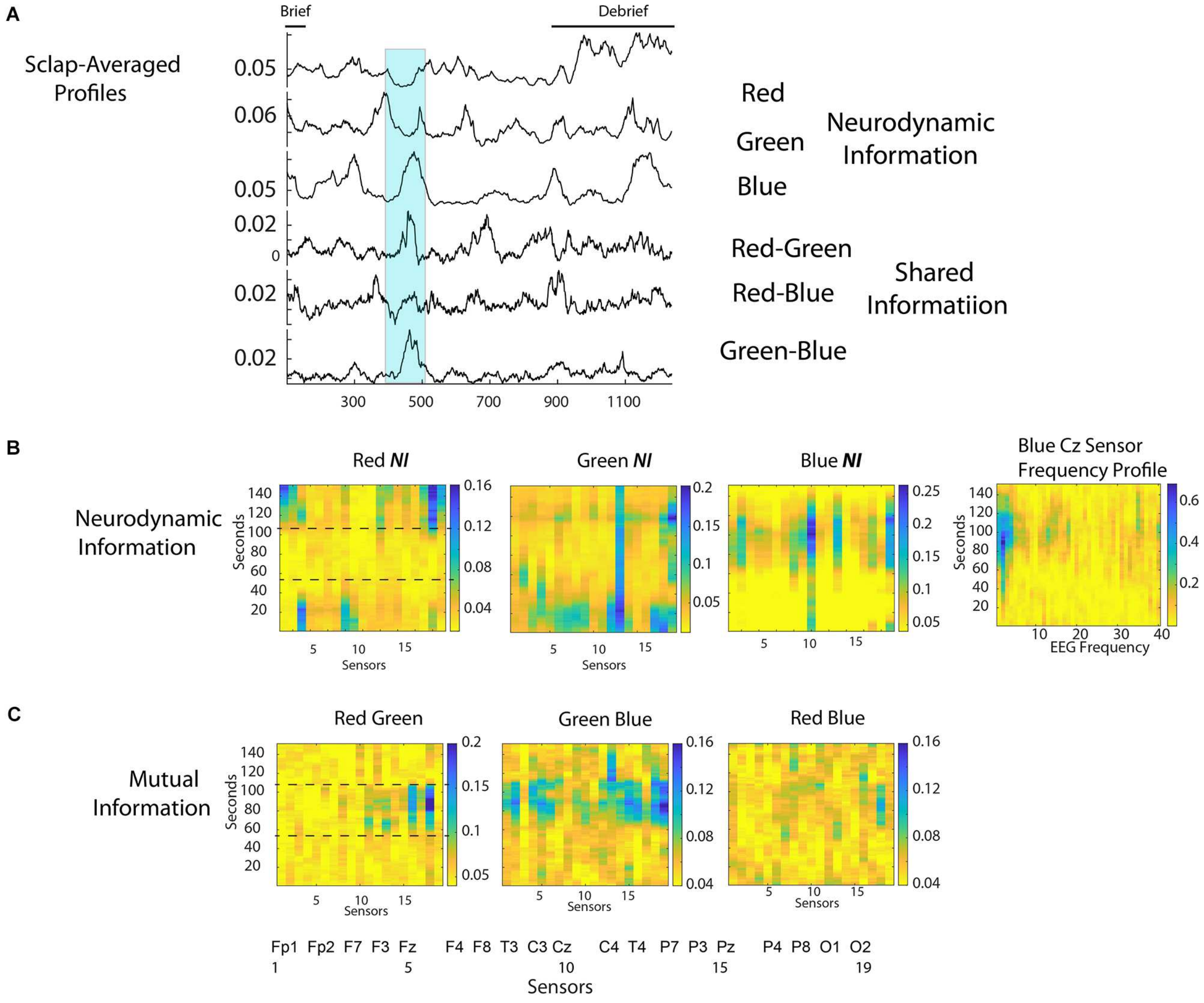

FIGURE 8
(A) The scalp-averaged *NI* levels for the Red, Green, and Blue team members, and the *MI* for the Red-Green, Red-Blue, and Green-Blue dyads respectively. **(B)** The *NI* levels for the Red, Green, and Blue team members during the 150 s interval when the patient was intubated (350 s to 500 s of the performance). The figure to the right of the first row is the 1–40 Hz frequency profile for the Cz sensor of Blue. **(C)** The *MI* for the Red-Green, Green-Blue, and Red-Blue dyads during the 151 s intubation segment.

profile along with others in the frontal [Fp1 (1), Fp2 (2), F4 (6) T4 (12), and parietal regions P3 (13), P7 (14), P8 (17)]. The *WCoh—MI* correlation was greatest at the Fp1 (1) and O1 (18) sensors.

Example 3 - three-person medical student team

The above experienced team studies showed that persistent periods of elevated *MI* and *WCoh* were present when elevated periods of *NI* were low. These persistent *IBCs* were often at sensor locations different from those contributing to elevated *NI* and were of smaller magnitude and shorter duration. There were also correlations between the mutual information and the wavelet coherence measures that differed with the sensor location.

The final example modeled the neurodynamics of three fourth-year medical students (designated Red, Green, and Blue) managing a patient with a benzodiazepine overdose. No team roles were assigned to the students, and individual activities were informally decided as the case evolved. For instance, the Blue team member calculated doses, while the Red team member led the intubation procedure with Green assisting.

The scalp-averaged *NI* values for Red, Green, and Blue were 0.039 bits, 0.052 bits, and 0.063 bits respectively, and the dyadic *MI* levels were: Red-Green, 0.054 bits; Red Blue, 0.055 bits, Green-Blue, 0.065 bits. Mutual information is used in this example as a measure of *IBC* as it provides more discrete peak profiles than *WCoh*. The scalp-averaged *NI* and *MI* profiles are

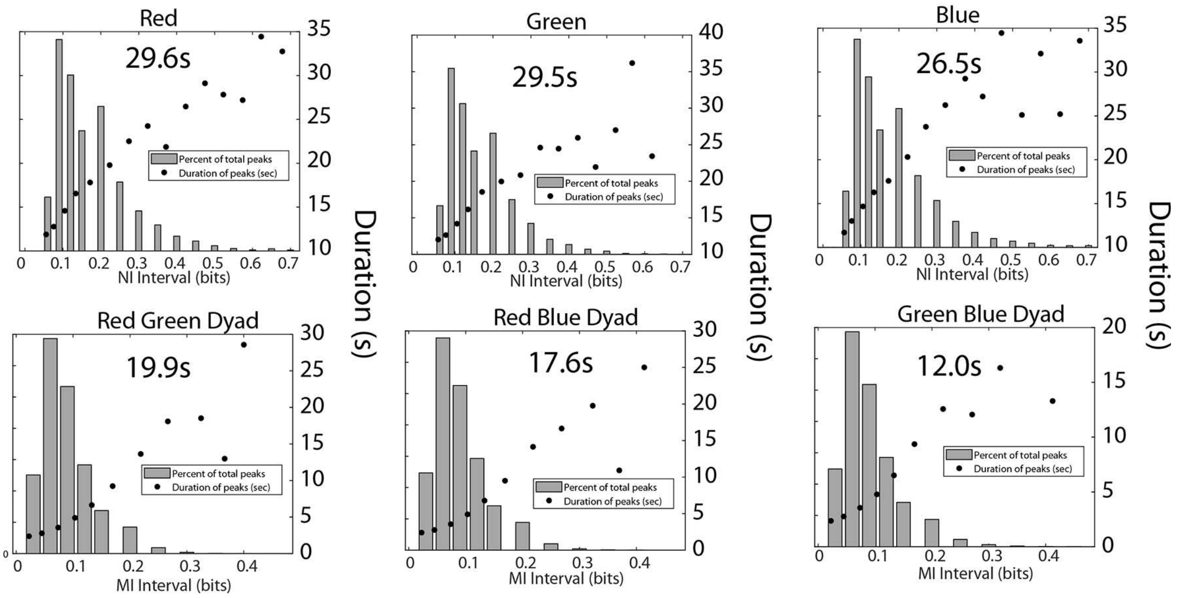

FIGURE 9
This figure shows the relationship between the magnitude and duration of the *NI* peaks for the Red, Green, and Blue team members (top), and for the *MI* peaks for the Red-Green, Red-Blue, and Green-Blue dyads (bottom). The mean duration was calculated for each panel from the top five data points for the top row figures, and the top four data points for the bottom row figures.

shown in **Figure 8A**. There was a short Briefing at the beginning, and a more extensive Debriefing at the end of the simulation than with the medical flight teams.

The most prominent *MI* peak coincided with the decision to intubate the patient and continued during the two attempts that followed (the second one was successful). This segment is shown by the highlighted region from 375 to 525 s. This 151 s segment was accompanied by elevations in *NI* and *MI* for different team members prompting the more detailed analysis in **Figure 8B**. During this 151 s period, the team was relatively quiet with Red speaking 28 s and Green and Blue speaking 40 s and 13 s, respectively.

The *NI* levels were greatest for Blue and Green when the decision to intubate was being made, and when the second attempt at the intubation procedure occurred. For Blue, there was a large peak of *NI* at the Cz sensor when the first intubation was unsuccessful and when the second attempt began. A further analysis at the frequency level indicated most of the activity was around 2–4 Hz. A similar peak of theta band activity around the Cz sensor has been associated with an interruption-based deterioration of task performance (Zikerick et al., 2021).

The lower dotted line in the first panel of **Figures 8B,C** indicates the point when the decision to intubate had been made, while the upper dotted line indicates when the second, and successful intubation procedure started. Most of the *IBC* occurred between these two lines. In other words, the greatest *IBC* occurred while the team watched/participated in the first, and unsuccessful intubation.

A final set of analyses were performed with the medical student team to estimate the frequency, magnitude, and duration of *NI* and *MI* of the team members (**Figure 9**). Consistent with the medical flight team findings in **Figure 6**, the average duration of the *NI* peaks was 28.3 ± 3.8 s while those of the *MI* was 16.0 ± 5.1 s ($t = 8.02$, $p < 0.001$).

Discussion

We have compared the neurodynamics of healthcare teams across time and brain regions during autonomous (individuals resolving uncertainty) and collaborative (wavelet coherence and mutual information) segments of activity to determine whether their dynamics were independent, interdependent, or perhaps mutually exclusive. Uncertainty, as measured by *NI*, is often a persistent state (>15 s; Stevens and Galloway, 2014, 2017, 2019), is multifractal (Likens et al., 2014), and can be decomposed into periods of shorter duration (**Figures 6, 9**). The practical benefits from obtaining evidence higher up the temporal hierarchy of cognition, and closer to observable behaviors is that the system may be amenable to change through interventions.

While both *NI*-related measures of uncertainty and inter-brain coherence have histories of operating at small time frames such as milliseconds-seconds, and while periods of elevated *NI* have been shown to persist over time frames of seconds to minutes, it was unclear how common persistent *IBC* states were during real-world task performance.

Evidence that persistent *IBC* states may exist has come from dissecting the structures of a neurodynamic organization during the continuously evolving tasks (Stevens et al., 2018b). These studies showed that continuous quantitative estimates of team *NI* could be deconstructed into those of the individual team members, and across 49 dyads performing in different teaming domains, the sum of the team member *NI* accounted for ∼90% of that of the team *NI*. There was always a residual amount (3%–15%) of information that was shared among the team members (Stevens et al., 2018a). These periods of neurodynamic mutual information were often distributed throughout the task and briefing/debriefing segments but were poorly correlated with changes in the *NI* of team members or the speech patterns of the teams (Stevens and Galloway, 2015; Stevens et al., 2017). In other words, it was not clear whether *MI* reflected inter-brain coupling in the sense of that modeled by other inter-brain measures like coherence (Bastos and Schoffelen, 2016), or whether it represented other forms of information sharing (or creation) activity among team members.

Persistent states of *WCoh* were observed in all teams in this study. The across subject scalp-averaged *MI* and *WCoh* levels of the seven performances were not correlated ($r = 0.27$. $p = 0.26$), but became so (i.e., **Figures 3, 7**) when individual teams were studied. When measured within subjects at the EEG sensor level (**Figures 4, 7**), correlations were large and significant. The *WCoh-MI* sensor-level correlations showed that although there was often a close concordance between *MI* and *WCoh* activities, they were not identical, showing both positive and negative sensor-level differences. This diversity may be from *WCoh* measures being derived from both the power and phase and *MI* being power-derived.

Nevertheless, examples of persistent (>15 s) *IBC*, both *WCoh* and *MI* derived, were found in all teams studied, and most frequently present during the briefings and debriefings where the simulation was being framed or discussed, respectively. Briefings are a critical part of simulation training as it is when the instructor gives the patient history (Petranek, 1994; Fanning and Gaba, 2007). During these times, the dyads were generally still and mostly silent. These segments may represent organizations that occur when the rhythm of the team members has been captured or entrained by task elements and/or the actions of other members, like the instructor (Adrian and Matthews, 1934; Galambos et al., 1981). As an extension, they also resemble periods of complex collective cognition while groups view emotionally-rich movie scenes (Hasson et al., 2004; Domachowski et al., 2012).

At any moment, increased *IBC*, as well as *NI* could be found in a single or across multiple sensor channels. Observationally, the number of sensors involved was related to the level of the measure. From a cognitive perspective, this would be consistent with the distributed nature of uncertainty (Grupe and Nitschke, 2013) and would represent an expansion from a local to a more global search (Lewis et al., 2019). From a network perspective, a larger and more connected network allows a perturbation to propagate across the network and results in more system amplification. At a critical point (critical amplification) a perturbation can grow to encompass a significant faction of system resources (Daniels et al., 2017). The neurodynamic magnitude and duration curves shown in **Figures 6, 9**, suggest that the critical amplifications for *NI* and *MI* may be reached ∼30 s for *NI* and half that for *MI* (∼15 s). These estimates may provide the durations within which to work for training interventions.

The most notable differences during periods of *IBC* and *NI* were their temporal dynamics. Previously we showed in a variety of teaming situations that *NI* levels elevate during periods of uncertainty, similar to those experienced by the equipment failure in **Figure 5** and the intubation attempts in **Figure 8**. Han et al.'s (2011) emphasis on uncertainty being a "subjective perception" highlights the singular nature of the state.

When measured at the aggregated scalp level there were no positive correlations between the *IBC* and *NI* suggesting that the factors elevating and resolving uncertainty are singular processes and that the involvement of increased *IBC* is minimal.

The closest example of simultaneous *IBC* and *NI* dynamics is shown in **Figure 5** during the over 3-min segment while the team tried to resolve the equipment failure. Even here, the elevated *IBC* occurred during a short gap when the *NI* decreased for both TM-1 and TM-2.

Elevated levels of *MI* were near, but not coincident with periods of *NI* (Stevens and Galloway, 2015). A similar relationship was seen in this study where the temporal difference of both *WCoh* and *MI* varied for tens of seconds away from *NI* peaks (**Figures 4, 5**) to a minute or more away (**Figure 7**). The significance of these temporal associations is unknown.

Neurodynamic information in the context of uncertainty exists, at least partially, as a conscious (i.e., to be verbalized) and observable aggregate behavior with hesitations and pauses. The possibility exists that the lack of success (to date) in linking *MI* with behaviors may mean that *MI* and *(WCoh)* are more unconscious intermediate representations between the micro and macro layers of teamwork, and are those that influence subsequent aggregate behaviors, but do not directly participate in them (Flack J., 2017).

Nevertheless, these studies show that the persistent expressions of *NI* and *MI* were not simultaneous, suggesting that it may be difficult for team members to maintain inter-brain coherence while simultaneously reducing their individual uncertainties (and vice versa).

A mechanism behind these observations might be resource allocation. While an attractive candidate for such a resource would be working memory (Huynh Cong and Kerzel, 2021), the temporal timeframe of working memory is generally much shorter than the time frames being modeled here. The models being generated in this study, however, are amenable to being studied over shorter time frames.

A second possibility is that individual and shared information represent phases of the collective decision-making process. From millisecond neuronal decision-making to crowd sourcing, collective decision-making shows bi-phasic properties (Daniels et al., 2017) with the accumulation of evidence by individuals preceding a more rapid group consensus-building phase.

During teamwork, the dynamics of individual information would represent the accumulation of evidence by each team member. In the second phase, the accumulated evidence would be integrated across team members into a decision through a more-rapid information sharing process. The attractiveness of this model is: (1) that periods of increased individual information would be temporally more prolonged than those of the shared information, and (2) much of the shared information would occur outside the times of the maximum individual neurodynamic organization, trends consistent with *NI* and *MI* dynamics.

Limitations and future studies

This is an exploratory study subject to the challenges and limitations of teams, tasks, sample sizes, and the large temporal scales over which the performances were collected. Nevertheless it provides evidence that teamwork and taskwork are not always interdependent and may be mutually exclusive when measured at scales close to observable functional outputs. It also suggests future directions. For instance, network graphs of the segments before, during, and after perturbations will provide quantitative estimates of the shifting network structures of both *NI* and *IBC*, and refined views of possible interdependencies. For *WCoh*, and particularly *MI*, similar analyses can be performed within smaller brackets of duration (and magnitude) to better understand the finer temporal dynamics leading to the critical amplifications characterizing uncertainty.

In this article, few attempts have been made to provide interpretations for the brain region spatial and connectivity expressions of *NI*, *MI*, and *WCoh* in the context of the task events. Our previous experiences suggest that the use of machine learning tools (Stevens and Galloway, 2019) might be a worthwhile approach for determining the neurodynamic relationships of *IBC* and *NI* across sensors and frequencies. The discrete nature of *NI* and *MI* peaks at a 1 s resolution would facilitate the search for these peaks/motifs.

Data availability statement

The datasets presented in this article are not readily available because the data will be available to the extent that it is allowed by the Institutional Review Board agreements. Requests to access the datasets should be directed to info@teamneurodynamics.com.

Ethics statement

The studies involving human participants were reviewed and approved by Biomed IRB, San Diego CA, and the Order of Saint Francis Hospital Institutional Review Board. The patients/participants provided their written informed consent to participate in this study. A comprehensive ethics statement is included in "Methods" Section.

Author contributions

RS and TG co-designed the study and wrote the article. Both authors contributed to the article and approved the submitted version.

Conflict of interest

RS received his PhD in Molecular Genetics from Harvard University and is Professor (Emeritus), UCLA School of Medicine and a member of the UCLA Brain Research Institute. RS was also employed by The Learning Chameleon, Inc., a for profit educational technology corporation. His recent research had focused on using EEG-derived measures to investigate team neurodynamics in complex, real-world training settings. TG was employed by, and was the director of cognitive electrophysiology research, and Facility Security Officer for The Learning Chameleon laboratory. She received her CPFDA, EFDA and CDA from Oregon Health and Sciences University in 1995 later specializing in several areas of process analysis.

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How to orchestrate a soccer team: Generalized synchronization promoted by rhythmic acoustic stimuli

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Interpersonal coordination requires precise actions concerted in space and time in a self-organized manner. We found, using soccer teams as a testing ground, that a common timeframe provided by adequate acoustic stimuli improves the interplay between teammates. We provide quantitative evidence that the connectivity between teammates and the scoring rate of male soccer teams improve significantly when playing under the influence of an appropriate acoustic environment. Unexpectedly, female teams do not show any improvement under the same experimental conditions. We show by follow-up experiments that the acoustic rhythm modulates the attention level of the participants with a pronounced tempo preference and a marked gender difference in the preferred tempo. These results lead to a consistent explanation in terms of the dynamical system theory, nonlinear resonances, and dynamic attention theory, which may illuminate generic mechanisms of the brain dynamics and may have an impact on the design of novel training strategies in team sports.

KEYWORDS

interpersonal coordination, entrainment, dynamic attention theory, tempo preference, rhythmic acoustic stimuli and cognition, generalized synchronization

Introduction

Team sport implies teamwork. This requires precise interpersonal coordination in a common timeframe, oftentimes with scarce or even without any verbal communication. In the field of dynamical systems, the behavior where two dynamical units perform differently but one in function of the other is termed as "generalized synchronization" (Rulkov et al., 1995) and is quantified by statistical interdependencies between corresponding phase spaces (Arnhold et al., 1999).

Usually, synchronization is understood as "doing the same thing at the same time" (complete 1:1 synchronization) or at least doing the same thing a time lag apart from (lag synchronization). However, modes like (2:1, 3:1, 7:8, in general m:n) are possible and realized (refer to, e.g., Hasson and Frith, 2016). In the cases, two systems with the same instantaneous frequency orbit the attractor, or one unit with an integer multiple of the frequency of the other.

However, more complex scenarios with more complex attractor topologies are also conceivable, in which the movement in the phase space of one system is coupled to that of another, so there is a functional relationship between both movements in phase spaces: $\vec{X}(t) = \vec{F}\left(\vec{Y}(t)\right)$. In this case, the temporal evolution of the two systems, i.e., their dynamics, may be completely different, but they are not independent of each other. That is, if one system is in a particular position in its phase space at a particular time, it implies that the other system is in a specific region in its phase space at the same time, i.e., the positions of both systems in their respective phase spaces are strictly correlated and, therefore, their respective dynamics. If we denote the phase spaces of each of the systems by DX and DY, the common phase space of the coupled systems is given by $DX \times DY$ (note that this space is much larger than just the sum of DX and DY). Nevertheless, there is dynamic compression (Riley et al., 2011, Araújo and Davids, 2016). Although the coupled phase space is significantly larger than both uncoupled spaces, the number of degrees of freedom of each subsystem is reduced by the coupling. The larger flexibility of each subsystem provided by the enlarged space DX × DY is reduced by the functional coupling and thus, ensures the stability of the coupled system (Gorman et al., 2017). A second ingredient for synergy is reciprocal compensation, which means that one dynamical subunit of the coupled system react to changes of the others (Riley et al., 2011; Araújo and Davids, 2016). Given that in the extended phase space the dynamics of each subunit is strongly correlated to the others, this requisite is automatically fulfilled for coupled nonidentical complex systems. Only the amount of correlations between subunits depends on the amount of coupling strength. This scenario is called "generalized synchronization" (Rulkov et al., 1995).

Transferring this mathematical picture to real-life situations of social systems means that the behavior of several interacting subjects, i.e., pursuing a common goal, can be strikingly different, but each one acts in function of the others. In this sense, the terms "generalized synchronization," "joint action," and "Synergy" (Riley et al., 2011; Araújo and Davids, 2016) are synonyms referring to the same phenomenon but are used in different scientific communities.

Prominent real-world examples of such generalized synchronization are orchestras or soccer teams. However, musicians benefit continuously from the score, the acoustic feedback of the whole ensemble and if present from the external driving of the conductor, while the coupling between teammates is much weaker and reduced to actions perceived in a limited visual sector and a restricted acoustic radius. Here, team play is promoted through clearly defined positions and functions of individual players and tactical advice from the coach. Moreover, shared intentionality might play an important role in uncertain or novel situations (Phillips-Silver et al., 2010; Araújo and Davids, 2016). However, particularly for modern association football, team play emerges largely in a self-organized manner and depends sensitively on actual game situations (Araújo and Davids, 2016). It is for this reason why we decided to take modern association football as a testing ground for a novel joint action experiment.

Precise spatiotemporal coordination is also required from the sensory-motor system. It is widely accepted that rhythmic acoustic stimuli promote motor control even in the case of patients with severe motor disorders (O'Callaghan and Turnbull, 1987; Aldridge, 1993; Thaut et al., 1993; Altenmüller and Schlaug, 2013; Ghai et al., 2018). Here, music improves particularly the precision of movement but not necessarily speed (Bernatzky et al., 2004). Specifically, when real recordings of a moving subject are provided instead of synthetic sounds, auditory stimulation improves performance in healthy subjects and patients with Parkinson's disease (Young et al., 2014; Bailey et al., 2018; Murgia et al., 2018). Furthermore, the tempo at which the rhythm is displayed can have a critical impact on athletic performance (Pizzera et al., 2017).

The positive effect of acoustic rhythms is attributed to the orderly time structure of musical rhythms, which may act like a kind of trigger for brain structures like the cerebellum that are supposed to be responsible for timing of motor actions (Molinari et al., 2003). Although other qualities of music like groove may influence this scenario (Stupacher et al., 2013), rhythmic time structure seems to play a central role in this process.

Auditory rhythms rapidly entrain extended neural networks involved in motor acts even unconsciously (Thaut, 2003) such that the time order of motor responses is guided by the rhythmic time structure of the music and coordinates the communication of different brain areas (Thaut, 2003). In addition, current studies show that acoustic motion information can directly influence executive motor functions in addition to perceptual functions (Schmitz et al., 2013), and that it can also have effects on motor functions that go beyond rhythmic adjustments (Effenberg et al., 2016; Effenberg and Schmitz, 2018). A review of physiological, psychological, and psychophysical benefits of music in sports can be found in Terry et al. (2020).

Communication, on the other hand, is inherently rhythmical (Bispham, 2006). An interpersonal interaction is not an erratic process, where information fluxes are interchanged in a stochastic manner but occurs in an oscillating fashion, which may imply the presence of a dynamic process in the development of social interactions. The observation that a communicative interaction between 3- and 5-month-old infants and their mothers occurs in cycles may indicate that such a behavior is innate and could constitute an important precursor for language acquisition (Lester et al., 1985). Thus, the oscillatory features of social interaction of 3-week-old infants have been attributed to attention/non-attention phases (Wolff, 1967). It has even been suspected that the irregularities of interaction rhythms may have a diagnostic value and may serve as a measure of neurological functioning and early detection of communicative deficiencies (Lester et al., 1985). Finally, also, a nonverbal communication between individuals, probably a driving force of self-organized team management, displays a rhythmic time structure of interactions between the protagonists (Froese et al., 2014). The current study indicates different effects of knowledge- vs. performance-based kinds of auditory real-time feedback on interpersonal coordination in a joint task (Hwang et al., 2018).

Acknowledging that (a) musical rhythms significantly improve intrapersonal coordination and (b) social interactions (verbal and nonverbal) are inherently of rhythmic nature, we ask in this contribution if, furthermore, adequate rhythmic acoustic stimuli may also promote interpersonal coordination such that a group of individuals act like a kind of a super-organism (Duarte et al., 2012; Müller et al., 2021). That this is true in terms of perfect synchronization of movement (Roederer, 1984; McNeill, 1995), or at least for similar rhythmic motor actions (Keller, 2012), is well known. However, here, we refer to more complex, self-organized systems in terms of generalized synchronization, where people may act quite differently but everyone performs in function of the others. Whether a common rhythmic acoustic timeframe also promotes interpersonal coordination in this generalized sense is unknown so far but is considered in this study. We hypothesize that an adequate rhythmic acoustic stimulus modulates the attentional level, which, in consequence, foster interpersonal coordination. Association football is chosen here solely as a convenient testing ground to probe interpersonal coordination in a self-organized fashion without major constraints by external rules. In this sense, this is not an article about soccer, although we hope it may have implications for future training strategies. *Via* a sequence of experiments, we collect sufficient materials to propose a model for brain dynamics, which is congruent with the dynamic attention theory (Riess Jones et al., 1981; Large and Riess Jones, 1999) and nonlinear resonances; thus, we hope to contribute to the field of theoretical neuroscience.

The soccer experiment

The experiments have been approved by the ethics committee of Centro de Investigación Transdisciplinaren Psicología of the Universidad Autónoma del Estado de Morelos, Mexico. All participants in the three experiments realized in this study have been clinically healthy at the time of experimentation, and none of them suffered from any overt perceptual or motor impairments.

Description of the soccer experiment

In total, 52 male and 42 female players with a mean age of 18.8 ± 2.2 and 21.6 ± 4.6 years, respectively, participated. All the participants have practiced soccer regularly for at least 10 years at least two times a week and play in district to regional German soccer leagues. They all gave their written informed consent for the study. The experimental protocol was in accordance with the ethical standards of the American Psychological Association. The players were given general information on the experiment. For instance, they knew that we aim to study the influence of "music" on soccer performance, but they did not know about the particular purpose of this project. Furthermore, the players were not aware that teammates or players of the other team were under the influence of the same or a different acoustic environment.

Randomly constituted teams of 5 players are advised to play on a reduced pitch (32 m × 40 m) with two goals (with a width of 3 m) on each side (**Figure 1A**) for a period of 30 min, which is divided in thirds of 10. Occasionally, some of the players participated several times in the experiment. The coach's instructions as well as the whole concept of this training exercise were to practice fast and efficient passing sequences. Therefore, scoring by long distance shots was not allowed. All the players were familiar with this training exercise because it is frequently used to improve precision and timing of fast pass-sequences.

One third was played without rhythmic stimulation (wR). During two-thirds of a match, rhythmic auditory stimulation (RAS) is provided collectively (cRAS) to all the players, to one team in a synchronous (Sy) condition, to the other one in a non-synchronous (nS) condition, and vice versa. "Synchronous" means that the sound is displayed phase-synchronously at 140 bpm (Simpson and Karageorghis, 2006; Karageorghis and Priest, 2012a,b) to all the players of one team. In the non-synchronous mode, the same rhythm is presented but for each player with its own tempo (119, 133, 147, 154, and 161 bpm). All games were video-recorded for posterior quantitative analysis.

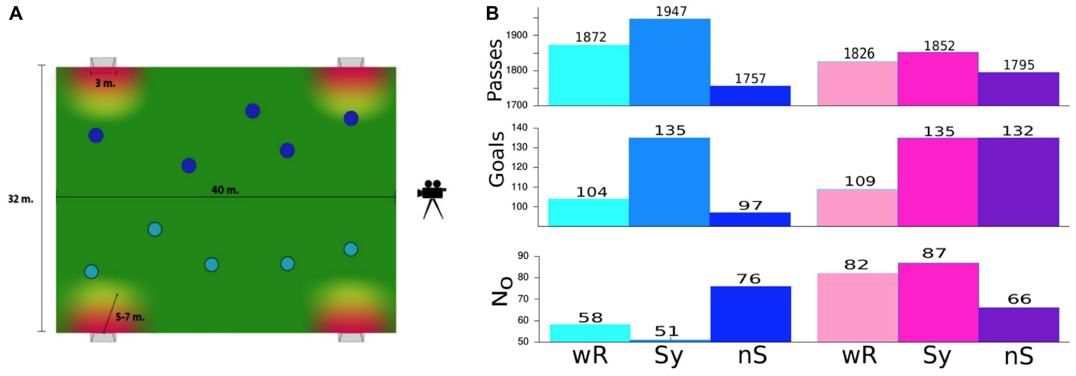

FIGURE 1

(A). Sketch of the soccer field. Scoring was only allowed within a critical radius around the goal. This is a typical exercise routine, which is commonly implemented in training sessions to improve interpersonal coordination expressed by fast and precise pass sequences or, in the terminology of this study, to improve the connectivity of a team. **(B)**. Total number of passes and goals for male (blue colors, left) and female teams (pink colors, right) were obtained under the three experimental conditions. N0 denotes the number of ball possessions of a team without any pass. wR = without rhythmic acoustic stimuli, Sy = rhythmic acoustic stimuli displayed collectively in a synchronous fashion at 140 bpm, nS = rhythmic acoustic stimuli displayed collectively but each player with another tempo.

In total, 16 matches with male and 14 matches with female teams were performed.

The chronological order of the three conditions was chosen in an almost balanced but randomized manner. Thirds without RAS has been applied 6 times at the beginning, 6 times in the middle, and 4 times at the end of a game for male teams; corresponding numbers for female teams are: 5, 5, and 4.

Because of the possible influence of individual music preferences on physiological performance parameters (Karageorghis and Priest, 2012a,b), we intended not to adopt any particular style. Instead, we derived the rhythm of the acoustic stimulus from the movement of a professional soccer player. Hence, we intend to stimulate soccer players with a football-affined rhythm, avoiding stylistic preferences to a maximal extent.

We used the time pattern of dribbling of South African offensive midfielder Teko Modise, a Premier Soccer League player from years 2008 and 2009. The temporal train of footsteps and ball contacts has been translated to a sequence of musical beats using the program "Logic Pro 9." This rhythm has been instrumented and looped with changing selection of instruments such that the resulting musical piece covers the period of one-thirds of a 30-min training session. Because of two reasons, the 140-bpm rhythm was chosen as the stimulus of the synchronous mode. First, it was reported that the performance of male 400-m racers improves significantly while hearing musical rhythms of this tempo (Simpson and Karageorghis, 2006). Setting the dribbling of several male soccer players to music further motivated the choice of 140 bpm for the synchronous condition, because we found that movement patterns are narrowly distributed around this tempo. Thus, the results of the 400-m racers and the soccer players seem to be congruent.

FM radio technology was used to ensure that both teams received the musical sequence in exact temporal synchrony (temporal difference <10 ms). The music was played back using the program Logic Pro 9. An interface (Echo AudioFire 12) was used to assign 1 of the 11 parallel soundtracks (for 10 players and one camera) to each transmitter (Sennheiser SRF 300 IEM G3-E-X). Four transmitting signals were fed to a directional antenna (Sennheiser A2003) through a combiner (Sennheiser Antenna Combiner AC 3). The players received the signals *via* a mobile receiver (Sennheiser EK 300 IEM G3 E-X) and headphones. The headphones (Adidas OMX 680) were specially designed to be used while playing sports and partially allow for transmission of ambient noise. To detect performance level, all the games were recorded with a video camera (Panasonic HDC SD100 EGK), which was located outside the playing field covering the whole pitch. Ball contacts, successful passes, and the number of goals were quantified during offline analysis.

Statistical analysis of the soccer experiment

The connectivity of a soccer team depicts the ability of the players to act together in the sense of generalized synchronization (Rulkov et al., 1995). It was introduced by the observation that nonidentical but weakly coupled chaotic oscillators may establish a nontrivial functional relationship between their dynamics, although they may not synchronize in a classical manner (doing the same thing at the same time).

Mathematically, such interrelationship is captured in a statistical sense such that instantaneous positions of the systems on the corresponding nonidentical attractors are correlated (Arnhold et al., 1999). These concepts have been generalized to many biological or social systems where a proper definition of a phase space and, hence, an adequate estimate of synchronization measures are impossible. In this spirit, movement patterns of individuals, as well as interpersonal coordination, have been frequently described in terms of dynamical systems (Schmidt and Richardson, 2008). Equivalent to nonidentical coupled chaotic oscillators, different players of a soccer team act differently, but there exists a functional relationship between players of the same team.

In the present experimental setup, effective team play is expressed by precise and fast pass sequences with a minimal number of ball contacts of each player. When the coupling between players is high, the ballcarrier knows about the position of his teammates, and his teammates try to disrupt the attacker's defense or position themselves in an open space so they can receive the pass. Thus, a fast pass sequence requires synergy in the team where all or almost all players participate and act like a super organism. Ideally, in this training exercise where fast passing sequences are required, the reception of the ball simultaneously represents the pass to a teammate (one touch play).

In this spirit, the connectivity of a team is quantified separately for each condition by the number of passes np divided by the number of ball contact ncs measured during a 10-min third $C^{Condition} = (np/nc)^{Condition}$, where "condition" refers to thirds without cRAS, the synchronous or the non-synchronous acoustical environment. Note, the number of passes between two teammates has already been used in Duch et al. (2010) in a graph theoretical context. Here, we used the quotient between the number of passes and ball context to consider the efficacy of team play.

Here, we are interested in which manner and on what amount the performance of a given team changes under the three conditions. To get rid of the absolute strength of a team in terms of connectivity and focus solely on relative changes, we contemplate relative connectivity values, which are normalized to those estimated from thirds without cRAS: $C = \frac{C^{RAS} - C^{wR}}{C^{wR}}$. In this way, the absolute strengths of the randomly constituted teams are eliminated from the statistics, and we focus exclusively on relative changes in the quality of their team play compared to the wR-condition, e.g., estimates of 0.1 connote a 10% increase in the connectivity value of a team in a Sy or an nS condition compared to the wR-mode. Therefore, although the results presented in **Figure 2** refer solely to the Sy- and nS-modes, the sign of the empirical estimates indicate additionally the comparison with the wR-condition. Of note, the difference between the relative connectivity values obtained for the Sy and nS settings can be understood as a kind of effect size. Significance values are estimated by nonparametric Mann-Whitney-Wilcoxon rank test.

To create **Figure 3**, we proceed with the same philosophy as before, *viz.*, we compare the performance of the same team under different conditions. To this end, we counted the number of times when the scoring difference of a team under different conditions is at least D (**Figure 3B**) and, further, how many times the scoring difference has been observed in favor of one or the other condition, e.g., comparing wR- and Sy-condition $kwR = 6$ times with a scoring difference of at least 1 was quoted in favor of wR and $kSy = 20$ times in favour of Sy (**Figure 3B**, upper panel). If one assumes the null hypothesis that scoring differences between conditions appear with equal probability $pwR = pSy = 0.5$, one might estimate the probability that our results occur by chance using the binomial distribution

$$P = \binom{kwR + kSy}{kSy} pwR^{kwR} pSy^{kSy}.$$

For the abovementioned number of comparisons of the wR and Sy-conditions, this probability is amazingly small with $p = 0.003431$.

To corroborate the significance of our experimental results obtained for connectivity values and scorings, we also applied a parametric test framework probing whether the average values of the samples are statistically equivalent. To this end, we conducted first a two-sample student t-test on the relative connectivity values shown in **Figure 2** (refer to **Supplementary material**). Thus, we reproduce almost quantitatively the results obtained by the nonparametric Mann-Whitney-Wilcoxon rank test (**Figures 2C,F**).

For the scoring statistics, we conducted a paired t-test where pairs of scoring rates are formed for the same team playing under different conditions (see **Supplementary Figure 2**). Again, we reproduced almost quantitatively the results obtained for the nonparametric statistics, namely, in the present case, the estimates for the binomial distribution (**Figure 3A**).

Results of the soccer experiment

In the first step, we considered two quantities commonly used for evaluating the dominance of a soccer team, namely, the number of passes played and goals scored. As a third quantity we introduce N0, the number of ball possessions of a team without making any pass and serves as an indicator of team segregation.

For the male teams, we obtained for the Sy-condition highest number of passes and goals and simultaneously reduced number of ball possessions without a pass, while for the nS-mode all the three statistics indicate poorest performance. Notable is the high increase in scores of about 30% in the Sy-condition as well as the 30% increase in N0 for the nS-condition for the male teams. For the female teams, the number of passes is highest for the synchronous and lowest for the nonsynchronous conditions, although the difference between the conditions is less pronounced. Scoring was notably higher in both conditions with cRAS (again about 30% higher than without RAS), while

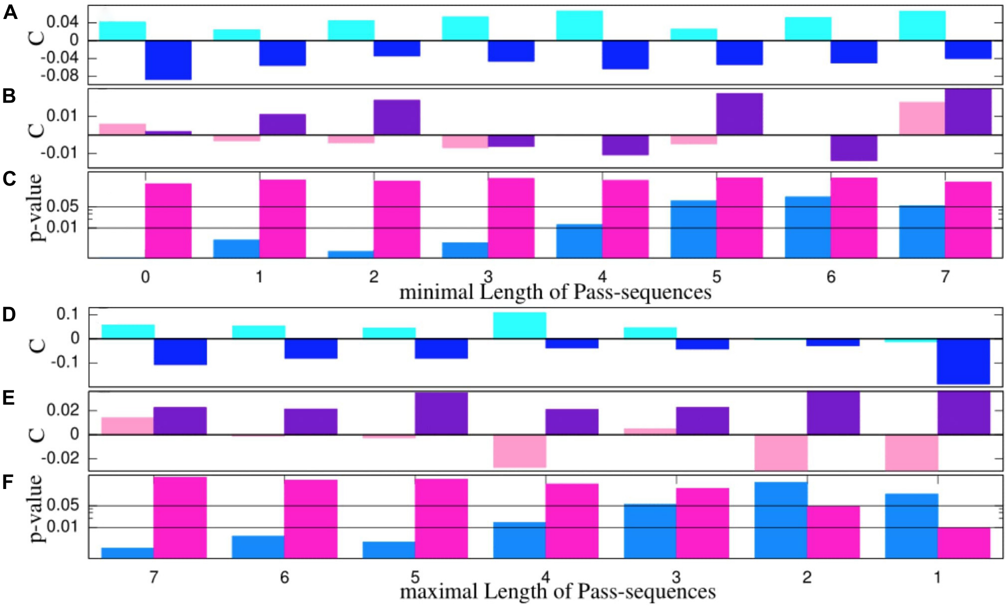

FIGURE 2
(A,B,D,E) Medians of relative connectivity values normalized to those estimated from the thirds without cRAS. Blue colors refer to male and pink color to female teams. Light pink/blue refers to the Sy-condition and dark pink/blue to the nS-condition. Panels **(C,F)** display the *p*-value on a logarithmic scale estimated by Mann-Whitney-Wilcoxon rank test, which provides the probability that the samples obtained for the Sy- and nS-modes stem from the same distribution. Horizontal black lines in panels **(C,F)** indicate the 1 and 5% significance level, respectively. The abscissa in panels **(A–C)** and **(D–F)** mark the minimal (maximal) length of pass sequences considered.

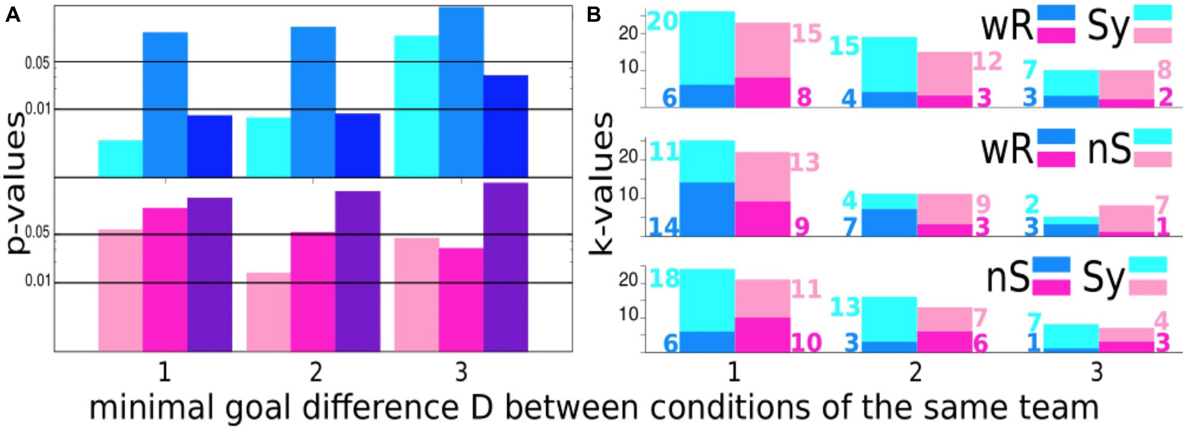

FIGURE 3
(A) Probabilities that the scoring differences D of a team playing under different conditions occur by chance according to the binomial distribution for the male (upper panel) and female teams (lower panel) on a logarithmic scale. We compare the setting without rhythmic stimulation (wR) with the synchronous displayed condition (Sy) (light pink/blue), wR- vs. the non-synchronous acoustic stimulation (nS-) condition (pink/blue) and the Sy-condition vs. nS-condition (dark pink/blue). Horizontal black lines indicate the 1 and 5% significance level. **(B)** Number of times where the scoring difference was in favor of one or the other condition. Each panel shows the comparison of two conditions for different values of the scoring difference D. Again, blue colors denote results for the male and pink colors for the female teams. The color code for the settings wR, Sy, and nS is indicated in the right border at each panel. wR = without rhythmic acoustic stimuli, Sy = rhythmic acoustic stimuli displayed collectively in a synchronous fashion at 140 bpm, nS = rhythmic acoustic stimuli displayed collectively but each player with another tempo.

team segregation seems to be highest in the Sy-mode and lowest in the nS-condition. The reduction of N0 in the nS mode in comparison with the Sy-mode is again about 30%.

Although this is not the main focus of this study, we also compared the performance between genders. For this purpose, we normalized the numbers in **Figure 1** according to the teams' playing time (the total number of matches was different for the male and female teams). A corresponding table is included in **Supplementary material**. Here, it can be seen that the indicators of the female teams are consistently higher than those of the male teams for all the three indices.

In summary, we obtained consistent results for the male teams, indicating a trend clearly in favor of the Sy- and lowest performance of the nS-condition, while the results for the female teams are puzzling and inconsistent. However, the results presented in **Figure 1** lack any objective significance test and are, thus, not conclusive.

As a step toward more substantiated statistics, we evaluate the interpersonal coordination or the connectivity of a team. Here, we are interested in which manner and on what amount the performance of a given team changes under the three conditions. For this reason, here, we refer to relative connectivity values with respect to the condition without cRAS. In this way, numerical estimates do not depend on the actual strength of the randomly constituted teams, but positive/negative relative values provide the percentage of the improvement/worsening of a team playing under the condition of cRAS with respect to the condition without music. The results are summarized in **Figure 2**.

The median relative connectivity values estimated for the male teams in the Sy-condition are systematically higher than those estimated without cRAS and are, in turn, above the medians estimated for the nS-condition in all the cases shown in **Figure 2A**. If all pass sequences are considered (the two very left boxes in panel A), we will obtain a p-value of $8.7x10^{-4}$ for distinction of the Sy and nS-modes for the male teams. In that case, we observe an increase of 4% for the Sy-mode and a decrease of about 8% for the nS-mode. Only if exclusively short pass sequences are examined ($n < 3$), the connectivity values derived for the synchronous mode decrease to values slightly below the estimates obtained for the wR-condition (**Figure 2D**). Including solely pass sequences with at most three passes, the p-value is slightly above the 5% level, and it grows further for shorter sequences (**Figure 2F**). The reason for this drop in significance level could be that a player, contrary to the instructions and the aim of the training exercise, takes the opportunity to dribble to one of the goals, possibly with the support of his teammates. Otherwise, given the specific training situation, it is more conceivable that this could also indicate a significant loss of connection between the players.

Also, if one dissects merely large pass sequences with $n > 5$ (**Figures 2A,C**), we notice a loss of significance. Again, one may question if in general sequences with more than 5 passes played on a reduced field within teams of only 5 players reflect synergy in a team. It is more conceivable that straight collective attacks are played quickly in approximately 3 to 5 passes. Otherwise, the opposing defense might intervene its forward action such that the team gets forced to move backward and the global stability of the synergic dynamical state gets disturbed (Riley et al., 2011; Araújo and Davids, 2016), which leads to decrease in connectivity index during the subsequent phase of reorientation before it may increase for even longer pass sequences. Consistently, for $n = 7$, the p-value already decreases again. Of note, the negative trends of the indicators when playing with RAS are expectable, acknowledging that the headphones conspicuously diminish the acoustical coupling between players. Naturally, such disturbances are absent in the mode without RAS. Thus, the clear positive results for the Sy-mode for the male teams are more surprising.

The results summarized in **Figure 2** pinpoint that the male teams are significantly more connected and less segregated in the synchronous mode, and that a non-synchronous cRAS promotes team segregation and impedes interpersonal space-time coordination. For the female teams, on the other hand, the results are puzzling and qualitatively different. The connectivity values obtained for, the Sy-mode and the nS-mode take occasionally positive and negative values in an irregular fashion without showing any systematic trend, and the significance values are far outside the 5% limit, which depicts a striking gender difference in interpersonal coordination under the experimental conditions of the soccer experiment.

"Winning is not everything, it's the only thing" (Overman, 1999). This famous quote, attributed to the American football player and coach Henry Russel Sanders, must be acknowledged, although the aesthetic appearance of a well-coordinated team play is pleasing to the eye. Therefore, we probe in the next step whether the scoring differences shown in **Figure 1B** are significant.

For the male teams, we detect a highly significant scoring advantage of at least one or two goals in the Sy-condition in comparison to the wR-mode and even more pronounced for the comparison of the Sy- and nS-conditions. For $D \geq 3$, the probability that goal differences between the Sy- and nS-condition will occur by chance is still less than 5%. From 8 events, 7 have been denoted in favor of the Sy-condition. Naturally, elevated scoring differences D occur less frequently, which influences the estimation of p-values for small samples. Hence, significance by trend decreases with increase in D. However, considering that for soccer games the scoring statistics is highly noise contaminated (Heuer et al., 2010; Tolan et al., 2013), which makes the outcome of a soccer game hard to predict (Skinner and Freeman, 2009), and that the participants have not practiced with headphones beforehand such that our results reflect the spontaneous reaction of the cRAS, we believe that the high significance of the goal statistics obtained for the male teams are astounding.

Like in the case of the connectivity index, for the female teams, no significant difference between the synchronous and non-synchronous conditions could be detected for any D shown in **Figure 3**. Counter-intuitively, for the comparisons with the wR-condition, p-values decrease with D. For$D \geq 3$, both p-values are below 0.05. In view of the results presented in **Figure 2**, the increased scoring rates of the female teams under acoustic stimulation might be provoked by decreased efficient team play and decreased coupling between players probably due to the obstructive influence of the headphones. The last statement is backed up by the observation that the number of goals per game decreases on average with the quality of the football league. (refer to, e.g., www.fussball.de).

We also tested for the influence of fatigue along the three thirds but did not measure any significant effect. To this end, we compared the connectivity values as well as the scoring rates and probe statistical equivalence by Mann-Whitney-Wilcoxon-rank test. No significant difference between the first and the last thirds could be detected. Furthermore, we repeated the statistical evaluation by employing parametric tests (namely the Student t-test and the paired t-test. For further information refer to **Supplementary material**) and obtained quantitatively similar results.

We conclude that the results presented so far are not due to a particular philosophy of the data analysis (parametric vs. nonparametric statistics) but reflect a genuine effect of (a) an improved interpersonal coordination under an adequate acoustic environment providing a common time frame, (b) a pronounced correlation between the connectivity index and the scoring rate for the male teams and (c) according to our knowledge a, so far, unobserved gender difference.

The question remains to be "which mechanism is responsible for the highly significant effect for the male teams and for which reason the female teams react so differently?". It is well-known that there is an elevated functional connectivity between the auditory cortex and the motor cortex in human brains (Thaut et al., 1999; Chen et al., 2008; Altenmüller and Schlaug, 2013), which leads to entrainment effects of motor skills such that, e.g., locomotion gets spontaneously modified (Molinari et al., 2003). This finding seems to be independent of physical body features (MacDougall and Moore, 2005).

It was shown that a more similar movement dynamics facilitates prediction of future actions (Vesper et al., 2011), and it has been pointed out that joint action is promoted if subjects share similar features of their motor dynamics (Stowinski et al., 2016; TsanevaAtanasova, 2016). Hence, a possible explanation of the above scenario is that the motor entrainment in the Sy-condition causes a more similar movement dynamics of the 5 players, while in the nS-condition where each player perceives its personal acoustic pacemaker, one may suppose that motor entrainment provokes larger spreading of, e.g., stride frequencies. What if the tempo adjustment of the Sy-mode is not appropriate for female players? Then, it cannot be expected that the rhythm displayed at 140 bpm will promote team play, and that the stimulus might have a disturbing influence on interpersonal coordination. Of note, this argument holds solely if motor entrainment, provoked by the acoustic rhythm displayed at 140 bpm, promotes assimilation of the moving frequency of male but not female subjects. We tested for this effect in a first follow-up experiment.

Notwithstanding, it is doubtable if this principle applies to association football in a strict sense where players must adjust their motor performance according to the game situation they encounter and, may be the most important, according to the movement of the players of the opposing team and only partly to that of their own teammates. Their behavior is context-dependent (Turvey, 2007; Araújo and Davids, 2016). One may also observe that a defending player synchronizes his motion to a certain extent with that of the ball-leading one, especially in areas close to their own goal, to block the opponent's way. Accordingly, this follow-up experiment clearly demonstrates that no assimilation of stride frequencies occurs because of motor entrainment (refer to **Supplementary material**). Hence, motor entrainment does not provide a possible mechanism capable of explaining the results observed in the soccer experiment. We provide empirical evidence for this conclusion in **Supplementary material**.

The Stroop experiment

The acoustic rhythm neither presents some feedback nor is directly related to the performance of soccer players. Instead, it provides a common time frame for organizing efficient interpersonal coordination. It influences the level of attention and promotes anticipation skills and adaptation of own actions (Riess Jones et al., 2006; Keller et al., 2014). It was shown that the sensory motor system is involved in selective attention and anticipatory mechanism (Schubotz, 2007; Morillon et al., 2014), which in turn fosters interpersonal coordination because it supports the fine-tuning of self-actions with those of interaction partners (Riess Jones et al., 2006; Keller et al., 2014). Such rhythmic modulation of attention level (Riess Jones et al., 1981; Large and Riess Jones, 1999; Trapp et al., 2018) draws a dynamical picture of attention driven by, e.g., external acoustic stimuli (Escoffier et al., 2010; Bolger et al., 2013). Thus, a preferred tempo of acoustic rhythms improving (motor) cognition (Keller et al., 2014) would provide a strong indication for a resonance-like behavior of brain dynamics (Large, 2008) and affords a plausible explanation of the outcomes of the soccer experiment.

If the attention dynamics of the players could be synchronized, e.g., *via* synchronously displayed acoustic stimuli, this would positively influence the joint action of the players (Sebanz et al., 2006). The prerequisite for this is that acoustic rhythms can modulate the level of attention. To obtain empirical evidence that supports these theoretical considerations, we designed and conducted a follow-up experiment.

Description of the Stroop experiment

To probe whether the level of attention can be influenced by acoustic rhythms and to explore whether we detect some tempo dependency, we used a modified version of the Stroop interference task known as the color-word matching Stroop task (Zysset et al., 2001). In this version of the Stroop test, the cognitive part is slightly more complicated, and the response is just by pressing a button. The participants had this test in the acoustic environment of the same rhythm used for the soccer experiment, but now we probe three different tempos, namely, 100, 140, and 180 bpm, while measuring the reaction time Δt of the participants.

In total, 60 male and 77 female subjects with mean age of 23.7 ± 3.5 and 23.5 ± 4.1, respectively, participated and performed a variant of the Stroop test already used elsewhere (Masataka and Perlovsky, 2013) while hearing the acoustic rhythms used in the soccer experiment with headphones. For each participant, we applied the rhythm with solely one tempo to avoid the influence of a probable memory effect.

The task consisted of 3 blocks. All of them were composed of two runs with 48 trials each. Both runs comprised 24 congruent and 24 incongruent randomized trials. The first run was named "neutral test" and worked as a control to estimate the reaction time of the participants for perception, reading, and pressing the response button. The second run, named "Stroop test," was presented to estimate the Stroop effect, which is meant to represent the effect elicited by the incongruence of the features. The first and third blocks were presented without music, and the second block was performed while listening to the rhythm used in the soccer experiment displayed at one of the following tempi: 100, 140, or 180 bpm. Hence, the dependent variable was the reaction time, and the independent variable was the musical tempo. For the data analysis presented here, only incongruent trials were considered. For each tempo, a group of men and women was recruited. After the first analysis, we sorted the female participants according to the phase of their menstrual cycle, which was obtained by forward-counting, and we repeated the analysis separately for each group. The number of participants for each phase of the menstrual cycle is shown in **Table 1**.

TABLE 1 Number of male and female subjects participating in the Stroop-experiment under the influence of different tempi.

Tempo/ bpm	Male	Female			
		Menstrual	Folicular	Ovulatory	Lutea
100	20	10	2	4	8
140	20	10	2	6	7
180	20	10	5	3	8

The female participants are listed separately for different stages of the menstrual cycle.

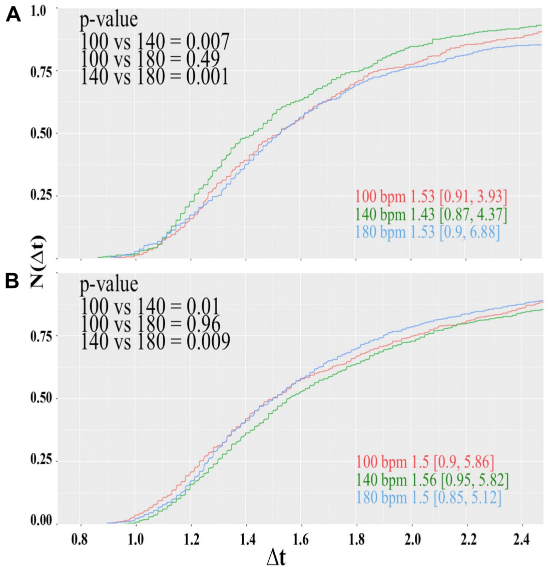

FIGURE 4
Cumulative distributions of the reaction times of the color-word matching Stroop task while the participants were under the influence of the acoustic rhythm used in the soccer experiment displayed at 100 (red), 140b (green), and 180 bpm (blue). Panels **(A,B)** show the results for the male and female subjects, respectively. Inserted numbers indicate the median value and borders of the 95% confidence interval. Furthermore, *p*-values for the pairwise comparison of the different samples according to the Mann-Whitney-Wilcoxon-rank test are indicated.

The quantitative comparison of the reaction times obtained for the different settings is performed by Mann-Whitney-Wilcoxon-rank test. Besides the estimated p-values, the median and borders of the 95% confidence interval of the samples are also reported to provide information about the effect of size. More details about the Stroop experiment can be found in the last part of **Supplementary material**.

Results of the Stroop experiment

The results obtained for the reaction times of the participants are summarized in **Figure 4**.

For the male subjects (**Figure 4A**), we observe a clear preference for 140 bpm. The difference of the central values of the distribution obtained for 140 bpm and the others is of the order $\Delta t \approx 0.1$ s, which connotes a decrease in the reaction time of about 6.5% and is highly significant. For the female subjects, on the other hand, the performance at 140 bpm is worse, but no clear difference between 100 and 180 bpm can be observed. By trend, reaction times obtained for 180 are slightly shorter given that the distribution for 100 bpm has a much longer tail toward large Δt; however, statistically, the central values of the distributions (**Figure 4B**) are indistinguishable.

A preferred tempo of the acoustic stimulus for male brains resembles a resonance-like behavior. It seems that neuronal circuits, which are responsible for attentional tasks, get entrained by the activity of neuronal ensembles that are processing acoustic information, a clear indication of the dynamical nature of attentional processes (Large and Riess Jones, 1999; Large, 2008). This behavior is like that of coupled, nonlinear oscillators where one dynamical unit triggers the response of the others (Vicente et al., 2008). If such resonance-like behavior is a generic principle for male brains, why do we not observe similar effects for female subjects albeit their preferred tempo might differ from 140 bpm. This last conjecture is based on indications that functional networks of acoustic information processing are different for men and women (Corsi-Cabrera et al., 2007).

A possible explanation for this incongruity might be that neural activity is altered during the menstrual cycle (Solís Ortiz et al., 1994). The influence of sexual steroids in different areas of the cortex where estrogenic receptors moderate acetylcholine production, which in turn is involved in selective attention processes (Corsi-Cabrera et al., 2007), might provoke that hormonal changes during the menstrual cycle influence the outcome of the Stroop experiment. Furthermore, it was documented that women, within the first days of their menstrual cycle, show a significantly improved performance in the Stroop task than those within days 21 and 22 (Hatta and Nagaya, 2009), which correspond to the luteal phase. To probe such hormonal dependency, we divided the group of female participants according to their actual phase of the menstrual cycle (refer to **Table 1**). The results obtained for women in the menstrual, follicular, ovulation, and luteal phases are shown in **Figure 5**.

Under the new selection criteria, the picture changes drastically. The women in the menstrual phase represent the largest group of the female participants with 10 subjects for each tempo; hence, the results shown in **Figure 4B** are somewhat biased by this group. Like in the former case where all female participants form one single group, the performance at 140 bpm is worse, but now the cumulative distribution for 100 and 180 bpm has the same shape. The best performance is now observed when the rhythm is displayed at 100 bpm, although the difference between 100 and 180 bpm is only in trend. The median values differ by only 0.03 s and turns out to be insignificant.

The women in the folicular phase, on the other hand, show a slight preference for 180 bpm and worse performance when the rhythm is displayed at 100 bpm. The subjects in the ovulation phase again seem to prefer 100 bpm, and slowest reaction times are observed at 140 bpm. The effect size for this group is considerably large. Differences between central values of adjacent distributions are slightly larger than 0.2 s and connote an effect of about 14%. However, the results of both groups should be taken with caution, because the number of participants for each tempo of 3 to 6 subjects is considerably low (**Table 1**).

Finally, the group in the luteal phase had 8 to 9 participants for each tempo. For this group, a clear preference for 140 bpm can be seen, while distribution functions obtained for 100 and 180 bpm are statistically equivalent. The central value of the cumulative probability distribution for 140 bpm is about 0.16 s lower than the values observed for the lower and faster tempos, yielding an effect of 11%, which proves to be highly significant.

We acknowledge that the group size when different phases of the menstrual cycle are distinguished is by far not sufficient for drawing definite conclusions. Therefore, we propose to repeat the whole Stroop experiment in a future study in a more controlled manner. Only women between 20 and 30 years old that do not take any contraceptive drugs, do not conduct any kind of hormone therapy, and are regular in the sense that their menstrual cycle does not vary more than plus/minus 1 day should be considered to improve the control of hormonal balance. With this inclusion criteria, a sufficiently high number of participants for each tempo should be recruited. Furthermore, to obtain a more detailed picture of a possible resonance phenomenon, more tempi should also be probed.

However, even the results presented in **Figures 4**, **5** provide at least a strong indication for a kind of entrainment of attention processes with a preferred tempo of the acoustic rhythm. In addition, this tempo preference seems to depend on the hormonal balance of the subjects. Given that this parameter was not controlled in the soccer experiment, one cannot expect to find a tempo preference for the female teams.

Discussion

The empirical data gained from the soccer experiment show a pronounced response of the male teams to a certain rhythmic acoustic stimulus. A successful play in terms of scoring rate could be significantly enhanced, a result that correlates strongly with the connectivity measure introduced by us. At the same time, it seems at a first glance that females do not show any sensitivity to their acoustic environment in terms of the connectivity of their team play or their efficiency regarding scoring rates. At this point, two questions arise: the first is “why does a certain rhythm, or rather a rhythm displayed to all teammates at a certain tempo, improve or worsen the team play of the male teams although one might expect that there is no interference between listening to music and performance on the soccer field? The improvement observed for the synchronous setting is surprising given the obstructive influence of earphones while doing team sport, because it hinders the acoustical coupling between teammates. In this context, it was shown that the intention of the game opponent can be inferred from the sound of his motor actions. This information can be used as a guide for one’s own reactions (Camponogara et al., 2017). Such

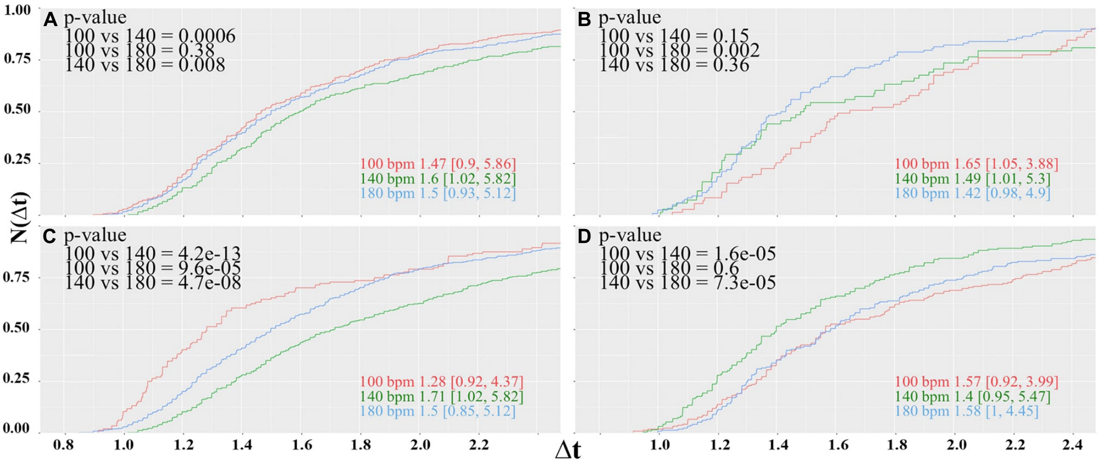

FIGURE 5
Same as Figure, but now the female subjects are divided according to the actual phase of their menstrual cycle. Cumulative distributions of reaction times of the female participants in the **(A)** menstrual, **(B)** folicular **(C)** ovulatory and **(D)** luteal phase

action-related auditory cues (Cañal-Bruland et al., 2018) are widely suppressed when RAS is supplied. The second question is "why do the female teams behave strikingly different?". Seemingly, the results obtained for synchronous and non-synchronous do not differ statistically for women.

The results of the Stroop experiment, however, imply that the same resonance-like mechanism is active in the male and female brains. An acoustic rhythm displayed at an appropriate (preferred) tempo enhances the level of attention of subjects, which in turn positively influences interpersonal coordination. This result is gender-independent, which indicates that the principal mechanism of men and women is the same as could be expected beforehand. However, in addition, we encounter a striking dependence on hormonal balance, an uncontrollable parameter in the soccer experiment. Hence, the Stroop experiment provides a consistent explanation for the initially surprising result. The increased connectivity of the male teams in comparison to the non-synchronous setting and, as a consequence, the improved scoring rate can be attributed to the improved attentional level provoked by the synchronously displayed rhythm at 140 bpm, the preferred tempo for the male subjects in the Stroop experiment. Furthermore, it was impossible to control for the seemingly strong dependence of the preferred tempo on the hormonal level in the soccer experiment. Based on these results, it cannot be expected that the female teams will show any effect.

However, is it tenable to think of a resonance phenomenon of the brain dynamics? Its hierarchical structure supports the hypothesis of a resonating brain. Sets of few neurons form microcircuits, which are assembled to larger modules up to the constitution of macroscopic structures like the thalamo-cortical system. All these hierarchically intertwined modules are feedback loops, which are oscillating with their preferred rhythm (Buzsaki, 2006). A hierarchical organization has also been observed for oscillations of the functional brain network where delta rhythm modulates activity of faster frequency bands up to the gamma band by phase-amplitude locking (Lakatos et al., 2008, 2013). In this context, it is important to note that cortical activity is entrained to acoustical rhythms (Fujioka et al., 2009; Large et al., 2015). Delta activity may synchronize to acoustic stimuli (Will and Berg, 2007; Stefanics et al., 2010; Gomez-Ramirez et al., 2011; Nozaradan, 2014), which in turn trigger theta rhythms (Will and Berg, 2007) as well as activity in the alpha, beta- and lower gamma-bands (Will and Berg, 2007; Gomez-Ramirez et al., 2011). Cyclic modulation of alpha activity is associated with effective social coordination (Naem et al., 2012) and attention processes in a way that alpha activity acts as an inhibitor of distracters while gamma activity focuses on attention (Ward, 2003).

Hence, it seems that the brain operates generally in a rhythmic mode, with frequency preferences in terms of nonlinear resonances of dynamical units acting on different scales of space and time where low frequency activity may control the dynamics measured in higher frequency bands, which in turn are responsible for a variety of cognitive processes and attention. Delta activity may act as an instrument for attentional selection (Schroeder and Lakatos, 2008). In this picture, entrainment of neuronal oscillating activity (Lakatos et al., 2008; Nozaradan, 2014) may also directly induce an improvement in cognitive skills (Xing et al., 2016) without involving motor areas. Thus, the brain can be understood as a finely orchestrated assembly of dynamical units able to resonate.

Musical stimuli have an immediate influence on attention and cognitive abilities (Lakatos et al., 2008, 2013), which may result in a kind of attentional entrainment that decays only gradually (Trapp et al., 2018). Importantly, the reaction time in a highly demanding visual attention task varies notably when subjects hear the same acoustic stimulus at different tempi (Amezcua et al., 2005; Husain et al., 2002) and may modulate the perception of physical exertion (Martins-Almeida et al., 2015; Patania et al., 2020). Therefore, it is also conceivable that appropriate adjustment of the tempo of an acoustic rhythm is imperative in the present context, as could be substantiated by the Stroop experiment.

In this spirit and given that the maximal time lag by which the synchronously displayed rhythm is perceived by the players is below 10 ms, it seems that the common acoustic framework not only elevates but also synchronizes the level of attention of the subjects and equivalently promotes interpersonal coordination of the whole team in a self-organized manner. In this dynamical picture, synchronized attention dynamics provides a common ground for joint action (Sebanz et al., 2006) and promotes synergy in a team (Riley et al., 2011; Araújo and Davids, 2016).This explains the significant positive effect measured for the male teams and simultaneously the initially counter-intuitive results for the female teams, which are possibly provoked by our finding that the preferred tempo of the female subjects apparently changes during the menstrual cycle.

At this point, we like to underscore that the results obtained for women in different phases of their menstrual cycle are still not conclusive but should be understood as a first experimental indication for this finding. To provide a substantial empirical finding, the number of well-selected participants in each group and for each tempo should be increased notably, which goes beyond the scope of this study and will be treated in a forthcoming study. However, this viewpoint is supported by the fact that functional brain networks during music perception are strikingly disparate between male and female subjects (Corsi-Cabrera et al., 2007; Flores-Gutiérrez et al., 2009). Therefore, it is plausible to assume that preferred frequencies of active functional networks are notably different between genders because of dependency on hormonal balance (Solís Ortiz et al., 1994; Corsi-Cabrera et al., 2007; Hatta and Nagaya, 2009). However, we should also take into consideration that the 140 bpm of the synchronous setting was optimized for male 400-m racers; thus, in principle, it could be inadequate for women.

The results obtained so far clearly indicate that (a) the connectivity and, hence, efficiency (goal statistics) of a soccer team is improved in the Sy setting compared to the nS condition, and that (b) the attention level of the male teams improves when exposed to the rhythm displayed at 140 bpm. However, it might be interesting to investigate in future experiments whether the positive influence of cRAS can compensate for the reduced acoustic coupling between players (Camponogara et al., 2017; Cañal-Bruland et al., 2018). Thus, although the results of the male subjects in the Stroop experiment clearly indicate a resonance phenomenon, it would be interesting in future experiments to have a team play in the Sy condition against a team without acoustic stimulation (wR).

Besides the theoretical considerations of underlying brain dynamics, this study might have additionally a major practical impact on training strategies. The long-term effect of music therapy, even for a short-lasting therapy duration (Thaut et al., 1999; Altenmüller and Schlaug, 2013), provides an optimistic projection in this direction, leading toward the conclusion that interpersonal coordination may also improve in a competing situation of a league game if a team is accustomed to practice systematically in an appropriate acoustic environment. The last statement holds to be true not only for aesthetic aspects of team sports but also quantitatively in terms of scoring rate.

Conclusion

We discover a basic mechanism of interpersonal coordination and succeeded to integrate the observed phenomena into an established theoretical framework, namely, the dynamic attention theory in combination with a resonance-like tempo preference of rhythmic acoustic stimuli. Furthermore, we unravel a, so far, unknown gender difference; additionally, our findings may open new avenues for development of novel training strategies in team sports.

It is all about rhythm!

Data availability statement

The datasets presented in this study can be found in online repositories. The data of the soccer experiment are available at: https://github.com/antonietamg/Soccer_experiment_data, the Stroop experiment can be found in: https://github.com/antonietamg/Stroop_Data_2022, and the stride frequency experiment are located at: https://github.com/antonietamg/Rhythm_and_Sync_Data.

Ethics statement

The studies involving human participants were reviewed and approved by Ethic Committee of the Autonomous University of Morelos (UAEM), Nu. of Folio 240918-05. All participants were informed about details concerning the execution and evaluation of our experiments and all participants were aware that they could stop participating at any time without any consequences. They gave their written consent to their participation and in case of minors; we got the permission of the legal guardians. None of the experiments conducted by us put any participant in danger or got harmed. For instance, the soccer players followed a well-known training scheme they are used to doing in their practice sessions while the Stroop experiment is a common attention test in psychological studies.

Author contributions

MAM formulated the initial idea of this research and the first experiment. MAM, AF, MH, AE, and GS designed the first experiment. AE and GS acquired the technical equipment. MAM and AF conducted the first experiment and revised the video tapes. MH produced the acoustic stimuli. IG-M and MFM designed the stride frequency experiment. IG-M conducted the stride frequency experiment. MAM and MFM conducted the corresponding statistical analysis and wrote the manuscript. MFM and AM-G designed the Stroop experiment and made the Figures. AM-G conducted the Stroop experiment and did the respective statistical analysis in accordance with MFM. MC-C contributed essentially to the interpretation of the results. MAM, MC-C, AM-G, and MFM constructed the psychological model. All authors revised the manuscript and took part in the discussion of the results.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fnhum.2022.909939/full#supplementary-material

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In touch: Cardiac and respiratory patterns synchronize during ensemble singing with physical contact

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Musical ensemble performances provide an ideal environment to gain knowledge about complex human interactions. Network structures of synchronization can reflect specific roles of individual performers on the one hand and a higher level of organization of all performers as a superordinate system on the other. This study builds on research on joint singing, using hyperscanning of respiration and heart rate variability (HRV) from eight professional singers. Singers performed polyphonic music, distributing their breathing within the same voice and singing without and with physical contact: that is touching each other's shoulder or waist. The idea of singing with touch was motivated by historical depictions of ensemble performances that showed singers touching each other. It raises the question of the potential benefit of touch for group performances. From a psycho-physiological point of view, physical contact should increase the synchronization of singing coordination. The results confirm previous findings on synchronization of respiration and HRV during choir singing and extend those findings to a non-homophonic musical repertoire while also revealing an increase in synchronization in respiration during physical contact. These effects were significant across different frequency ranges. The effect of physical contact was stronger when all singers were singing in comparison to the partial ensemble. Importantly, the synchronization could not be fully explained by the singing action (i.e., singing the same voice, or singing vs. listening) or by the standing position or touch. This finding suggests a higher level of organization of all singers, forming a superordinate system.

KEYWORDS

joint action, HRV, respiration, singing ensemble, polyphonic music, supersubject, hyperscanning

Introduction

Joint human interaction requires highly synchronized behavior to achieve individual or group goals (Valdesolo et al., 2010; Konvalinka et al., 2011). Interactions have often been investigated in dyadic constellations (Konvalinka and Roepstorff, 2012), for instance, to better understand unidirectional effects (Goldstein et al., 2017), sender-receiver relations (Montague et al., 2002), leader-follower relations (Konvalinka et al., 2011; Sänger et al., 2012), and also to investigate ongoing, real-time, mutual coordination (Tognoli et al., 2007; Lindenberger et al., 2009). Importantly, interacting entities are not only separate units but are coupled (Konvalinka and Roepstorff, 2012). Systematic research on the coordination of larger groups is still in its beginnings and has often occurred in a musical context (Babiloni et al., 2011, 2012; Müller and Lindenberger, 2011, 2019; Müller et al., 2013, 2018a,b, 2019; Vickhoff et al., 2013; Glowinski et al., 2015; Osaka et al., 2015; Hemakom et al., 2016, 2017; Kaneshiro et al., 2016). To gain knowledge about complex human interaction, investigating musical performance might be ideal because of the inherent variety of individual and group goals. In ensemble music, musicians have to adapt their individual voices within the musical context and in relation to the interpretation of the other voices. This requires a constant adaptation of own and joint goals in terms of tempo, intensity, and timbre to arrive at a joint and coherent musical interpretation of a piece.

Coordination between musicians performing in ensembles has been shown on different levels. For example, on the behavioral level, head movements cue musical structure and different performance practices (Glowinski et al., 2015; Bishop et al., 2019). Interestingly, coordination has also been demonstrated on the level of physiological processes that are less obvious, for example, respiratory and cardiac responses (Müller and Lindenberger, 2011; Vickhoff et al., 2013; Hemakom et al., 2016, 2017; Müller et al., 2018a, 2019), and brain responses (Lindenberger et al., 2009; Babiloni et al., 2011, 2012; Sänger et al., 2012; Müller et al., 2013, 2018b, 2019; Osaka et al., 2015), suggesting that coordination extends to implicit processes. Neural and physiological oscillations have shown inter-person and intra-person couplings and have revealed an underlying complex network structure within and between brains (Müller et al., 2018b, 2021). On the one hand, it is conceivable that these network structures reflect specific roles of individual musical performers, and on the other hand, a higher level of organization of all performers as a superordinate system (Noble, 2012) or superorganism.

Our study builds on previous research on joint singing, using hyperscanning (e.g., simultaneous recording of several psychophysiological measures from several participants; see Müller et al., 2021) of respiration and HRV from an ensemble of eight singers. Studies have demonstrated increased phase synchronization of respiration and HRV during singing in comparison to a resting condition (Müller and Lindenberger, 2011) or breaks during a concert (Hemakom et al., 2017). Phase synchronization was higher in a choir during singing in unison, in comparison to singing a canon in parts (Müller and Lindenberger, 2011). However, singing in canon resulted in the coupling of singers singing the same voice,[1] revealing a modular structure based on the musical score (Müller and Lindenberger, 2011). Coupling between singers has been shown to be higher than between members of the audience (Hemakom et al., 2016), suggesting that the act of singing results in more synchronized physiological processes than simply perceiving music.

However, synchronized respiration in monophonic and homophonic music may not seem very surprising, given that singing is uniquely related to a characteristic use of respiration. The exhaled air vibrates the vocal cords, and the controlled adjustments of the resonance apparatus and articulators result in different timbres (Kang et al., 2018). Breathing has to be coordinated with the musical progression and musical phrase endings or breaks, offering suitable time points for breathing. Further, as respiration and heart rate are coupled physiological signals (e.g., suppression of heartbeat during exhalation), synchronized breathing can also result in synchronization of HRV. Indeed, strong relations between synchronized breathing during singing and coupled HRV have been demonstrated, when comparing three conditions (Vickhoff et al., 2013): singers hummed a tone without breathing instructions and the tone did not include musical structure, or singers sang a hymn at a specific tempo related to 0.2 Hz, or, finally, they sang a mantra with breathing instructed at 0.1 Hz in relation to the musical structure (breaks). During humming, singers showed inter-individual differences for specific periodicities within respiration and HRV. While singing the hymn, respiration and HRV synchronized at 0.2 Hz (as well as at 0.05 and 0.1 Hz). Singing the mantra resulted in the strongest synchronization across conditions with a peak at 0.1 Hz. In other words, singing the same musical voice coordinates breathing which, in turn, results in systematic synchronization of respiration frequencies. However, turning back to the results of Müller and Lindenberger (2011), singing songs in parts and canons resulted in synchronized respiration and HRV on several oscillation frequencies, suggesting that synchronization is not limited to frequencies inherent in the musical structure.

We follow up on previous studies on singing with the goal of replicating and extending results on synchronization of respiration and HRV. A professional ensemble performed polyphonic a-cappella music from the Renaissance, which can be considered one of the most complex and intricate forms of European multi-part music. Each voice typically has an identity of its own: specifically, the beginning and end of phrases often overlap between voices and do not happen

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[1] With voice, we are referring to the individual voices of a polyphonic composition, e.g., soprano, alto, tenor, and bass.

simultaneously. The voices are woven into each other, blending into a continuous stream of a musical sound. To achieve an uninterrupted flow of musical sound, professional choirs make use of distributed breathing, avoiding breathing at the same time (see Supplementary Figure 1 depicting no inter-subject synchronization of the audible breathing onsets in our data sets). Our first research question was, can we replicate the synchronization of respiration and HRV even when the sung music is polyphonic, i.e., when the phrases of the musical voices are mostly independent of each other?

We further extended the study to include a feature that is often shown in pictorial representations of singing and other music ensembles from the fourteenth to seventeenth centuries. Singing ensembles are displayed standing close and even in an embrace and with physical contact (Tammen, 2013). An investigation of historical sources resulted in a large corpus of these depictions (Wald-Fuhrmann et al., 2014; Max Planck Institute for Empirical Aesthetics, 2017). Embraces between members of a chapel seem to be unusual. They were required to cross the upper arms in front of their breast, above or below the mantle. Also, almost no other historical sources exist that corroborate that singing with physical contact was actually a common feature of the performance practices of that time. However, in the context of Christian sacred music, some reasons for physical contact are plausible: For example, singing from only one music book that was placed on a large note stand made standing close and eventually physical contact unavoidable (Figures 1A,B). In addition, physical contact might benefit keeping time: The mensural notation system in which this repertoire was written down did not provide any visual cues for temporal coordination across voices in polyphonic compositions. The four or more voices were notated in individual blocks, e.g., the upper left quadrant showed notation for the Superius, upper right Altus, lower left Tenor, and lower right Bassus (Figure 1C). In modern notation, voices are ordered in horizontal lines, and bar lines are used as a visual cue for temporal alignment (Figure 1D). In most historical depictions, physical contact is applied either by putting the hand on the shoulder or head of the singer in front, or the arm around the shoulder of a neighboring singer, i.e., contact is established between singers of the same as well as of different voices. Sometimes, the position of the pointing finger invites the interpretation that part of the contact was to periodically tap on the shoulder to provide an external pacemaker in the absence of a conductor, an aspect of historical performance practice for which at least scarce literary sources exist (Frobenius, 1972). Given the complexity of polyphonic music and its traditional notation, however, additional means for temporally coordinating the singers' actions might have been used. If an effect of touch on singers and singing were to be shown, this could indicate that physical contact might have been one such additional means. It should be noted, however, that instead of a literal understanding of the depictions, several other interpretations are conceivable, too. The hand on the shoulder might symbolize the unifying forces of musical performance, the group identity of the clergy, the harmonious character of their performance, or an act of consecration (Tammen, 2013).

From a psycho-physiological point of view, physical contact can indeed be expected to increase the synchronization of singing coordination on several levels, for example by increasing the synchronization of motor behavior (Lagarde and Kelso, 2006; Harrison and Richardson, 2009; Sofianidis et al., 2012), which in turn might enhance beat perception (e.g., Phillips-Silver and Trainor, 2007), or by vibrotactile support of timbre and pitch perception (e.g., Russo et al., 2012). In general, it has been shown that tactile stimuli activate the auditory cortex, suggesting that physical contact might alter auditory perception (e.g., Schürmann et al., 2006). With regard to respiration and HRV, static hand holding increased inter-personal coupling in the context of pain research (e.g., Goldstein et al., 2017). In addition, indirect effects might benefit synchronization. For example, touch benefits emotional communication and increases social bonding (e.g., Hertenstein et al., 2006; for reviews see Gallace and Spence, 2010; Morrison, 2016).

In our study, we compared the synchronization of respiration and HRV of professional singers performing polyphonic music from the Renaissance in three standing conditions: (i) Modern performance practice, distributed across the stage, each singer using their own music stand (no touch, standing far: *ntf*); (ii) Standing close, all singers using one large music stand, with physical contact *via* putting the hand onto the neighboring singers (touch, standing close: *tc*); (iii) Standing close, using one music stand, but without physical contact as a control (no touch, standing close: *ntc*; see Figure 2). We applied a hyperscanning approach to measure respiration and HRV from all eight singers at the same time (Müller and Lindenberger, 2011). To avoid comparisons of single measures and their underlying potential confound, we repeated measures on three days in a balanced order. We predicted a stronger synchronization during singing in comparison to a resting condition, and an additional increase in synchronization during touch while singing. Further, we expected to see synchronization effects at different frequency bands of HRV.

Materials and methods

Participants

The ensemble consisted of six men and two women in addition to a male conductor with an age range of 29–45 years. The singers had 4–34 years of professional singing experience and were particularly experienced in Renaissance music, having sung such music for 3–30 years. The ensemble has a changing cast with, over the years, some members participating on a regular basis and others more infrequently. The singers in this
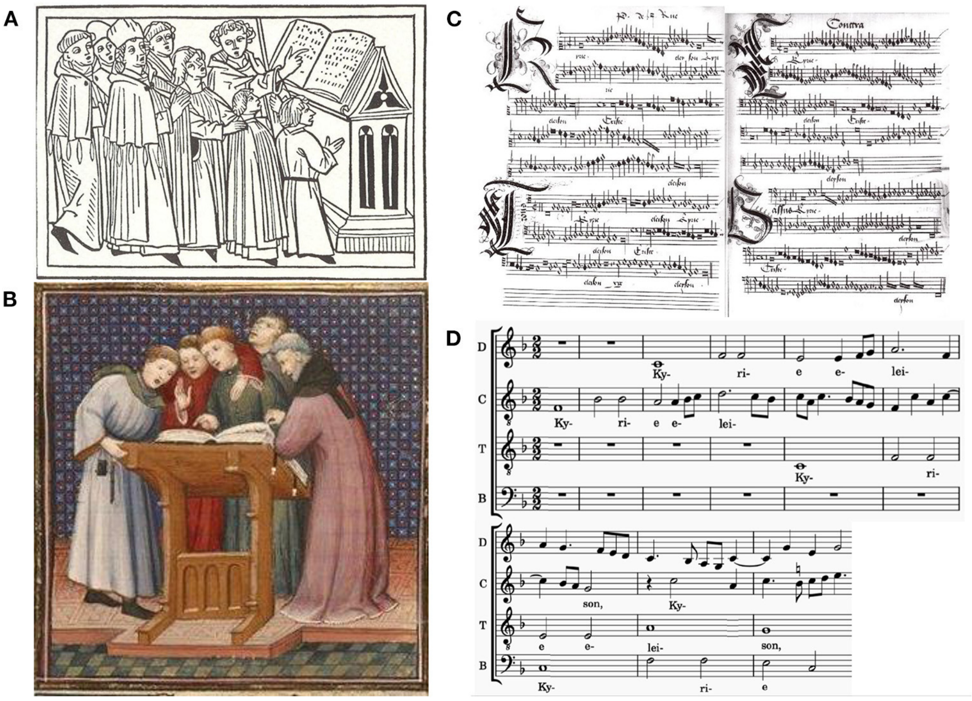
FIGURE 1
(A) Initial to the entry "Cantus," Rodericus Zamorensis, Speculum vitae humanae, 1468; **(B)** Miniature at the beginning of Psalm 150, Grande bible historiale complétée (1395–1401), Maître du livre d'heures de Johannette Ravanelle, Paris, Bibliothèque nationale, Ms. fr. 159, f. 277v. (source: gallica.bnf.fr / BnF); **(C)** Mensural (Historic musical) notation of Pierre De la Rue: *Missa Almana, Kyrie* (before 1518) with the four voices separately in blocks, upper left, upper right, lower left, lower right (source: Brüssel, Koninklijke Bibliotheek van Belgie, ms. 9126, 58v und 59r.); **(D)** Modern notation of the same composition with the four voices in horizontal lines and the vertical indicating time.

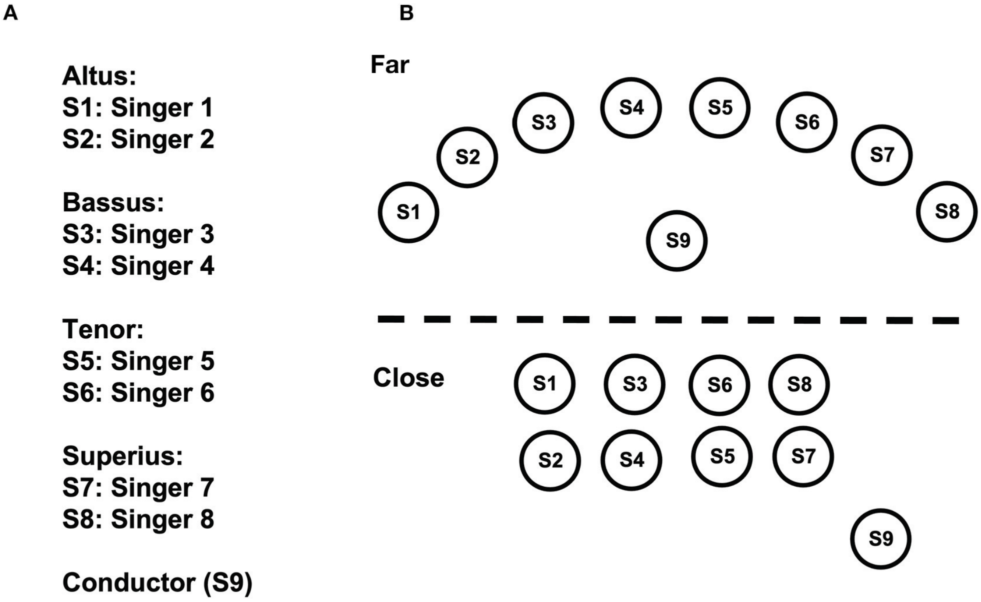

FIGURE 2
Configuration and assignment of the ensemble. The singers were placed in three standing conditions, with *ntf* relating to the depicted "far" positions, and *ntc* and *tc* to the close positions (see Methods for more information). **(A)** Assignment. **(B)** Configuration of the singing ensemble.

study had been performing in the ensemble for a range of 1.5–12 years, and the conductor had taken the lead of the ensemble 12 years before our study commenced. The ensemble volunteered to participate in our study while they were on tour in Germany in May 2016 in exchange for accommodation expenses and a fee for their time. Data collection spanned three complete days.

Apparatus

Physiology was acquired with a Brainamp ExG system. Three electrodes were placed on the chest of each of the eight singers in order to measure their heart rate: the first medially over the first rib between the two collarbones, the second left-lateralized just below the last rib, and the ground electrode next to the second but more medial. Respiration was measured by picking up the breathing extraction of the chest using a respiratory belt (BP-BM-10 by BrainProducts). This belt was placed on the upper chest but below the cables of the heart rate electrodes. No abdominal signal was recorded because particularly in singing both chest and abdomen breathing are coupled. The sampling rate at data acquisition was 1,000 Hz. Additionally to HRV and respiration, electroencephalography was acquired from two singers and the conductor, and motion capture was taken from the head of each singer and the conductor. The audio was recorded for all pieces. These additional measures are not part of the current analysis.

Stimulus material

Pieces were selected from the repertoire of the ensemble: Josquin Desprez: the motets *Virgo prudentissima*, and *Tu solus qui facis mirabilia* (only second part: *D'ung aultre amer*); Guillaume Du Fay: *Kyrie*, *Gloria*, and *Agnus Dei* from the *Missa Ecce ancilla domini/Beata es Maria*. Pieces were arranged into three sections. In some cases, pieces or parts of pieces were repeated to reach sections of a minimum duration of 6 min. The sections contained (1) the two motets of Josquin in the order *Virgo prudentissima, D'ung aultre amer, Virgo prudentissima*; (2) *Agnus Dei* I, II, III, I, II; (3) *Kyrie* I, II, *Gloria*. In the following, we refer to the three sections as (1) *Motets*, (2) *Agnus Dei*, (3) *Kyrie/Gloria*. Modern notation was used to accommodate the choir's usual practice and to keep a high performance level.

For the most part, the chosen musical pieces represented the typical polyphonic style of the time, i.e., with imitative and free polyphonic passages and alternations of two-, three-, four-voices sections. However, the chosen musical pieces also included some homophonic passages (e.g., in *D'ung aultre amer*).

Procedure

The day prior to data collection, the ensemble visited the laboratory concert hall to get instructed, practice the three standing positions, and give informed consent. Each of the three days started with setting up the participants with the physiology equipment, and on the second and third day, three of them with an EEG cap. The duration of preparation took 70–85 min. Then, as a practice run, all pieces were sung once in the same serial order (*Agnus Dei, Motets, Kyrie/Gloria*). This was followed by the experimental blocks, one for each of the pieces, and an additional resting control block on days one and three. However, due to technical problems we only collected two musical sections on day one (*Kyrie/Gloria* was excluded). In each of the experimental blocks three standing positions (conditions) were completed: (a) modern tradition: each singer with their own music stand, positioned in a semicircle, conductor centrally (*ntf*); (b) historical tradition: all singers gathered close together in two rows of four, singing from one monitor (on which the sheet music was digitally presented instead of a music stand), having no physical contact, conductor placed next to them (*ntc*); (c) historical plus physical condition: Same as in (b) but with the physical contact of arms and hands (*tc*). Positions for ensemble members were marked on the floor for accuracy across repeated measures. However, as keeping positions and the physical contact points in (c) constant turned out to be too challenging and exhausting for the singers, they were allowed to adjust according to their needs on days two and three.

Due to technical problems, we diverged from the planned Latin Square of the serial order of pieces slightly but kept it for the standing positions. As a result, the serial positions of the pieces on day one were: rest, *Agnus Dei, Motets*; on day two were: *Motets, Kyrie/Gloria, Agnus Dei*; and on day three were: *Kyrie/Gloria, Agnus Dei,* rest, *Motets*. In total, we recorded 30 trials, based on eight musical blocks, two resting blocks, and each block in three standing conditions. Data collection took place from about 10 am to 4 pm. A longer lunch break was included and the ensemble indicated whenever they needed additional rest.

Data preprocessing

We adjusted the length of each trial recording to be 360 s by clipping the end of the recording. Using BrainVision Analyzer software (Brain Products GmbH, Gilching, Germany), the QRS complexes in the ECG signals were identified and used for the determination of heartbeat locations. Once the timing of beats was determined, an instantaneous Heart Rate (HR) signal was created. Thereafter, HR and respiration signals were down-sampled to 10 Hz. Spencer's 15-Point Moving Average method was used to smooth a time series in order to highlight the underlying structure. Thereafter, mean and trends were removed from the HR and respiration data, and then the data were normalized to a unit variance. Note that heart rate variability (HRV) is determined by the time between heartbeats, known as RR intervals.

Data analysis

The data analysis was strongly guided by an earlier study on synchronization of respiration and HRV of singers (Müller and Lindenberger, 2011). To investigate phase synchronization, we applied an analytic or complex-valued Morlet wavelet transform to compute the instantaneous phase in the frequency range from 0 to 1 Hz in 0.005-Hz steps. The complex mother Morlet wavelet, also called the Gabor wavelet, has a Gaussian shape around its central frequency f:

$$w(t, f) = (\sigma^2\pi)^{-1/4} exp(-t^2/2\sigma^2) exp(3/2\pi jft), j = \sqrt{-1}$$

where σ is the standard deviation of the Gaussian envelope of the mother wavelet. The wavelet coefficients were calculated with a time step of 1, leading to a time resolution of 0.1 s.

In order to identify the phase relations between any two subjects/channels during the task, the instantaneous phase difference $\Delta\phi_{mn}(t, f)$ was computed from the wavelet coefficients for all possible subject/channel pairs. Three different synchronization measures were obtained from these phase differences for frequency of interest (FOI) f_i. Initial power spectral density (PSD) analyses showed no clear peaks and therefore provided no guideline for selecting relevant FOIs. We therefore decided to use the same ten frequencies as in an earlier study (Müller et al., 2018a), which were chosen with regard to the fixed relation between frequencies (1:2, 1:3, 2:3, etc.): 0.025, 0.05, 0.075, 0.10, 0.125, 0.15, 0.20, 0.25, 0.30, and 0.40 Hz. These ten frequency components practically cover the whole frequency spectrum of breathing and HRV during singing.

We obtained the Phase Synchronization Index (PSI), which is defined as the mean vector length of the angular dispersions of the phase difference in a complex space. It was calculated by $\mathrm{PSI}_{\Phi}(f_i) = \left|\left\langle e^{j \cdot \Delta\Phi^k(f_i)} \right\rangle\right|, j = \sqrt{-1}$, where $\Delta\Phi^k = \mathrm{mod}\left(\Phi_m^k(f_i, t) - \Phi_n^k(f_i, t), 2 \cdot \pi\right)$, which is the phase difference with instantaneous phases of these two signals across k data points during the task condition; $\Phi_m^k(f_i) = \arg\left\{y_m^k(f_i)\right\}$ and $\Phi_n^k(f_i) = \arg\left\{y_n^k(f_i)\right\}$. The PSI is most widely used in research applying electroencephalography (Müller et al., 2013; Hemakom et al., 2017; Borovik et al., 2020) but also with respiration and HRV (Müller and Lindenberger, 2011).

With the estimates of the phase difference between pairs of signals (participants), it is then possible to ascertain how long the phase difference remains stable in defined phase angle boundaries by counting the number of points that are phase-locked at a defined time window. Analogous to Müller and Lindenberger (2011; see also Kitzbichler et al., 2009), we divided the range between $-\pi/4$ and $+\pi/4$ into two ranges, one marked the negative deviations in the range between $-\pi/4$ and 0 (coded with "−1," see blue color in Figure 5), the other the positive deviations in the range between 0 and $+\pi/4$ (coded with +1, see red color in Figure 5). Phase differences beyond these ranges represent non-synchronization (coded with "0," see green color in Figure 5). By counting the relative number of phase-locked points within the range $-\pi/4$ and $+\pi/4$, we obtained the Absolute Coupling Index (ACI). In addition, we derived the Integrative Coupling Index (ICI), which combines information of the ACI and the relative number of phase-locked point within the positive range (Positive Coupling Index, PCI) and is an asymmetric coupling measure: $\mathrm{ICI} = ((\mathrm{PCI} + \mathrm{ACI})/(2^*\mathrm{ACI}))^* \sqrt{\mathrm{PCI}}$. The ICI equals 1, when all phase-locked points are in the positive range, and zero, when they are in the negative range.

We report results on the three coupling measures PSI, ACI, and ICI. To determine the effects of singing and touch on the coupling of respiration and HRV measures across participants, we made use of two-way repeated measures ANOVAs with the factors Frequency and Condition, comparing either singing to rest in *ntf*, or touch to no touch in *tc* and *ntc*. We concentrated on these two comparisons because for an effect of singing, we did not want to include the rather unusual close standing conditions (*tc* and *ntc*), while for an effect of touch, the regular standing condition *ntf* is not a suitable control. We grouped the ten frequencies in three ranges that relate to specific physiological processes. Very low frequencies (VLF: 0.025, 0.05 Hz) and low frequencies (LF: 0.075, 0.10, 0.125, 0.15 Hz) support the sympathetic nervous system, and high frequencies (HF: 0.20, 0.25, 0.30, 0.40 Hz) the parasympathetic. We applied the Greenhouse-Geisser epsilon for non-sphericity, wherever necessary. We used IBM SPSS v25 (SPSS, Chicago, IL, USA) for statistical analysis. In addition to rigor testing, we explored the relationship between coupling and musical structure in a descriptive way, looking into dynamic changes across time.

Results

Effect of singing on synchronization

The two-factor ANOVA with the factors Condition (singing vs. rest) and Frequency (VLF, LF, HF) included data from the regular standing position only (*ntf*) to avoid any confounding effects of standing close and having physical contact. Table 1 lists the statistical results for all three coupling indices: PSI, ACI, and ICI. The results are clear. The factor Condition was significant as well as the factor Frequency, with the interaction being not significant (with one exception: HRV, PSI; pairwise *post-hoc* comparisons revealed that the interaction was due to a missing effect of singing for VLF, $p > 0.10$). Figure 3 shows that, indeed, the coupling of respiration and HRV was higher during singing than at rest, and this effect was similar across different frequency ranges.

TABLE 1 Results of the two-factor ANOVA on the effect of singing.

		Condition (singing, rest) $(df = 1, 7)$			**Frequency** $(df = 2, 14)$			**Cond. * Frequ.** $(df = 2, 14)$		
		F	p	η^2	F	p	η_p^2	F	p	η_p^2
Respiration	PSI	37.44	<0.001	0.842	432.31	<0.001	0.984	1.89	0.201	0.213
	ACI	28.30	0.001	0.802	13.41	0.002	0.657	0.011	0.958	0.002
	ICI	21.39	0.002	0.753	10.82	0.007	0.607	0.35	0.705	0.048
HRV	PSI	9.22	0.019	0.568	338.27	<0.001	0.980	7.74	0.017	0.525
	ACI	30.57	0.001	0.814	9.23	0.006	0.569	1.17	0.326	0.143
	ICI	27.25	0.001	0.796	38.64	<0.001	0.847	0.442	0.554	0.059

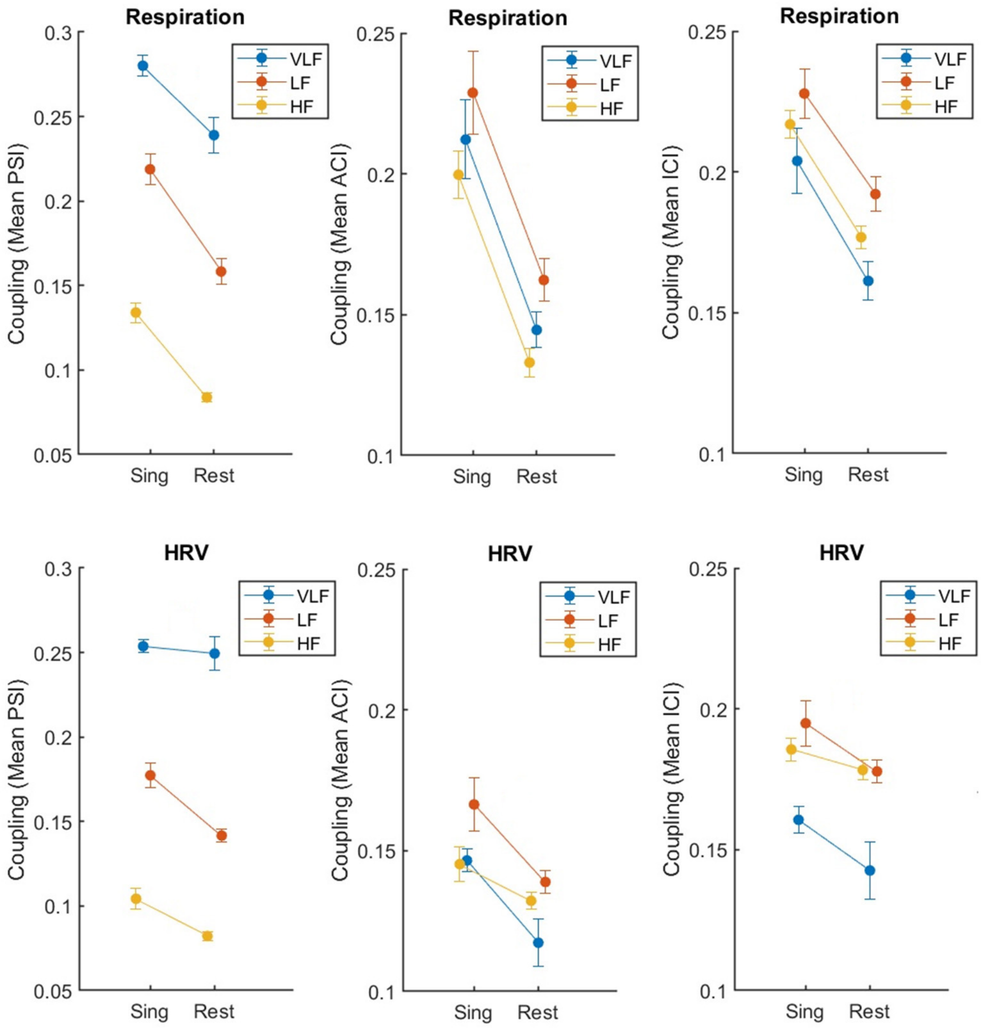

FIGURE 3
Synchronization of respiration (upper part) and HRV (lower part) between eight singers recorded during singing or resting (both in standing condition *ntf*), measured by mean PSI, ACI, and ICI (from left to right). The error bars depict the standard error of the means.

TABLE 2 Results of the two-factor ANOVA on the effect of touch.

		Condition (*tc, ntc*) (df = 1, 7)			**Frequency (df = 2, 14)**			**Cond. * Frequ. (df = 2, 14)**		
		F	p	η^2	F	p	η_p^2	F	p	η_p^2
Respiration	PSI	8.17	0.024	0.539	297.91	<0.001	0.977	4.95	0.051	0.414
	ACI	9.54	0.018	0.577	20.29	<0.001	0.743	1.15	0.329	0.141
	ICI	3.96	0.087	0.361	6.08	0.020	0.465	0.26	0.718	0.036
HRV	PSI	3.28	0.113	0.319	576.85	<0.001	0.988	1.18	0.333	0.144
	ACI	0.09	0.769	0.013	7.85	0.016	0.529	1.69	0.228	0.194
	ICI	0.135	0.724	0.019	26.16	<0.001	0.789	1.14	0.329	0.140

Effect of touch on synchronization

We tested for the effect of touch, comparing synchronization of respiration and HRV in the two close standing conditions, with and without touch (*tc, ntc*). Again, the results are clear (see Table 2). For respiration, there was an effect of touch (significant for PSI and ACI, and a tendency with $p < 0.10$ for ICI), while for HRV there was no such an effect (all p's > 0.11). The main effect of Frequency was significant for all three measures and both physiological recordings. None of the two-way interactions reached significance (but there was a tendency with $p < 0.10$ for PSI in respiration; the *post-hoc* pairwise comparison indicated no difference between touch conditions for HF, $t < 1$). Overall, Figure 4 shows that the effects were as expected: Singing with physical contact resulted in a higher coupling of respiration than singing without. For HRV, some tendencies in the same direction were revealed but were far from significant (i.e., for PSI $p = 0.113$).

Changes in synchronization across time

Figure 5 depicts examples of the synchronization of respiration across time for all frequencies from one recording (Kyrie/Gloria in *tc* on day three). On a descriptive level, it is obvious that the synchronization of an ensemble singing a polyphonic piece is less stable across time than what has previously been reported with an amateur choir singing canons (see Müller and Lindenberger, 2011, Figure 3). In our data and this specific example, one can visually identify several time intervals showing synchronization between singers across different frequencies. For instance, there is high pairwise synchronization across most singers in the time interval 130–150 s for periodicities around 0.05, 0.075, 0.10, 0.125, and 0.40 Hz, with some synchronization (but not across all singers) for 0.15, 0.20, 0.25 and 0.30 Hz. Further, a second time window of 240–260 s shows strong synchronization in the higher frequencies from 0.125 to 0.40 and some synchronization also for lower frequencies. That is, synchronization occurs for a diverse range of frequencies and is not limited to a specific frequency. Synchronization also occurs for different frequency ranges at different time points. Note that the two time intervals mentioned above, are related to musical sections such as the beginning of Kyrie II (at around 137 s) and the end of Kyrie II (240–260 s). The beginning is special as after a short break all singers start simultaneously for the first time in that piece and then sing relatively homophonous for a few measures. In addition, the entry of the cantus firmus in the Tenor ("Beata es Maria") marks the first musical climax in Du Fay's *Missa Ecce ancilla domini/Beata es Maria*, and was also performed with particular emphasis by the singers of the tenor. The end has a purely chordal, i.e., homophonic structure with chords that change only very slowly. That is, the compositional structure is revealed in the synchronization pattern.

We also see differences between singers regarding their synchronization. For instance, in the time window of 180–200 s and at the frequency of 0.075 Hz the subgroup of singers S3–S8 was connected with each other, but connections from S3–S8 to S1 and S2 were missing, whereas S1 and S2 were coupled. However, at this time S1 and S2 as well as S7 and S8 were singing in a duo, with S1 and S2 singing one voice (Altus) and S7 and S8 the other (Superius). S3–S6 listened (see also Figure 5 lower subplot, depicting singing activity for each singer across time). It is interesting that S3–S6 (Bassus, Tenor) were connected to S7 and S8 (Superius) and not to S1 and S2 (Altus). There seems to be no musical explanation for preferably connecting with the Superius. Importantly, synchronization is not systematically organized by the singing action but also occurs between singers and listening ensemble members. As a further example, at the frequency of 0.25 Hz (and other frequencies), horizontal lines reflect a sustained synchronization between S1 and S2, S4 and S5 as well as S7 and S8. While S1 and S2 as well as S7 and S8 were actually singing the same voice, S4 and S5 were not, but rather stood in neighboring positions and were connected by touch (see Table 3). Hence, for this pair (S4, S5) not singing together but touching each other seemed to increase synchronization. Note, too, that the connectivity was intermittent for S1 and S2, as well as S7 and S8, even though these singers were singing most of the

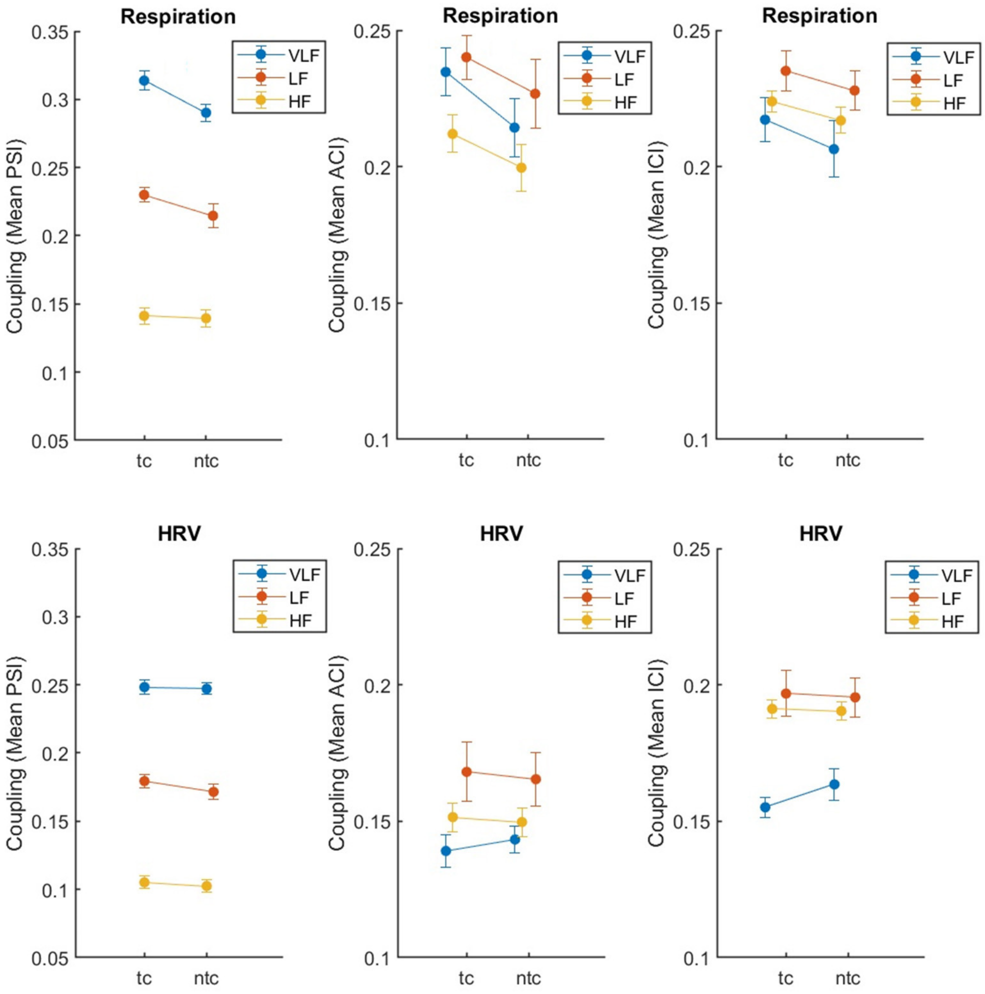

FIGURE 4

Synchronization of respiration (upper part) and HRV (lower part) between eight singers recorded during singing with (*tc*) and without (*ntc*) physical contact, measured by mean PSI, ACI, and ICI (left to right). The error bars depict the standard error of the means.

time (i.e., compare the vertical, intermittent line patterns in the upper part of Figure 5 with the depicted singing activity in the lower subplot of Figure 5).

To further explore how synchronization in respiration was related to the fact that all singers were singing or not, we decided *post-hoc* on a comparison between synchronization measures during time intervals when all singers were singing in comparison to when only part of the ensemble was singing. Given the observations above, synchronization should be stronger for passages with all singers in comparison to only part of it. Regarding the effect of touch, both outcomes are possible: A stronger effect of touch when part of the ensemble was singing. Eventually, touch is particularly effective when there is no other means for coordination like singing; or, a stronger effect of touch when all are singing, as the joint action of singing might be the base for physical contact to be effective.

For this analysis, we report on ACI as a synchronization measure for respiration only and focus on recordings from the conditions *ntc* and *tc*. We annotated which singer was singing within the 360 s recordings, based on seconds as time unit. We marked sequences when all singers were singing (condition: total). To keep the lengths of the passages about the same, we compared these sequences with times, when the number of active singers was below eight but not zero (condition: partial). We dropped time units, when only a single unit differed from the other surrounding ones (e.g., 1 s, in which only seven singers instead of eight were singing). The mean number of time units across all recordings in the condition total was 168 s ($SD = 10$) and for partial 142 s ($SD = 14$). We then calculated the mean ACI in the same way than before, but separately for total and partial singing. We fit the data into a three-way ANOVA with the within-subject factors Touch (*ntc*, *tc*) and Ensemble (*total*, *partial*), and Frequency (VLF, LF, and HF). The main effect of

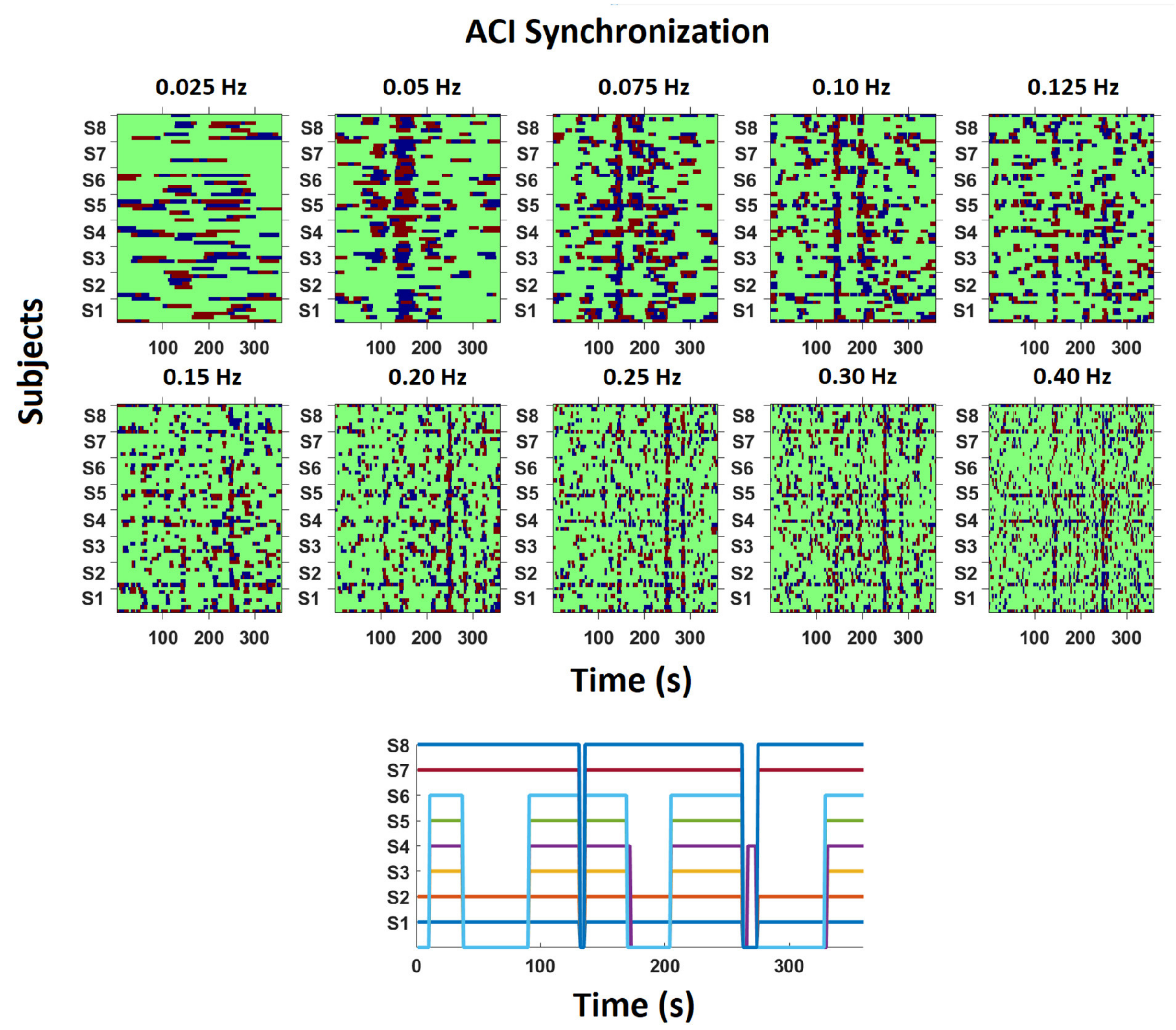

FIGURE 5
Example of phase synchronization patterns of respiration at different frequencies across 360 s. The ACI between each singer (S1–S8) and every other singer was calculated pairwise for ten frequency bins. Red depicts that one singer's oscillation is leading, blue that the other singer is leading, and green depicts no synchronization within the defined range of the phase difference (see Method for more information). In this recording, the ensemble was singing the *Kyrie/Gloria* in *tc* on the 3rd day. The subplot on the bottom depicts which singer was singing across time, with singers S1, S2, S7, and S8 singing throughout the musical piece, and S3 to S6 having longer passages without singing.

TABLE 3 Overview of the singers' neighboring positions and realized touch conditions in the trial depicted in Figure 5.

Singer	Neighbor	Physical contact
S1	S2, S3, S4	Touched hands with S2, Touched shoulder of S3
S2	S1, S3, S4	Touched hands with S1
S3	S1, S2, S4, S5, S6	Touched waist of S1, Touched shoulder of S4
S4	S1, S2, S3, S5, S6	Touched waist of S5
S5	S3, S4, S6, S7, S8	Touched waist of S4, Touched shoulder of S7
S6	S3, S4, S5, S7, S8	Touched waist of S3, Touched waist of S1
S7	S5, S6, S8	Touched shoulder of S5
S8	S5, S6, S7	Touched waist of S6

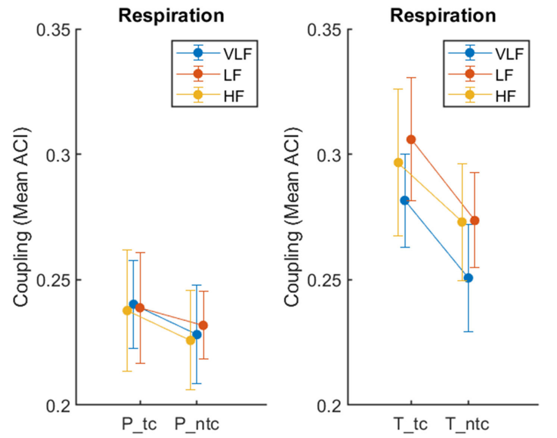

FIGURE 6
Synchronization of respiration during passages when only part of the ensemble was singing (P: partial, left) in comparison to all singers (T: total, right), recorded during singing with (*tc*) and without (*ntc*) physical contact, measured by ACI. The error bars depict the standard error of the means.

touch was significant, $F_{(1,7)} = 22.71$, $p = 0.002$, $\eta_p^2 = 0.764$, with touch resulting in higher synchronization ($M = 0.27$, $SE = 0.02$) than no touch ($M = 0.25$, $SE = 0.02$). The main effect of ensemble was significant, $F_{(1,7)} = 191.13$, $p < 0.001$, $\eta_p^2 = 0.965$, with synchronization being higher for total ($M = 0.28$, $SE = 0.02$) in comparison to partial ($M = 23$, $SE = 0.02$). The main effect of frequency failed to be significant ($p = 0.059$). The two-way interaction ensemble-by-touch was significant, $F_{(2,14)} = 19.45$, $p = 0.003$, $\eta_p^2 = 0.735$. Figure 6 shows that the effect of touch was stronger for total than partial. In addition, the two-way interaction ensemble-by-frequency was significant, $F_{(2,14)} = 35.37$, $p < 0.001$, $\eta_p^2 = 0.835$, which was based on a slightly smaller effect of ensemble for VLF than for LF and HF.

To test whether the effect of touch was still present when only part of the ensemble was singing, we limited the analysis on the two factors Touch and Frequency and the data from the partial condition. The main effect of touch only showed a non-significant tendency, $F_{(1,7)} = 4.75$, $p = 0.066$, $\eta_p^2 = 0.404$. The effect of frequency was far from significant as well as the interaction, both F's < 1.

Discussion

Our results confirm previous findings on synchronization of respiration and HRV during ensemble singing and extend those findings by revealing an increase in synchronization under physical contact. Singing increased the coupling between singers in comparison to rest in both respiration and HRV. This effect was significant across the different frequency ranges. With these results, we replicate the findings by Müller and Lindenberger (2011). Importantly, we show that singing synchronizes respiration and HRV, even in the current setup where a professional ensemble is singing polyphonic music with distributed breathing. We also extended previous findings by showing that singing with touch led to higher synchronization than singing without touch. This effect became significant in respiration but not for HRV. Moreover, the effect of touch was particularly pronounced during parts when all singers in the ensemble were singing at the same time in comparison to the partial ensemble.

As this study breaks new ground regarding joint singing with touch, parallels can only be drawn to studies of the effects of physical contact on other behaviors. The synchrony effects of touch during singing might stem from a higher activation of the auditory cortex through the vibrotactile support (e.g., Schürmann et al., 2006), which in turn enhances support of timbre and pitch perception (e.g., Russo et al., 2012). This might explain, why the effect of touch was particularly effective when the full in comparison to the partial ensemble was engaged in the joint action of singing. In addition, physical contact such as hand-holding has been shown to increase respiration in inter-personal coupling (e.g., Goldstein et al., 2017), indicating that the current measures reflect these processes. Of course, these theses would need further support from brain imaging techniques. In any case, touch has various (indirect) effects on people which might benefit synchronization through (emotional) communication and social bonding (e.g., Hertenstein et al., 2006, for reviews see Gallace and Spence, 2010; Morrison, 2016), but might also hinder synchronization in situations where people do not want physical contact or their natural movement behavior is too restricted by maintaining contact.

Some observations from the descriptive time analyses need to be discussed. Firstly, we see that synchronization in our study is less stable across time than what has previously been reported by Müller and Lindenberger (2011). One reason might lie in the music selection, another in the experience level of the singers. While we selected highly intricate polyphonic music, in other studies the music was chosen because of its simple structure (i.e., Vickhoff et al., 2013), clear tempo, and distinct phrase endings. With these simple stimuli, tempo and breathing rhythm are related strongly to the synchronization of specific frequencies in respiration and HRV. On a side note, we looked into a potential relation between musical tempo and the respiration signal in our own data, but did not find supporting evidence. Also, singing in unison resulted in higher coupling than singing a canon in parts (Müller and Lindenberger, 2011), indicating that the lower complexity of the music has a positive impact on synchronization. In addition, we invited an ensemble with professional singers that applied distributed breathing, whereas the study from Müller and Lindenberger (2011) involved an amateur choir. Both the complex musical structure and distributed breathing onsets might have lowered synchronization between singers in our study.

Looking at the changes in synchronization over time, synchronization was seen to occur for a range of frequencies at various moments. In some of these moments, all singers were synchronized, in some only subgroups were synchronized. While this can in some cases be explained by the musical structure (homophonic vs. polyphonic parts, only some voices singing vs. all voices singing), most of the time, synchronization was not systematically organized by the singing action (e.g., singing the same voice), but also occurred between active and "passive" singers, that is those resting at certain points. While research has shown that coupling between singers is higher than between members of the audience (Hemakom et al., 2016), we see that listening as a singer is a very engaging activity as singers who rest need to follow the other singers in order to get the cue for their next entry. Hence, subgrouping is not simply due to the fact of singing being contrasted with non-singing activity. Here, the musical experience might also come into play. It might very well be that a professional singing ensemble is able to create such a superordinate system, indicated by the strong coupling between active singers and the other singers of the ensemble (cf. Müller et al., 2018a).

However, we indeed found an effect of total vs. partial ensemble singing in our *post-hoc* analyses. Synchronization of respiration was higher, when all singers sang, in comparison to only part of the ensemble. Note that most of the time the music was polyphonic when the full ensemble sang, with a complex structure and distributed breathing. Then, this analysis does not compare homophonic with polyphonic singing—an analysis, which was not possible, because the homophonic parts were rather rare and data then too sparse.

Synchronization was present across different frequency ranges at the same time, spanning very low to high frequency bands. From a physiological perspective, VLF and LF support the sympathetic nervous system and HF the parasympathetic. There is also evidence that LF can be modulated by both sympathetic and parasympathetic activities (Ernst, 2017). Then, synchronization was present in the sympathetic and parasympathetic nervous systems and was not limited to either of the two. Whereas, the sympathetic system controls the dilation of the bronchi and acceleration of the heart rate, the parasympathetic system constricts the bronchi and slows the heart rate (Eckberg, 2000). As reported (Bonsignore et al., 1995; Yasuma and Hayano, 2004), heart rate increases at inspiration and decreases at expiration, reflecting respiratory-circulatory interactions. Heart rate variability in synchrony with respiration is a biological phenomenon known as respiratory sinus arrhythmia (RSA), playing a role in the HRV coupling occurring in singing interactions (Müller and Lindenberger, 2011; Vickhoff et al., 2013).

As the current project was interdisciplinary in nature, historical sources that pointed to the practice of singing with body contact were of interest. However, since pictorial representations cannot be taken at face value and corroborating sources are missing, one cannot say for sure whether historical ensembles really touched during their rehearsals and performances. A reason for touch in medieval and early modern times might have been the need to ensure high-precision coordination among singers in the absence of cues in the music notation and a conductor. Scholarship on the cultural history of touch (Classen, 2012), cultural anthropological studies on group singing worldwide (Hayward, 2014), but also results from social psychological research on the effects of interpersonal touch on action coordination and feelings of social connectedness (Gallace and Spence, 2010; Cekaite and Mondada, 2020) make it seem plausible to assume that physical contact and vibrotactile perceptual input can serve as a source of coordination and entrainment during joint singing. The current findings support these claims as touch increased connectivity during singing, at least for respiratory activity.

However, as touch only added to the already strong increase in connectivity that was seen from rest to singing, the function of touch in the current study needs to be discussed. Different from Renaissance practice, the current ensemble sang from modern scores and had a conductor who took over the coordination. Hence, in our study, touch did not need to serve an intentional function besides following the instructions of the experimenter, which may explain the smaller synchrony effect for touch vs. no touch. Touch is a multidimensional, socially coded behavior and communicates a variety of contents, like love, intimacy, bonding, solidarity, friendship, comfort, sexual intention, aggression, dominance, status, or power (Hertenstein et al., 2006), via a variety of features, such as duration, intensity, location, etc. (Major, 1981). There are strong inter-individual differences in the ways people feel and interpret touch, particularly outside a romantic relationship (Major, 1981). In a context like ours, where the singers were asked to maintain physical contact, singers might have a wide range of reactions, with some of the singers feeling more pleasure and others irritation (as some singers of our ensemble actually mentioned after data collection). This divergence might have contributed to inter-individual differences in physiological coupling via touch. Forcing singers to maintain physical contact also created some difficulties, e.g., the radius of free movements was restricted, and touching while concentrating on singing might have created some difficulties, and hence dual-task costs (onto the singing performance). One might speculate whether touch might have been more disturbing during passages when only part of the ensemble was singing than when the ensemble was unified in the joint action of singing. However, despite potential difficulties, the coupling increased as a result of physical contact, showing a general benefit of touch for respiration synchronization.

Our study showed increased physiological synchronization between singers. However, it is difficult to disentangle what exactly drove synchronization. Joint action requires several processes and representations to overlap between co-actors (Vesper et al., 2017), such as the mental representation of action goals and monitoring task progress, the sharing of sensorimotor information including ongoing multisensory perceptual and emotional processes, sensorimotor predictions of the own and others' actions, and general mechanisms supporting coordination. However, we tentatively argue that some simple underlying reasons for synchronization can be ruled out. We see mixed patterns of synchronization between singers that could not be explained by either singing the same voice, having physical contact or spatial distance between singers. Importantly, therefore, our findings suggest a higher level of organization of all singers, forming a superordinate system (Noble, 2012) or superorganism, here in the form of a music ensemble (Müller et al., 2018a, 2019). With this, we propose that our findings follow the theoretical model of the human supersubject (Müller et al., 2021) reflected in professional ensemble members who are familiar with each other and the sung music, and that share the same goals.

Conclusion

While it had previously been shown that joint singing increases the synchronization of respiration and HRV, the current study extends these findings by revealing an additional increase in synchronization of respiration when singing with body contact. By taking an interdisciplinary approach, the current study stands out in the field of synchrony during singing. Investigation of singing with physical contact was inspired by historical accounts and the professional ensemble recruited sang intricate polyphonic music. We showed that synchrony increased even under these highly specific circumstances. Interestingly, synchrony was not shown to be systematically related to the singing activity such as singing the same voice, or either standing position or touch. The ensemble seemed to organize itself on a higher level, possibly creating a superordinate system where singers share the same goals.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found at: https://osf.io/tejvy/.

Ethics statement

All procedures were conducted in accordance with the 1964 Helsinki Declaration and its later amendments, and approved by the Ethics Council of the Max Planck Society (number 2702_12). All participants provided their written informed consent to participate in this study.

Author contributions

MW-F conceived the research. EL, DO, and JM designed the research. EL, DO, MW-F, and JM collected the data. EL, DO, CT, and VM performed the analyses. DO, CT, and VM contributed to the Methods and Results Sections. EL and JM wrote the manuscript. All authors revised the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fnhum.2022.928563/full#supplementary-material

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Inter-brain plasticity as a biological mechanism of change in psychotherapy: A review and integrative model

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Recent models of psychopathology and psychotherapy highlight the importance of interpersonal factors. The current review offers a biological perspective on these interpersonal processes by examining inter-brain synchrony—the coupling of brain activity between people interacting with one another. High inter-brain synchrony is associated with better relationships in therapy and in daily life, while deficits in the ability to achieve inter-brain synchrony are associated with a variety of psychological and developmental disorders. The review suggests that therapy improves patients' ability to achieve such synchrony through inter-brain plasticity—a process by which recurring exposure to high inter-brain synchrony leads to lasting change in a person's overall ability to synchronize. Therapeutic sessions provide repeated situations with high inter-brain synchrony. This can lead to a long-term increase in the ability to synchronize, first with the therapist, then generalized to other interpersonal relationships, ultimately leading to symptom reduction. The proposed inter-brain plasticity model offers a novel biological framework for understanding relational change in psychotherapy and its links to various forms of psychopathology and provides testable hypotheses for future research. Understanding this mechanism may help improve existing psychotherapy methods and develop new ones.

KEYWORDS

brain-to-brain coupling, neuropsychology, psychotherapy, synchrony, therapeutic alliance

Introduction

The effect of the patient-therapist relationship has been the focus of theoretical and clinical writing for the past century. Almost five decades of research suggest that the patient-therapist relationship, as evaluated using self-report measures and behavioral coding systems, is a consistent predictor of treatment outcome (Doran, 2016; Flückiger et al., 2018). In the past decades, researchers have explored more objectively observable indicators of the quality and strength of the relationship. One promising line of research is the study of interpersonal synchrony, defined by Koole et al. (2020) as "the temporal coordination of social agents' mutual behavioral, physiological, and neurological functions."

Various approaches have been implemented to evaluate multiple aspects of synchrony between the patient and the therapist during therapy sessions, such as movement energy (Ramseyer and Tschacher, 2011), hormonal (Zilcha-Mano et al., 2021), physiological (Kleinbub et al., 2020), and acoustic markers (Imel et al., 2014). Recently, studies that examined the simultaneous brain activity of patients and psychotherapists have shown that inter-brain synchrony emerges during psychotherapy (Zhang et al., 2018), suggesting that coupling between brain activities of interaction partners may underlie behavioral levels of synchrony and connectedness. Narrative and systematic reviews of the overall literature on synchrony in psychotherapy (Koole and Tschacher, 2016; Koole et al., 2020; Wiltshire et al., 2020; Mende and Schmidt, 2021) have found that a high level of synchrony is associated with the formation of a strong working alliance between the patient and the therapist, as well as with greater treatment efficacy and effectiveness, although there are occasional caveats which call for further research (e.g., Wiltshire et al., 2020; did not find a connection between linguistic synchrony and outcome).

The current review proposes that patient-therapist synchrony might directly increase patients' ability to establish inter-brain synchrony in the future when interacting with their therapist, and ultimately, with other people.[1] This can happen through *inter-brain plasticity*; as explained in detail below, inter-brain plasticity (Shamay-Tsoory, 2021) is a phenomenon in which after regions in the brains of two (or more) people are repeatedly activated in close succession (i.e., one immediately after another), connectivity in each brain will become stronger such that these two regions will have a higher chance to be activated together in the future. In synchrony terms, this means that when two people are engaged in an activity involving high inter-brain synchrony, their ability to synchronize will increase, and inter-brain synchrony between them will be greater in the future. We suggest that as psychotherapy is a situation which involves high inter-brain synchrony for extended periods of time, it can trigger inter-brain plasticity.

Importantly, inter-brain synchrony has been associated with better functioning in interpersonal situations and relationships (Hu et al., 2017; Gvirts and Perlmutter, 2020). Thus, improving patients' ability to synchronize through inter-brain plasticity may be a biological mechanism which can explain how therapy improves patients' relationships and interpersonal interactions. Many forms of psychopathology are associated with interpersonal difficulties (Girard et al., 2017) and multiple theoretical frameworks of psychopathology and psychotherapy revolve around interpersonal relationships. Examples include contemporary integrative interpersonal theory (CIIT) (Hopwood et al., 2021), relational and intersubjective psychoanalytical theory (Mitchell and Aron, 1999; Stolorow et al., 2014), and interpersonal psychotherapy (Blagys and Hilsenroth, 2000), among others; even when they are not the focal point of treatment, the role of interpersonal components is often recognized, such as in recent research on CBT (Castonguay et al., 2018; Kazantzis et al., 2018). Inter-brain plasticity may help explain some of these key interpersonal processes on a biological level.

We begin by briefly detailing our method and discussing the definitions of synchrony. We then introduce inter-brain synchrony and review studies linking it with prosocial behavior, deeper interpersonal relationships, and stronger therapeutic alliances. We continue by describing inter-brain plasticity and review studies documenting its occurrence. We then review clinical literature showing how various psychological and neurological disorders are associated with low inter-brain and behavioral synchrony, and how, following therapy the synchronization ability may increase. We conclude by presenting a model for inter-brain plasticity in psychotherapy. We discuss implications for clinical research and practice, as well as addressing alternative explanations for our findings and providing directions for future research.

Methods

The current review is a non-systematic narrative review. This approach was chosen as our aim is to demonstrate how indirect evidence from a variety of research programs possibly points to a phenomenon. Such broad discussion of an evolving concept, as opposed to a review of literature on an established topic, is better suited to a narrative review (Collins and Fauser, 2005). In a more practical sense, as we integrate findings from multiple lines of research, performing a systematic review of each one of them would be infeasible.

Still, following Ferrari's (2015) suggestion to include some methods of systematic review in narrative reviews, we detail some attempts we made to stratify our article search methodology. In general, literature searches were performed on Google Scholar and PsycArticles. Each search was repeated once using brain-specific terms ("Inter-Brain Synchrony" OR "Inter-Brain Synchronization" OR "Brain Coupling"[2]) coupled with a

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[1] While in the interest of brevity we sometimes discuss a general "ability to synchronize," a person's ability to synchronize is always context-dependent, as detailed here. We expand on this more below when discussing generalization.

[2] The reason we used "inter-brain" with "synchrony" and "synchronization" but used "brain" with "coupling" is that "brain synchrony" usually refers to synchronization between two regions in the same brain. "Brain coupling" is almost exclusively used for inter-brain

relevant additional term (e.g., "Psychotherapy," "Depression"), and once simply using "Synchrony" to examine behavioral and other forms of synchrony. When discussing plasticity, we included either studies which contrasted synchrony at multiple timepoints, or who correlated synchrony with an individual difference variable which could indicate differences in repeated exposure to a situation, e.g., experienced vs. novice professionals (Zhang et al., 2020), people with existing relationships vs. strangers (Kinreich et al., 2017), different types of repeated contact with caregivers during development (Yaniv et al., 2021). However, the large number of searches required to cover all of the topics discussed meant that we could not systematically categorize all results of each search. To somewhat counteract possible biases, we highlight existing systematic reviews and meta-analyses on specific topics whenever possible.

Interpersonal synchrony: Definitions

As mentioned above, the definitions of synchrony (Koole et al., 2020), imply that the phenomenon in question must have some temporal variance, which is shared between participants; the specific behavior, physiological or neural measure at a specific point in time does not have to match. For example, two people standing on a basketball court would not be considered synchronized in movement just for performing the same action, as there is no variance in behavior over time. However, if they started throwing the ball back and forth, they would be considered synchronized in movement; although they are never simultaneously performing the same action, their actions are perfectly correlated over time (whenever person A is throwing, person B is catching, and vice versa).

From a temporal perspective, there are multiple subtypes of synchrony with different definitions of "temporal coordination" (For a full review, see Butler, 2011). One important distinction is between trend, concurrent and lagged synchrony (Helm et al., 2018). Trend synchrony is a correlated trend between people in a measure (behavioral, physiological or neural) over a long period of time. Concurrent synchrony is a common fluctuation of the measure around a trend. Lagged synchrony is similar to concurrent synchrony, but with one of the participants "leading" the other, i.e., one participants' measures are correlated with the other participants' measures at a previous time-point. Studies of interpersonal synchrony in conversation settings, as the ones detailed below, generally measure concurrent synchrony, while allowing for short lags in either direction (e.g., by averaging results with lags between −5 and +5 s; Paulick et al., 2018). Short lags must be accounted for as they may stem from a variety of reasons, including small discrepancies in measurement timing, differences in inherent delays such as an approximately 6 s delay between neuronal activity and blood response (Liao et al., 2002), and differences in reaction times and in movement speeds between participants. Trend synchrony is of less theoretical interest—as detailed above, theories of synchrony in interpersonal interaction focus on the moment-to-moment interaction between people, and not on general similarity over long periods of time. Another common distinction is between in-phase synchrony, in which participants' levels of measures are positively correlated (e.g., dancers performing the same moves at the same time), and anti-phase synchrony, in which participants' actions are negatively correlated (e.g., a conversation in which whenever one person talks the other is silent). As interpersonal interaction studies must account for lags in either direction, the distinction between in-phase and anti-phase synchrony is murkier, and they are usually aggregated.

How do people establish synchrony with one another? Prominent theories highlight the importance of being able to perceive each other's behavior, and by having a consistent reaction which is perceived by the other person (Hasson et al., 2012; Wheatley et al., 2012). Thus, the occurrence of synchrony is an indicator of participants' ability to perceive each other, and their willingness and ability to react to each other. Once synchrony has been established, it also has the direct benefit of making predictions of the other person easier, freeing cognitive resources for other tasks (Hoehl et al., 2021). Indeed, multiple systematic reviews and meta-analyses (Rennung and Göritz, 2016; Mogan et al., 2017; Czeszumski et al., 2022) have linked behavioral and neural synchrony to a variety of positive outcomes.

Importantly, while we could find no studies linking inter-brain synchrony and negative relational outcomes, there are studies from other modalities which show negative effect. Systematic reviews and meta analyses of physiological synchrony in the autonomous nervous system show mixed results (Palumbo et al., 2017; Mayo et al., 2021). In psychotherapy, while reviews find general positive effects (Koole et al., 2020; Wiltshire et al., 2020), some studies of behavioral synchrony have reported mixed results (Ramseyer, 2020; Tschacher and Meier, 2020). As mentioned above, a study by Paulick et al. (2018) has even found negative associations between behavioral synchrony and outcome for patients with anxiety disorders. A prominent explanation behind these more mixed results is context dependence (Danyluck and Page-Gould, 2019). Indeed, it could be the case that in some cases, a flexible balance between synchrony and non-synchrony is more important than constant high synchrony (Mayo and Gordon, 2020).

While these mixed results should be taken in mind, the current review follows the aforementioned systematic reviews and meta-analyses which show overall positive outcomes of

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synchrony, and the search term "brain coupling" also captures papers with the term "inter-brain coupling".

interpersonal synchrony. Still, we certainly do not expect increased inter-brain synchrony to be a panacea, and we expect that as research on inter-brain plasticity progresses specific disorders, subtypes of synchrony, or session contexts may emerge as contra-indications.

Inter-brain synchrony, relationships, and therapeutic alliance

Inter-brain synchrony, also referred to as brain-to-brain coupling, represents synchronized activity patterns between the brains of two (or more) people. Inter-brain synchrony is a widely observed phenomenon, thought to occur through the transfer of various signals between brains using external channels such as speech, gestures, and facial emotions (Hasson et al., 2012). It is usually examined using hyperscanning—the simultaneous acquisition of the cerebral data from two subjects (Montague et al., 2002; Babiloni and Astolfi, 2014). Current hyperscanning methods include functional near-infrared spectroscopy (fNIRS) (Ferrari and Quaresima, 2012), dual-EEG (Liu et al., 2018), and more rarely, fMRI (Misaki et al., 2021).

Inter-brain synchrony is associated with several positive interpersonal outcomes. In one study in which participants played a prisoner's dilemma game, participants who displayed greater inter-brain synchrony (as measured via dual-EEG) were more cooperative (Hu et al., 2017). In a study of teams engaged in cooperative problem solving, inter-brain synchrony measured using EEG hyperscanning predicted cooperative behavior even beyond self-reported team identification (Reinero et al., 2020). Gvirts and Perlmutter (2020) propose a mechanism for this effect, suggesting that inter-brain synchrony may help increase mutual attention and social alignment—the tendency of individuals to align their motions, emotions and cognitions (Shamay-Tsoory et al., 2019). Recent studies have examined these questions using dyadic neurofeedback paradigms, in which participants' brain activity is visualized (e.g., by displaying coherence metrics between two people's EEG readings; Chen et al., 2021), allowing them to see whether it is synchronized or not. Participants who are instructed to use this feedback to increase their inter-brain synchrony over time are able to do so (e.g., Susnoschi Luca et al., 2021). Dyadic neurofeedback studies in humans (Müller et al., 2021) and in pigeons (Yang et al., 2020) have demonstrated causal links between inter-brain synchrony and prosociality; the researchers increased inter-brain synchrony using dyadic neurofeedback and demonstrated that this increased synchrony was associated with more pro-social experiences (Müller et al., 2021) and behavior (Yang et al., 2020).

Research on inter-brain synchrony shows that it may occur between various brain networks. The literature points to two networks which may be especially relevant: the theory of mind network and the observation-execution system (see **Figure 1**).

The theory of mind network involves reasoning about, considering and simulating the mental states of others and is key to social interaction (Rilling et al., 2004). Theory of mind is a broad term, encompassing various processes in many brain regions. A "core" theory of mind network (Carrington and Bailey, 2009; Schurz et al., 2014) encompasses the temporal-parietal junction (TPJ) and the medial prefrontal cortex [both the dorsomedial (dmPFC) and the ventromedial (vmPFC) prefrontal cortex, with some differentiation between tasks; Shamay-Tsoory and Aharon-Peretz, 2007]. Both regions have been shown to be activated in a wide range of theory of mind related tasks (Tamir and Mitchell, 2010; Schurz et al., 2017; Paracampo et al., 2018), and comprise part of the cognitive empathy system (Abu-Akel and Shamay-Tsoory, 2011).

Another system that may support emotional communication is the observation-execution system. This system was identified in the inferior frontal gyrus (IFG) and the inferior parietal lobule (IPL) and premotor (PM) cortices, with the IFG pertaining to motor representations of actions, whereas the IPL is linked to the actual sensory-to-motor mapping of visual input, and own-body vs. other coordinates. This system is activated in multiple interpersonal contexts, such as emotional contagion, vicarious pain, and emotion observation (Shamay-Tsoory et al., 2019), and overlaps with the emotional empathy system (Abu-Akel and Shamay-Tsoory, 2011).

Synchrony in both systems has been associated with improved communication and cooperation and with better relationships. A recent meta-analysis found evidence of synchrony in the temporo-parietal and prefrontal cortex during collaborative tasks (Czeszumski et al., 2022). More specifically, synchrony in the TPJ and the medial prefrontal cortex was found during collaborative tasks such as drawing (Xie et al., 2020) and

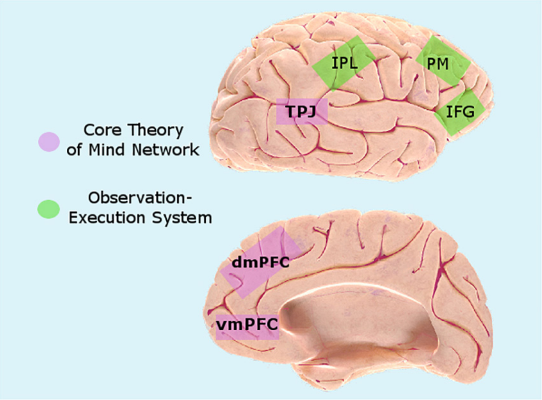

FIGURE 1
Target regions for inter-brain plasticity. Figure based on brain images © Society for Neuroscience, copied with permission from www.brainfacts.org.

problem solving (Lu et al., 2019), and in freeform conversations between romantic couples, as opposed to conversations between strangers (Kinreich et al., 2017).

As for the observation-execution system, an increase in inter-brain synchrony of the left IFG, compared to rest, was found during coordinated face-to-face dialog between partners (Jiang et al., 2012). Dual-EEG studies further confirm the relevance of inter-brain synchrony in the alpha/mu band (8–12 or 13 Hz) that is considered a biomarker of the observation-execution system (Astolfi et al., 2010; De Vico Fallani et al., 2010), during imitation (Dumas et al., 2010). Such synchrony also predicts the level of analgesia during handholding (Goldstein et al., 2018).

Finally, a small number of studies were able to demonstrate links between inter-brain synchrony and psychotherapy, and that synchrony was associated with high levels of working alliance. Zhang et al. (2018) used fNIRS to perform brain imaging on therapist-patient dyads in a single session. Thirty-four students who presented to a college counseling center (with no specific diagnosis) were randomly assigned to a single therapy session or to a social chatting session. Therapists provided therapy in an integrative orientation (Stricker and Gold, 2008). Inter-brain synchrony in the right temporo-parietal junction (rTPJ) was higher in the therapy condition. These findings indicate that inter-brain synchrony is higher in treatment sessions than in day-to-day social encounters. Importantly, within the therapy condition, inter-brain synchrony and working alliance were associated—higher inter-brain synchrony was recorded for participants who reported a stronger working alliance. In an additional study by the same team, Zhang et al. (2020) found that experienced, licensed therapists developed significantly stronger inter-brain synchrony with their patients than novice therapists (First-year graduate students with 15–24 h of experience), as well as a stronger working alliance reported by the patient. For experienced therapists, but not for novice ones, inter-brain synchrony was associated with a stronger working alliance. This indicates that therapists' training may improve their ability to create strong inter-brain synchrony in a session. Lecchi et al. (2019) examined 14 therapist-patient dyads in single sessions using dual-EEG. Patients reported low mood or anxiety issues during the preceding fortnight. High interbrain synchrony was associated with greater congruence between patient and therapist ratings of the working alliance, and with high patient working alliance ratings. Interestingly, synchrony was the same whether sessions were conducted in person or through video conference. Thus, in both studies inter-brain synchrony was associated with better therapeutic relationships in single sessions.

Importantly, indirect insight into the causes and effects of inter-brain synchrony can also be gained from the broader behavioral and physiological synchrony literature. While behavioral synchrony and neural synchrony are not identical, they have been shown to coincide (Dumas et al., 2010), with neural synchrony having a causal influence on behavioral synchrony (Novembre et al., 2017). Thus, behavioral synchrony may be seen as an (imperfect) proxy measure for inter-brain synchrony, and in areas of research where studies explicitly measuring inter-brain synchrony are scarce we discuss behavioral synchrony studies as well.

Inter-brain plasticity

As detailed above, inter-brain synchrony is associated with prosocial behavior and better relationships, within psychotherapy and without. This raises the question—can a person's general ability to achieve inter-brain synchrony be changed? At the neural level, existing research has established that connectivity between brain regions in a single brain can change. Experience-dependent short- and long-term changes in connectivity in several networks (i.e., changes in inter-*system* synchrony) have been reported to underlie various types of learning (e.g., Garrido et al., 2009). According to the spike-timing-dependent plasticity (STDP) principle, which has been widely supported (Caporale and Dan, 2008), when two neurons, or whole brain regions, fire one after another in close succession, synaptic strength will increase. For example, a study of infants aged 5–8 months (King et al., 2021) has shown that exposure to language was associated with higher connectivity between regions in the auditory cortex, the left inferior frontal gyrus (IFG), and the bilateral superior temporal gyrus (STG). Recent studies have managed to purposefully activate such plasticity by using transcranial magnetic stimulation (TMS) to stimulate two brain regions in rapid succession (Suppa et al., 2022); for example, in one study researchers were able to improve participants' hand dexterity after stroke by stimulating the cerebellum and the motor cortex (Rosso et al., 2022).

While there are many cellular-level pathways which can lead to STDP, one of the most studied ones is through N-methyl-D-aspartate receptors (NMDAR), which can only be activated by the pre-synaptic neuron when the post-synaptic neuron is depolarized—allowing it to detect the specific timing of activation typical to STDP learning. When activated, the NMDAR releases large amounts of calcium, which in turn causes long-term potentiation of the synapse (Malenka and Bear, 2004; Caporale and Dan, 2008). Interestingly, this process may be modulated by various neurotransmitters, including Oxytocin (Lin and Hsu, 2018) a neurohormone associated with the regulation of social interactions (Froemke and Young, 2021).

The notion of STDP was recently expanded by taking an inter-brain approach to plasticity (Shamay-Tsoory, 2021). The inter-brain (or second brain) approach (Redcay and Schilbach, 2019) views multiple brains of interacting individuals as parts of an extended network in which nodes, or units, represent different individuals (Hari and Kujala, 2009). Thus, the concept of inter-brain plasticity posits that in a manner similar to regions in the same brain, when regions in two brains are activated in close succession, as is the case in inter-brain synchrony, synchrony between them will grow stronger.

Importantly, inter-brain plasticity as a concept does not posit a new biological or physical fact beyond single brain plasticity, and the possibility of interpersonal communication. Consider person A's inner mental state (A_i) leading, through neural processes in their own brain, to specific behavior (A_b). For example, as depicted in panel 1 of Figure 2, a therapist might experience empathy and caring toward a patient, leading them to smile. That behavior is then perceived by person B (e.g., through vision), and registered in their own brain (B_p)—the patient sees the therapist's smile. Through their own neural processes, that may lead to changes in their own inner mental state (B_i)—seeing the therapist smile leads the patient to feel validated. As long as this process is repeated, we would expect the connections A_i-A_b and B_p-B_i to grow stronger, through plasticity processes within a single brain. Assuming that person B's perceptual capacities (i.e., the connection A_b-B_p) have stayed the same over repeated interactions, this would naturally lead the direct inter-brain association $A_{i-}B_i$ to increase (via the pathway A_i-A_b-B_p-B_i). Of course, in actual interpersonal relationships, person A's inner mental state might be reflected in a variety of behaviors. For example, as depicted in panel 1 of Figure 2, a therapist caring for her patient may smile, support them verbally, or adopt a relaxed speaking tone. The notion of inter-brain plasticity allows us to avoid cataloging changes in numerous behavioral-perceptual pathways (A_i-A_{b1}-B_{p1}-B_i, A_i-A_{b2}-B_{p2}-B_i, etc.), focusing instead on the gradually increasing association between a single pair of mental states (A_i-B_i). Note that this example does not involve or require behavioral synchrony (e.g., both people smile)—only the possibility of perception (e.g., when one person smiles, the other person is able to see their smile). Of course, sometimes synchronized mental states might lead to synchronized behavior (e.g., synchrony between a therapist feeling empathy and a patient feeling validated might lead them both to smile).

Several lines of research have demonstrated inter-brain plasticity in various types of interpersonal interaction.

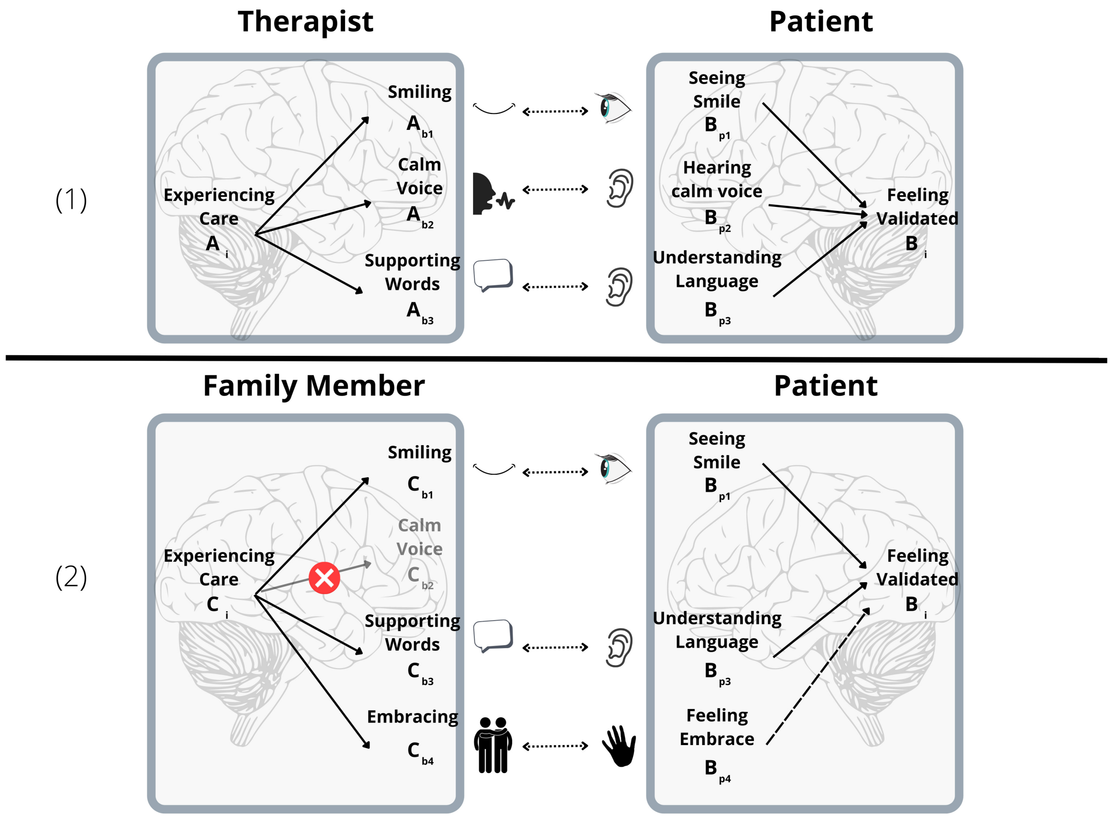

FIGURE 2
(1) Inter-brain pathways, including neuronal and behavioral links. As neuronal pathways grow stronger, if the behavioral links stay constant, inter-brain pathways grow stronger as a whole. The link between two mental states involves multiple inter-brain pathways, which might all grow gradually stronger through inter-brain plasticity. (2) After a period of therapy, in a new encounter with a family member, not all pathways are present (e.g., the family member uses an excited, no calm, voice). However, enough pathways are present to link the two mental states. This can allow a new pathway (e.g., through embracing), which was not present during therapy, to start forming.

Yaniv et al. (2021) have shown in a longitudinal study that the ability to *behaviorally* synchronize increases throughout development, from infancy to young adulthood. Babies who were carried to full term had a better ability to synchronize at all ages. Importantly, babies born pre-term whose mothers employed kangaroo care (increased amounts of skin-to-skin touch between mother and baby) at infancy had a higher capability to synchronize throughout development than matched controls whose mothers did not employ this method. This shows that care-taking behaviors can have long-term effects on the capability to synchronize, at least behaviorally, suggesting that inter-brain plasticity may have taken place.

With respect to relationships, research has shown that inter-brain synchrony is stronger in closer relationships. Multiple studies have shown that inter-brain synchrony is correlated with social closeness (Dikker et al., 2021); that romantic partners have higher inter-brain synchrony with each other than strangers (Kinreich et al., 2017), and that students who feel closer to their teachers are also more synchronized with them (Bevilacqua et al., 2019). These findings support the notion that inter-brain plasticity occurs over the course of the relationship, gradually increasing inter-brain synchrony.

Studies of more specific interpersonal interactions also support this idea. For example, changes in brain synchrony have been documented after a teaching session (Zheng et al., 2020), and therapy was shown to cause changes in behavioral synchrony (e.g., Venuti et al., 2017; Galbusera et al., 2018). Thus, series of professional encounters with a teacher or a therapist can change people's ability to synchronize. Importantly, there are indications that this kind of improvement can generalize to interactions with other people. In addition to the aforementioned study showing that experienced therapists have stronger inter-brain synchrony than novice ones (Zhang et al., 2020), a study of teaching sessions has shown that expert teachers synchronize better with new students than novice teachers (Sun et al., 2020). These two studies suggest that as teachers and therapists gain experience, inter-brain plasticity occurs.

A major consideration regarding inter-brain plasticity is that in order to lead to significant change in patients' lives, it must involve consolidation and generalization. Consolidation is the process through which new memories, which are initially susceptible to be overwritten with new information, become stable for long periods of time (McGaugh, 2000). For inter-brain plasticity in therapy, this would mean that increases in synchrony achieved in one session would be retained in future sessions.

Generalization (Ghirlanda and Enquist, 2003) is the process through which the response to one set of stimuli becomes associated with a new set of similar stimuli. Synchrony is highly context dependent (see above for examples concerning synchrony in cooperative vs. non-cooperative situations, as well as in therapy vs. in small talk). Thus, when discussing changes in a person's "ability to synchronize," we are referring to changes in the amount of synchronization they tend to achieve in a specific set of contexts. We expect changes due to inter-brain plasticity to be limited at first to the exact context in which the initial synchronous experiences occurred. However, this could gradually generalize to similar situations.

For inter-brain plasticity in therapy, this would mean that changes in patients' ability to achieve inter-brain synchrony *in therapy with their specific therapist* would lead to changes in their ability to synchronize (a) *with people other than their therapist* and (b) *in different contexts*, such as various day-to-day interactions. Extending the earlier example, generalization may take the following form: Following a variety of interactions with a therapist A (A_i-A_{b1}-B_{p1}-B_i, A_i-A_{b2}-B_{p2}-B_i, . . .), patient B meets another person, C, in a different context, such as a social meeting with a family member, as detailed in panel 2 of **Figure 2**. Although C may have a mental state analogous to one encountered in therapy (C_i), as this is a different person in a different context, C might only engage in a subset of the behaviors experienced in the interaction with A (C_i-C_{b1}-B_{p1}-B_i, C_i-C_{b3}-B_{p3}-B_i, but not C_i-C_{b2}-B_{p2}-B_i). For example, while both the therapist and the family member might smile at the patient and support them verbally when they experience caring for them, the therapist might have been speaking in a calm and reassuring tone of voice, which the family member does not use. However, as this subset of associations (B_{p1}-B_i,B_{p3}-B_i, . . .) were strengthened for B in therapy, the association C_i-B_i will still be stronger than it might have been before therapy. What if C's mental state is also reflected in an entirely new behavior (e.g., C_i-C_{b4}-B_{p4}), which may have been absent from therapy, such as embracing the patient? Considering that B's internal state representation B_i is already activated through the pathways which were trained in therapy, B_{p4} and B_i will be activated at the same time. According to the STDP principle, we expect that this will lead the pathway B_{p4}-B_i to become stronger, and ultimately B will be able to synchronize with C through this new behavior, which was not present in therapy at all.

While a full review of consolidation and generalization is beyond the scope of this article, one of the major findings of the literature concerning consolidation and generalization is the spacing effect—the fact that consolidation and generalization are stronger when information is presented repeatedly in spaced intervals (Smith and Scarf, 2017). As psychotherapy is often delivered in intervals (e.g., weekly sessions), it has a high potential to encourage consolidation and generalization.

Behavioral and inter-brain synchrony in psychopathology

Many forms of psychopathology are associated with a reduced ability to achieve inter-brain synchronization in various contexts. Therapy can help patients mitigate this deficit.

The following section reviews the transdiagnostical role of deficiencies in patients' ability to synchronize, and evidence that psychotherapy improves this ability.

Autistic spectrum disorder (ASD) has often been associated with reduced interpersonal synchrony, including reduced inter-brain synchrony (McNaughton and Redcay, 2020). Autistic individuals repeatedly exhibit difficulties in tasks that involve movement synchrony (Feldman, 2007; Fournier et al., 2010; Marsh et al., 2013; Fitzpatrick et al., 2016; Cheng et al., 2017). Concerning neural synchrony, two hyperscanning fMRI studies reported that autistic individuals show reduced brain-to-brain coupling of the IFG compared to typically developing (TD) individuals (Tanabe et al., 2012; Wang et al., 2020). A recent fNIRS hyperscanning study found similarly reduced synchrony in the TPJ during a conversation for autistic individuals as compared to TD individuals (Quiñones-Camacho et al., 2021).

Importantly, some studies have shown that various forms of therapy can improve the ability of autistic individuals to synchronize. For example, autistic children treated with dog-assisted therapy (Griffioen et al., 2020) showed more synchrony with the therapy dog's movements. In a study of music therapy for autistic children, not only did interpersonal synchrony of emotion and behavior improve over the course of therapy, but this improvement generalized to synchrony with an unknown adult administering a diagnostic interview (Venuti et al., 2017). This suggests both inter-brain plasticity and generalization following therapy.

Borderline personality disorder (BPD) has also been associated with reduced synchrony. Individuals with BPD showed reduced behavioral synchrony during a music improvisation task (Foubert et al., 2017). A neuroimaging study revealed reduced inter-brain synchrony in the rTPJ in conversations between individuals with BPD and healthy controls as opposed to conversations between two healthy controls (Bilek et al., 2017). Crucially, the study found that individuals with BPD *in remission* had the same synchrony capability as healthy controls, suggesting that inter-brain plasticity has occurred.

Symptoms of schizophrenia have been associated with reduced movement synchrony (Kupper et al., 2015) and overall interpersonal behavioral coordination (Dean et al., 2021). Interestingly, in a study of human-robot interactions, positive social feedback helped healthy controls, but not schizophrenia patients, improve their motion synchrony with a robot, indicating that it might be especially difficult to induce inter-brain plasticity in such patients (Cohen et al., 2017). Nevertheless, in accordance with inter-brain plasticity as a mechanism of change, a study of body-oriented psychotherapy found that the ability of patients with schizophrenia to achieve movement synchrony increased after therapy (Galbusera et al., 2018).

Major depressive disorder (MDD) has been associated with synchrony deficits, such as reduced movement and facial synchrony in clinical interviews (Altmann et al., 2021). Mothers with a history of major depression were shown to be less synchronized with their children both behaviorally (Granat et al., 2017) and physiologically (Woody et al., 2016). In the context of psychotherapy, a recent study has shown that coupling of the levels of the neurohormone oxytocin between the patient and the psychotherapist is associated with better psychotherapy outcomes for depression (Zilcha-Mano et al., 2021). Another recent study has demonstrated that patients diagnosed with a depressive disorder were less synchronized behaviorally with their therapists than patients with anxiety disorders (Paulick et al., 2018). As with other conditions, the latter study demonstrated that for depressed patients, behavioral synchrony increased as treatment progressed, suggesting that inter-brain plasticity may have occurred.

Social anxiety has also been linked to reduced movement and heart rate synchrony (Asher et al., 2020, 2021). In a recent study, higher movement synchrony was associated with better treatment outcomes for clients with social anxiety (Altmann et al., 2020). However, studies examining anxiety disorders in general, without looking at specific disorders, reported different results; mothers with anxiety disorders had increased synchrony with their children (Granat et al., 2017) and patients with anxiety disorders demonstrated *reduced* synchrony following cognitive-behavioral psychotherapy (Paulick et al., 2018). As the evidence for the significance of behavioral synchrony in anxiety disorders is mixed, special care is required when examining the role of inter-brain plasticity in psychotherapy for these disorders.

The inter-brain plasticity in psychotherapy model and its implications

To integrate the various lines of research reviewed above, we propose a model of inter-brain plasticity in psychotherapy, detailed in **Figure 3**. We posit that (1) Psychotherapy involves high inter-brain synchrony between patients and therapists; (2) by helping patients repeatedly achieve high inter-brain synchrony, therapy increases patients' ability to synchronize with the therapist, and ultimately with others, through inter-brain plasticity and generalization; and (3) this increase in the ability to synchronize underlies some of the beneficial effects of psychotherapy.

As evidence for claim (1), we have reviewed both direct studies (Zhang et al., 2018; Lecchi et al., 2019) showing high inter-brain synchrony during psychotherapy, as well as general research linking inter-brain synchrony with strong relationships. As evidence for claim (2), we have reviewed studies showing increases in inter-brain and behavioral synchrony over the course of parent-child and peer relationships; over the course of learning in a classroom;

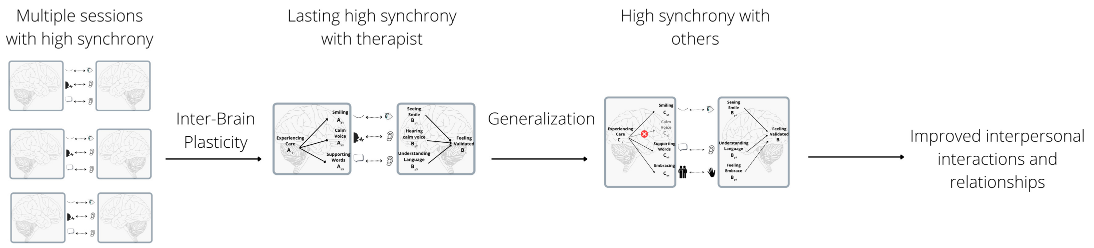

FIGURE 3
The inter-brain plasticity in psychotherapy model. Multiple sessions with high therapist-patient synchrony improve synchrony with therapist. This generalizes to improved synchrony with others, which allows for improved interpersonal interactions and relationships.

and over the course of psychotherapy, as evident in studies showing higher behavioral synchrony after, as opposed to before, psychotherapy. As evidence for claim (3), we have reviewed studies showing that symptom levels of various disorders are correlated with inter-brain and behavioral synchrony deficits, and that changes in behavioral synchrony over the course of therapy are correlated with changes in symptoms (Paulick et al., 2018).

While the model focuses on therapeutic relationships, it does not preclude inter-brain plasticity from happening outside of therapy—to the contrary, we have reviewed many studies showing inter-brain plasticity in other contexts; the proposed model simply focuses on how inter-brain plasticity might operate in a therapeutic setting. However, it does suggest that therapy can potentially lead patients to more inter-brain plasticity than other activities, for two main reasons. First, it posits that therapy is a high-synchrony activity (claim 1). Second, having a positive interpersonal interaction for about an hour with no distractions can be rare in many people's lives; people with synchrony deficits, which are common in many disorders (claim 3), may find it especially difficult to establish relationships in which they have such long, positive, high-synchrony interactions with others regularly. A therapeutic setting allows them to have this type of interaction week after week.

Implications

The inter-brain plasticity in psychotherapy model has three major implications for psychotherapy research and practice. First, as inter-brain plasticity stems out of single brain plasticity, it follows that biological conditions which affect plasticity will have corresponding influence on the efficacy of psychotherapy. Some of these conditions may be difficult or impossible to alter—for example, old age, as well as some neurological conditions, are associated with reduced plasticity (Pascual-Leone et al., 2011). However, some conditions may be alterable, and could be incorporated alongside psychotherapy to increase its effectiveness. For example, having enough sleep (Abel et al., 2013) and engaging in physical activity (Erickson et al., 2012) may increase inter-brain plasticity.

A second implication of the model is that it suggests that directly inducing inter-brain synchrony may have beneficial, long-lasting effects on patients' interpersonal relationships and interactions through inter-brain plasticity. Several methods have been demonstrated to increase inter-brain synchrony. For example, listening to music together was shown to increase inter-brain synchrony (Abrams et al., 2013; Khalil et al., 2022). Performing synchronized arm movements was shown to improve synchrony in a later teaching session, demonstrating that synchronizing can precede the interpersonal interaction (Nozawa et al., 2019). In another study, inter-brain synchrony was increased by administering Oxytocin (Mu et al., 2016). Other researchers examine the capabilities of dyadic neurofeedback to increase interpersonal synchrony and influence interpersonal interactions (Duan et al., 2013; Kovacevic et al., 2015; Dikker et al., 2021; Müller et al., 2021). Finally, in a recent study (Pan et al., 2020b) researchers used dual transcranial alternate current stimulation (tACS) to manipulate synchrony between music instructors and students. Increasing participants' inter-brain synchrony improved learning compared to controls. Interestingly, this improvement was mediated by increased interpersonal behavioral synchrony. Similar manipulations should be examined in the context of psychotherapy—either by incorporating synchrony increasing exercises such as joint music listening into psychotherapy sessions, or by complimenting psychotherapy with separate sessions incorporating dyadic neurofeedback or synchronized movement. While existing models of inter-brain synchrony may also provide mechanisms through which increasing synchrony in-session could improve outcomes (e.g., by improving the therapeutic alliance; Zhang et al., 2018), the inter-brain plasticity model suggests an additional mechanism which may underlie this phenomenon; it also uniquely predicts that separate synchrony-inducing sessions with others, even if they do not include therapy, would be beneficial, as they would also increase patients' ability to synchronize and ultimately lead to better interpersonal interactions and relationships.

A final implication is that inter-brain plasticity could serve as a measure of therapy improvement. While for clinical purposes the high cost of imaging devices may render them impractical, in research settings measuring inter-brain synchrony and plasticity can serve as a measure which is less affected by subjective biases than self-report; imaging during psychotherapy sessions has the additional advantage of providing a continuous measure with which the effects of specific moments in the session may be examined.

Alternative explanations and caveats

Behavioral mechanisms of change

The proposed model does not replace behavioral models of change, such as mediations of therapeutic change by the working alliance (Baier et al., 2020). In fact, for inter-brain plasticity to occur, it must be reflected behaviorally, as behavior (and the perception of it by the other person) is the only way for information to be conveyed between two brains. However, as detailed above, this biological perspective can help understand the contribution of biological factors to therapeutic change (e.g., sleep and physical activity), design supplementary biological interventions (e.g., inducing synchrony by listening to music), and incorporate biological measures into psychotherapy research.

Inter-brain plasticity as a confound

While any psychological change must be reflected somehow in the brain, one could argue that changes occurring during psychotherapy are better understood through a single-brain perspective, and that changes in inter-brain synchrony are mere confounds. Indeed, previous neuroscientific research on change in psychotherapy has identified changes in patients' brains over the course of therapy (Barsaglini et al., 2014). We agree that some of the effects of psychotherapy would be better construed as single brain plasticity. For example, a recent study has identified changes in the neural reaction to spiders after exposure therapy (Rosenbaum et al., 2020). However, we believe that when attempting to document the relational effect of psychotherapy from a neural perspective, a single brain approach would require documenting neural reactions to an extremely wide range of relational stimuli (words, gestures, facial expressions, body postures, etc.). Recognizing that this range of stimuli stem from the presence of another person (and another brain) is a much more parsimonious and allows for a more informative explanation. A recent study supporting this notion attempted to compare single and dual brain explanations in a teaching paradigm (Pan et al., 2020a). Dual brain information was significantly better than single brain information in identifying the teaching style employed in a study session.

Another alternative explanation could be that inter-brain plasticity is a measurement confound, e.g., that it simply reflects statistical properties of measurement, or effects of double measurement of neural data. However, there is evidence that this is not the case. First, some studies show that people who have underwent interpersonal processes which should, according to the model, result in inter-brain plasticity, demonstrate increased synchrony when measured in a single measurement. As detailed above, experienced teachers (Sun et al., 2020) and therapists (Zhang et al., 2020) achieved stronger synchrony than their novice counterparts; in the context of specific relationships, people in stronger relationships exhibit more synchrony (Kinreich et al., 2017; Dikker et al., 2021); and participants with borderline personality disorder in remission show higher synchrony that participants with an active disorder (Bilek et al., 2017). Second, studies looking at synchrony over short time frames (e.g., within a single long interaction) often show that synchrony is stable or even declines (Reinero et al., 2020; e.g., Galbusera et al., 2018). If increases in synchrony were purely due to measurement, we would expect synchrony to increase over short time-frames, perhaps even more than after long periods of time with no measurement (as is the case with evidence of inter-brain synchrony). Still, to fully reject these alternative explanations, future studies should be performed in which the number of measurements varies between participants, to demonstrate that it is not driving inter-brain plasticity.

Future directions

Full model tests

While we have reviewed evidence for the various claims made by the proposed model, no study has directly tested the complete model. Future studies should measure inter-brain synchrony over the course of psychotherapy, ideally both between patients and therapists and between patients and others (to establish generalization). We expect inter-brain synchrony to increase over the course of therapy, and to be associated with symptom reduction. We expect these increases to be associated with the quantity of synchronous experiences (i.e., number of sessions). We also expect such increases to be associated with the levels of synchrony in each session, such that high synchrony in a session would lead to higher gains in synchrony. However, researchers should take care to avoid ceiling effects, as people with a high ability to synchronize might not have much room to improve. Finally, integrating external methods to improve synchrony (e.g., having patients and therapists listen to music together before sessions) could help demonstrate causality.

Moderating factors

As cited above, reduced ability to synchronize is a feature of multiple psychological conditions. However, these conditions might respond differently to improvement in synchrony ability via inter-brain plasticity. In some conditions, difficulties in synchrony may be core features, underlying the condition; in those conditions, improving the ability to synchronize can lead to general psychological change. In other conditions, difficulties in synchrony may be the result of other processes; in these conditions, while improving the ability to synchronize may carry some benefits, these may be rather limited. Importantly, some conditions, such as anxiety disorders, might be characterized by over-synchrony (Paulick et al., 2018) although, as detailed above, evidence is inconclusive. If this is indeed the case, methods to *avoid* increases in synchrony, or to better adapt the level of synchrony to the specific patient, should be developed.

Another important possible moderator is the type of treatment—both the general treatment modality (e.g., psychodynamic vs. cognitive-behavioral therapy, group vs. individual therapy), and the techniques employed in a specific session. A recent study has found that levels of synchrony, as well as the associations between synchrony and outcome may differ between types of treatment (Altmann et al., 2020)—specifically, in cognitive-behavioral therapy, as compared to psychodynamic therapy, movement synchrony was stronger and was more strongly associated with reductions in interpersonal problems, but less associated with the therapeutic alliance. There may well be similar differences in the extent to which different treatment modalities lead to different levels of inter-brain plasticity, or in the extent to which inter-brain plasticity is associated with outcome measures in these various modalities. Similarly, different treatment modalities might foster different types of synchrony (e.g., patient-led or therapist-led synchrony).

Some modes of treatment may foster less inter-brain synchrony, which should lead to less inter-brain plasticity. For example, in treatments which utilize virtual reality (Emmelkamp and Meyerbröker, 2021) or psychoactive drugs (De Gregorio et al., 2021) the therapist usually does not take part in the specific key activity (using a virtual reality device or a psychoactive drug) alongside the patient. This may result in less time spent in high inter-brain synchrony and reduce inter-brain plasticity, at least in the specific sessions in which these activities take place. Other techniques may increase generalization—for example, therapeutic techniques which attempt to simulate outside circumstances, such as imagery rescripting (Arntz, 2012) or role-playing (Kipper, 1986), may help inter-brain plasticity generalize to situations outside of the clinic and increase its impact. Biological factors may also come into play. For example, applying sleep deprivation as part of therapy (Dallaspezia and Benedetti, 2014) may reduce neural consolidation, and as a result reduce inter-brain plasticity. Of course, these ideas should first be examined by future research.

Finally, irrespective of their current ability to synchronize, some patients may have a reduced aptitude for inter-brain plasticity itself, as a result of certain psychological or neurological conditions. According to our model, these patients may gain little from psychotherapy. If such conditions exist, identifying them should be an important research focus.

Implications in other contexts

Inter-brain plasticity as a mechanism of change has implications beyond traditional therapy sessions. First, complex plasticity dynamics may arise when more than two people are present, as in couples or group therapy. Research on group learning has established that groups of students are able to synchronize with a teacher and with one another (Bevilacqua et al., 2019), but synchrony was not associated with material retention. A recent study of physiological synchrony in couples therapy (Tourunen et al., 2020) highlights unique complexities that may arise in these situations; while in general physiological synchrony between couple members increased over the course of therapy, an increase which was associated with better outcomes, female clients' outcomes improved when synchrony between male clients and female therapists *decreased*. These findings demonstrate that in a group setting, participants are not only in or out of synchrony with other participants, but might also be affected by relationships between other participants which do not involve them. Future studies could examine whether inter-brain synchrony in group therapy leads to inter-brain plasticity, look at the ways in which each participant's ability to synchronize influences group processes, and examine the effects of observing other participants being in a high-synchrony interaction.

Second, inter-brain plasticity may have implications for therapist training. As mentioned above, a study by Zhang et al. (2020) has demonstrated that therapists who have completed their training had stronger synchrony with their patients than those just beginning, indicating that the ability to synchronize improves as one trains as a therapist. Future studies may find ways to fine-tune training programs to maximize this kind of improvement.

Conclusion

The current review has presented evidence demonstrating that inter-brain plasticity may be an important mechanism of change in psychotherapy. Effective psychotherapy involves inter-brain synchrony, and repeated interpersonal interactions with high inter-brain synchrony can induce inter-brain plasticity, increasing the ability to synchronize in future interactions. This may be especially true for the core theory of mind network and the observation-execution system.

Finally, inter-brain plasticity may underlie known outcomes of psychotherapy, such as improved coping with various psychological conditions which involve deficiencies in patients' ability to synchronize as well as general improvements in patients' interpersonal functioning. Thus, incorporating the inter-brain plasticity approach can offer new directions for the study of change in psychotherapy.

Author contributions

HS and SS-T conceptualized the proposed model. HS wrote the first draft. SZ-M and SS-T offered critical revisions. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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Positive emotions foster spontaneous synchronisation in a group movement improvisation task

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Emotions are a natural vector for acting together with others and are witnessed in human behaviour, perception and body functions. For this reason, studies of human-to-human interaction, such as multi-person motor synchronisation, are a perfect setting to disentangle the linkage of emotion with socio-motor interaction. And yet, the majority of joint action studies aiming at understanding the impact of emotions on multi-person performance resort to enacted emotions, the ones that are emulated based on the previous experience of such emotions, and almost exclusively focus on dyadic interaction. In addition, tasks chosen to study emotion in joint action are frequently characterised by a reduced number of physical dimensions to gain experimental control and subsequent facilitation in data analysis. Therefore, it is not clear how naturalistically induced emotions diffuse in more ecological interactions with other people and how emotions affect the process of interpersonal synchronisation. Here, we show that positive and negative emotions differently alter spontaneous human synchronous behaviour during a multi-person improvisation task. The study involved 39 participants organised in triads who self-reported liking improvisational activities (e.g., dancing). The task involved producing improvisational movements with the right hand. Participants were emotionally induced by manipulated social feedback involving a personal ranking score. Three-dimensional spatio-temporal data and cardiac activity were extracted and transformed into oscillatory signals (phases) to compute behavioural and physiological synchrony. Our results demonstrate that individuals induced with positive emotions, as opposed to negative emotions or a neutral state, maintained behavioural synchrony with other group members for a longer period of time. These findings contribute to the emerging shift of neuroscience of emotion and affective sciences towards the environment of social significance where emotions appear the most—in interaction with others. Our study showcases a method of quantification of synchrony in an improvisational and interactive task based on a well-established Kuramoto model.

KEYWORDS

interpersonal synchronisation, joint action, emotion, improvisation, non-verbal behaviour

Introduction

Rhythm entrainment is a social glue that helps humans to function and cooperate in large groups, constituting societies (Duranton and Gaunet, 2016). Since ancient times, people have engaged in rhythmic activities, such as singing or dancing, to improve their collective performances, such as hunting (von Zimmermann and Richardson, 2016). More recent historical records disclose that the introduction of synchronous drills into the Dutch Armed Forces in the late 16th century led to building a higher spirit of camaraderie and resulted in developing effective military units on the battlefield that altogether provided an edge for the Dutch army over other armies of the continent (McNeill, 1995). Interestingly, the drilling that made units more effective was believed to have established an emotional resonance between individuals. Consider this testimony of a person engaged in such drills: "Words are inadequate to describe the emotion aroused by the prolonged movement in unison that drilling involved. A sense of pervasive well-being is what I recall; more specifically, a strange sense of personal enlargement; a sort of swelling out, becoming bigger than life, thanks to participation in a collective ritual." (McNeill, 1995, p. 2). This quote draws attention to a surprising interplay between synchronous movements and human emotions, which is the object of the present study.

Synchronisation examples are everywhere around and inside us: from planets orbiting in different galaxies to fireflies firing in perfect unison to pacemaker cells in the human heart. The emergence of spontaneous order is a result achieved through order in space and time. While spatial ordering can be explained and demonstrated by the development of tangible and frequently understood architectures, temporal ordering is more elusive (Strogatz, 2003). For synchronisation to occur, several conditions must be met, such as the production of individual rhythm or oscillations, behavioural proximity, allowing for the exertion of physical or chemical influence and the coupling function (Strogatz, 2003). Fireflies communicate with flashing lights, have their inner rhythm, and adjust it in response to the flashing of others to attain synchronisation. In this light synchronisation analysis is based upon the extraction of individual frequencies and their relation to the group frequency, as well as the extraction of phases, i.e., moments where an event occurs in a time series (Pikovsky et al., 2001).

The phenomenon of human emotion intrigued ancient philosophers and has progressively transformed into a modern field of psychological research. However, the field is suffering from ongoing challenges. The realisation that "There will never be an integrative theory of emotion. . ." (Niedenthal and Brauer, 2012, p. 275) is a surprising way to start the conclusions section of recent Annals publication on the social functionality of human emotion. The difficulty is that there are myriad ways to approach the concept of emotions depending on research interests such as relevance for survival, the implication of cognition, morality, social engagement, or even the tendency for action that gives or seizes power. Despite some agreements on such essential topics as whether to approach emotion as discrete, separate entities (e.g., anger, surprise, and happiness) or in terms of dimensions (e.g., valence, arousal) as well as agreement on the distinction of emotion from other affective states (Ekman, 2016), there is no widely accepted definition after already 100 years of research (Russell, 2012). This poses a problem because the progress in studying a concept with fuzzy borders and subsequent experimental studies can be ineffective without an accurate and clear definition. Thus, it is of utmost importance when studying emotions to outline the aimed concept to explain. We phenomenologically understand emotions as relevance detectors occurring at behavioural, cognitive and physiological modalities that guide the decision process (Sander et al., 2003). Emotion interpretation as a relevance detector has essential consequences concerning the emotion induction method, which will be discussed in more detail in the relevant section. There is, however, an agreement (Sander, 2013) that emotions are a complex phenomenon resulting from clearly identified stimuli and followed by a reaction that brings about change not only in the cognitive modality but is expressed through other modalities as well, such as behaviour and physiology, of relatively short duration. This exemplifies the need to consider the different modalities of human experience for understanding emotions.

Previous research shows that there is a higher chance of losing rapport and creating misunderstandings in the absence of synchronous rhythmical movements. The rhythmic convergence occurring spontaneously between people, without conscious and deliberate efforts to develop synchrony, was reported in experimental studies in which individuals, while sitting next to each other, tend to synchronise swings of their legs (Schmidt et al., 1990), rocking in chairs (Richardson et al., 2007), and side-by-side walking (Nessler and Gilliland, 2009). Interestingly, interpersonal motor synchronisation was found to increase social affiliation (Hove and Risen, 2009), enhance self-esteem (Lumsden et al., 2014), and develop the ability to cooperate (Valdesolo et al., 2010) and even improve tolerance to pain (Tarr et al., 2015). Once we understand the benefits of perceiving movement synchronisation, a logical question is how humans perceive synchronisation? In a dyadic Tai Chi experiment, it was found that the perception of phase synchrony, among other metrics such as mutual information or dynamical time warping, is the most prevailing metric humans use to identify synchronisation (Bente and Novotny, 2020). Continuing this line of thought, one might ask what comes first, is it the affect that causes improved synchronisation or is it the synchronisation that brings about a pleasant feeling? Fujiwara and Daibo (2018) found no evidence that changes in valence produced tangible changes in synchronisation levels. The authors supposed that one possible reason for the absence of effect is that emotion induction did not produce affective changes. Indeed, it is possible that watching parts of movies or specific picture sets, while being an effective induction procedure for some individuals, is not personally relevant when standardised for a multitude of different people. Even if the change in valence occurs, it does not automatically imply that emotion was evoked. Emotion does not only portray changes in valence (Quigley et al., 2014), which alone would describe mere changes in preferences (Scherer, 2005), but they activate special machinery acting through different modalities to prepare the body for the execution of specific actions (e.g., anger—to attack, fear—to run away, and sadness—to seek for help), the process referred to as action tendencies (Frijda, 2007).

The link between synchronisation and physiological arousal was empirically tested previously. For instance, watching a family member engaged in a dangerous activity, the heartbeat of both people tends to synchronise (Konvalinka et al., 2011). Similarly, during dialogue, the brain waves of the listeners tend to synchronise with the speaker's (Hasson and Frith, 2016). What is not yet clear is how the emotional state impacts motor synchronisation. Besides a handful of studies (e.g., Varni et al., 2010; Paxton and Dale, 2013; Tschacher et al., 2014; Fujiwara and Daibo, 2018), the link between emotion and synchronisation remains largely unexplored, and the results are inconsistent. For instance, while Fujiwara and Daibo (2018) did not find evidence for an influence of affective valence on synchrony in a dyadic interaction, Varni et al. (2010) documented that the positive emotion (i.e., pleasure) facilitated synchronisation within a group of musicians in comparison to the negative emotion (i.e., anger).

In a recent review (Bieńkiewicz et al., 2021), we emphasised the need for reconciliation between emotion and joint action research. In line with this proposal, this study aims to show the effects of experimentally induced emotional valence (positive emotion vs. neutral state vs. negative emotion) on group motor synchronisation (arm movements between three people). Given the exploratory nature of this work, we held no quantified expectation about the amount of interactional change following emotional induction but a general hypothesis about the direction of this relationship. Based on the state-of-the-art reviewed above, we expected that positive emotions would improve synchrony and that negative emotions would disrupt it.

Considerations for emotional induction in the lab

In this study, we used a method for emotional induction based on manipulated social feedback. Fundamentally, regardless of the chosen emotion induction method, it is a trade-off between ecological validity and experimental control (Levenson, 2003). Conservative procedures, such as watching video clips (Fakhrhosseini and Myounghoon, 2017), displaying powerful or amusing photos or listening to music, do not entail personal implications. For this reason, we assessed that those methods are suboptimal for our experiment, which concerns the manifestations of emotion in movement and cardiac signals. There are other methods to induce emotions such as autobiographic recall, also known as relived emotions, imagery of specific events and situational procedures such as adapting certain facial expressions to evoke a particular emotion, changing the environmental conditions such as heating the room to an uncomfortable temperature to induce anger, or to provide an enjoyable gift to induce happiness (Siedlecka and Denson, 2019). Deception studies, such as Harmon-Jones and Sigelman's (2001) work on anger and aggression, arguably provide the closest to a real-life type of emotional induction in laboratory settings. The approach we have used in our study that affords high ecological validity relies on deception, based on success-failure manipulations owing to the personal involvement of participants in the process (Nummenmaa and Niemi, 2004), coupled with a picture type of emotion induction.

In this approach, each participant's performance is subjectively evaluated by other members and followed by the presentation of a manipulated (in predetermined order) feedback of being perceived as the best, a tie, or the worst. The feedback is directed explicitly at the individual and their efforts, making the induction more personal. On top of that, if the task based on which the person receives feedback is of personal value, then the induction is expected to generate even a greater effect.

In summary, the original contribution of the present research is an experimental paradigm for studying the natural interplay between synchrony and emotion (positive, neutral, and negative), in the different modalities of behavioural, psychological, and physiological modalities, based on a new analytical tool for adjusting raw, three-dimensional and non-stationary signals to extract phase synchronisation. Specifically, we used a social feedback emotion induction technique based on a personally relevant task. Moreover, we developed an experimental paradigm in which participants explored space in three dimensions (instead of one or two) and suggested a five-step process to analyse group synchronisation for $N > 2$.

Materials and methods

Participants

Thirty-nine adults (21 females, mean age = 25.4 years, SD = 5.7) participated in the study. Participants were volunteers (authors' network and students from various universities in Montpellier) who self-reported enjoying dancing as their leisure pastime or were professional dancers. Thirty-six were right-handed, and three were ambidextrous and obtained an Edinburgh Handedness Questionnaire (EHQ) score > -50. All participants were naïve to the goal of the study. They reported having no physical disabilities of any kind and had normal or corrected-to-normal vision. They did not benefit from any financial or material indemnity and participated with the goal of the advancement of scientific knowledge.

Participants were organised into groups of three people (triads) to perform the task together. These triads were randomly generated in groups of same-sex participants with no prior acquaintances within either of the group members. Most participants ($N = 33$) had no prior improvisational (e.g., dancing, gymnastics) experience other than leisure pastime, and six participants had intermediate experience with occasional group performances.

Before the start of the experiment, all participants read the information letter and gave written informed consent. The Institutional Review Board (IRB #2002A) approved the research protocol of the EuroMov Digital Health in Motion research unit, Montpellier, France.

Experimental setup

The experiment was held in the Motion Capture laboratory of EuroMov. Calibration and data acquisition were performed with the closed shutters daily before the experimental sessions. Body kinematics were recorded with the Vicon motion capture system (Nexus MX13 Vicon System), with eight infrared cameras and a sampling frequency set at 100 Hz. In the experiment, we used nine retroreflective markers placed on each participant, but in the light of the research question addressed in the present article, we used only three markers: right forehead (RFHD), left forehead (LFHD), and right head of the second metacarpal bone (RFIN), providing global information about hand movement. Those body points were selected during pilot runs as meaningful for extracting the participants' body kinematics for the computation of group synchronisation. In addition, we captured participants' cardiac activity *via* the Delsys Trigno wireless biofeedback system with Avanti EKG sensors (placed according to Delsys guidelines). The sampling frequency of cardiac data acquisition was set to 2,148 Hz, with recordings being triggered by the analogue board of the Vicon System to synchronise temporal data alignment. We used the Delsys Trigno Research + system for synchronous recordings of multiple devices. The Vicon system was connected to the Delsys system *via* the Vicon analogue board and a Delsys trigger box. The Delsys System was launched once from the beginning until the end of the experiment. Each time a Vicon recording was launched, the Delsys trigger generated an electrical spike to start acquiring ECG data and dropped to baseline level when the recording stopped. Afterward, these spikes in activity were used to identify the start and end of the trial. The Delsys ECG electrode signal and the Vicon motion capture data were automatically aligned regarding time stamps *via* the Vicon analogue board. Mobile devices were not connected to the Delsys as they were controlled from the Mentimeter website[1] and launched manually for all the participants at the exact moment. We developed a Python code to change the slides simultaneously. For this, we needed to keep the different Mentimeter presentations for each of the participants on separate tabs within a browser. With each click of the letter R, a series of commands were generated: Ctrl 1 (to open the first tab), then right arrow (to go to the next slide), then Ctrl 2, then right arrow, then Ctrl 3 and right arrow.

Before each experiment, the participant number was attributed to each individual in order to anonymise their data for processing. Participants were invited to stand in the part of the triangle in all trials, on a demarcated space for each participant (1.2 m distance in a straight line from each other), with the right hand slightly extended toward the centre of the formed equilateral triangle (angles 60° each). Participants were also asked to charge and bring their phones to the experiment to be used for the emotional induction procedure.

Experimental task

The current experiment was developed based on the mirror game paradigm for dyadic interaction (Noy et al., 2011) and extended to a group interaction (Himberg et al., 2018). Importantly, in our experiment (**Figure 1**), no specific instruction to synchronise was provided. This was to attribute the rise in synchronisation level to spontaneous entrainment

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[1] mentimeter.com

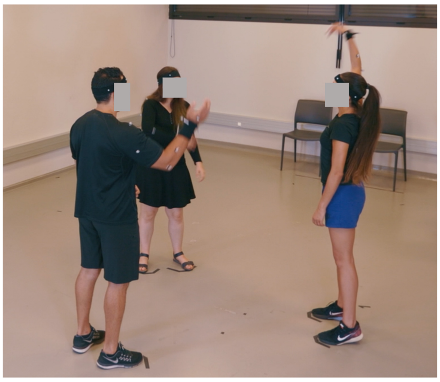


FIGURE 1
Experimental setup with three participants engaged in the movement improvisation task.

between participants. However, during the trial, we kept the original, explicit instruction used in the modified mirror game task to create complex, varied and interesting movements with the right hand. Additionally, we instructed participants not to communicate during the experiment. Finally, participants were asked not to move their feet and only to express themselves with the movements of their right hand.

Experimental procedure

Before coming to the laboratory, the participants received general information about the experiment. To them, the experiment was about personality extraction from movement and the development of group synergies in dancing. Upon arrival at the laboratory and after giving their written informed consent, they were equipped with the motion capture markers and instructed on how to place the Delsys Trigno ECG sensor correctly. Next, the accuracy of the recorded ECG data and specifically a salient QRS complex was verified visually before the experiment's launch. There were 15 trials of 30 s each (7 min and 30 s in total). The order of trials was randomised and counterbalanced across groups. Specifically, two random orders of trials were generated; seven triads were induced accordingly to the first order and six triads were induced accordingly to the second order. Jumping or turning around during the trials was not allowed.

After each trial, participants were asked to rank the performance of each triad member (including themselves) for that particular trial. When all scores were submitted, each participant would receive a (pre-programmed) feedback score for their own performance coming from their triad mates. This feedback based on the group evaluation of one's performance was part of the emotion induction method. The detailed emotion induction method, cover story, and rationale are described in section "Emotion elicitation". Following each trial, all three participants received the same feedback (i.e., all positive, neutral, or negative). Participants could not see the others' scores and thus were unaware that the (pre-programmed) results were the same for everyone.

After each emotion induction, we sought to detect resulted changes in the following trial. A particular case was the first trial which was not included in the analysis because there was no emotion induction before it. As of the second trial, the participants began to evaluate each other's performance in the preceding trial and received an emotion induction followed by a trial that uncovered the induction effect.

The ranking was performed using the participants' own phones connected to menti.com. Mentimeter is a website designed for interactive presentations but was precisely adjusted here by the experimenter for emotion elicitation. Once connected to the Mentimeter presentation, the computer screen was shown to illustrate the outcome of the triad vote (**Figure 2**). Before starting the experiment, participants were asked to answer the questions *via* menti.com and familiarise themselves with the process of answering them on their smartphones.

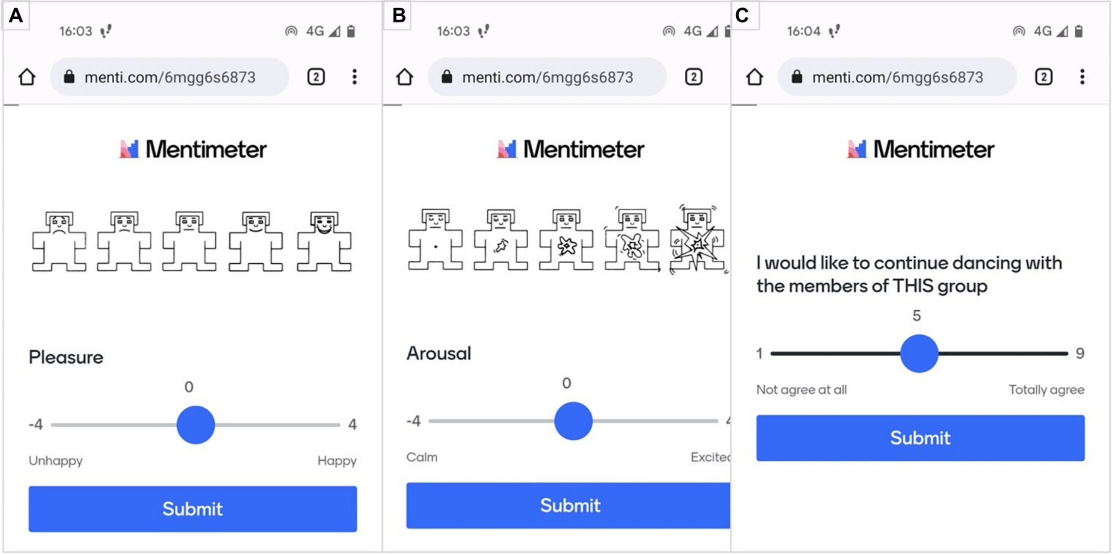
When feedback was submitted, three more questions were prompted on a screen to evaluate two emotion scales—pleasure and arousal—and their social consequences (see **Figure 3**). The first two questions were the scales of affective dimensions derived from the Self-Assessment Manikin (Bradley and Lang, 1994) on valence (**Figure 3A**) and arousal (**Figure 3B**) for assessment of the emotion associated with the participants' performance and the manipulated feedback they received. The third question (**Figure 3C**) assessed the social consequences of the preceding emotional elicitation. In part, it contains the motivational aspect of the individual to perform the task. For this article, the participants' Mentimeter is presented in English, whilst participants received their feedback in French.

Then, the experimenter discussed with participants their impression of the experiment to verify whether anyone understood that obtained feedback was manipulated. Finally, the deception procedure for emotion elicitation of the study was uncovered for participants, as well as the necessity of such a deception design.

Emotion elicitation

All participants were subjected to a social deception procedure with a cover story presented before the launch of the experiment that all participants in the triad would be asked to provide rankings of the performance of their triad mates and receive one themselves, based on the esthetical value and complexity of their movements. Being ranked "the best" provides three points, "second" two points and "third" one point. In such a manner, the range of possible points was between three (everyone ranked a person as the worst) and nine (everyone ranked a person as the best). The cumulative score

FIGURE 2
The first screen was visible before the experiment started to explain to the participants how the feedback worked, first before the votes **(A)**, then after the polls **(B)**, with the possibility that sometimes the scores could be tied **(C)**.



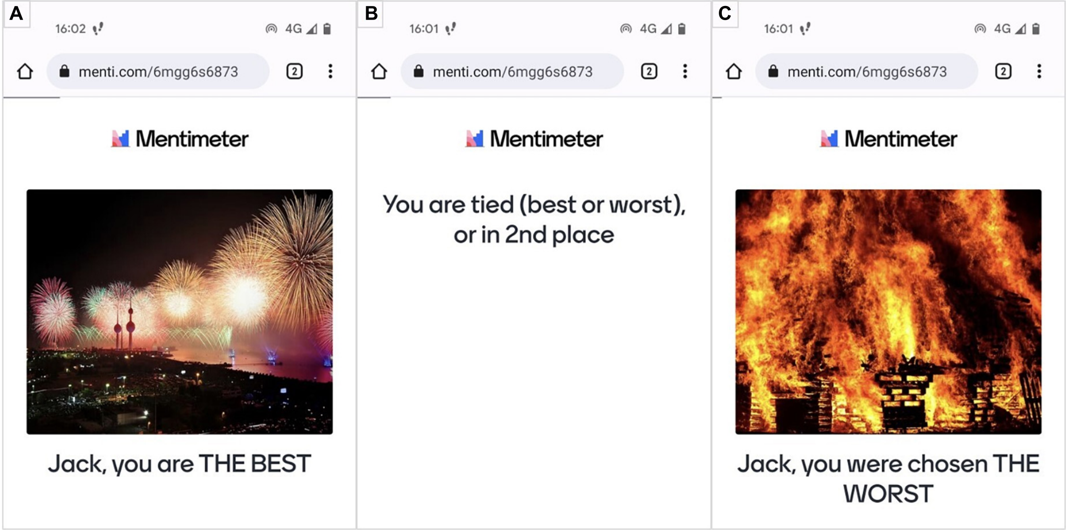
I would like to continue dancing with the members of THIS group

FIGURE 3
Evaluation of emotional [**(A)** pleasure; **(B)** arousal] and social **(C)** consequences after each performed trial.

of rankings of three participants was said to be automatically calculated and then provided personally to each individual.

As stated in the introduction, the emotion induction method is a compromise between ecological validity and experimental control, and we discuss the two aspects. Firstly, for the induction method to have high ecological validity, the goal is to create an elicitation environment in which the induction is personally relevant. For this reason, the task in which the participants are engaged must be of importance to them. Our experimental task is based on expressive improvisation dancing. The emotional induction was achieved through feedback concerning perceived dancing performance. The feedback starts with the participant's name to render the evaluation person-oriented. Specifically, after each trial, the participants received personalised positive or negative feedback: "Name, you are the BEST" (**Figure 4A**) and "Name, you were chosen the WORST" (**Figure 4C**). Receiving evaluative feedback from competent peers of being chosen as "the best" in a personally valuable task (i.e., dancing for dancers) would result in a more positive affect. Conversely, being selected as "the worst" would result in a more negative affect. Moreover, to enhance the feedback's evaluative form and facilitate interpretation by making the evaluation more salient, the words "BEST" and "WORST" were in capital letters. In addition, to reinforce the induction, we used images from the Open Affective Standardized Image Set (OASIS) (Kurdi et al., 2017) of the same arousal level but opposite valence level. In this way, the positive visual stimulus (e.g., fireworks) has a valence score of 6.27 and arousal of 4.98; the negative stimulus, e.g., parts of a house on fire, has a valence score of 1.73 and arousal of 5.28.

The control condition was used as a baseline. We opted for feedback that contained uncertainty for the participants: They would receive the feedback "You are tied (best or worst) or in 2nd place" (**Figure 4B**). We expected that this ambiguity of possibly being the best and the worst simultaneously would result in a more neutral induction.



Jack, you are THE BEST

You are tied (best or worst), or in 2nd place

Jack, you were chosen THE WORST

FIGURE 4
Emotion induction with positive feedback and positively valenced image from the OASIS database **(A)**, neutral state **(B)**, and negative emotion induction with negatively valenced image from the OASIS database **(C)**.

Variables, data processing, and statistics

For our independent variable, there were three experimental conditions for eliciting emotions (within-subject factor): positive emotion (P), neutral state (Nt), and negative emotion (Ng). The stimulus was the feedback received on the smartphones about the ranking score. This score was manipulated, and everyone in the triad received *de facto* the same feedback.

For our dependent variables, three modalities were analysed: behavioural [i.e., Time-in-Synchrony (TIS) scores of velocities], psychological (i.e., Self-Assessment Manikin (SAM) scale (Pleasure, Arousal) and Social Consequences scores), and physiological (i.e., TIS of time series of intervals between two successive heartbeats called the RR interval).

Behavioural data

The three-dimensional coordinates of hand movements were acquired. The hand was decided to be used as a reference point because the task consisted of hand movements, and the information provided by the cinematics of the hand marker was enough to extract the movement richness in the improvisational task. Then, the data were inspected and labelled. Data inspection was performed with the software Vicon Nexus 1.8.5. The labelling of each of three retro-reflective markers (one on hand and two on the head) was performed manually. If the gaps in trajectories were identified, the built-in gap-filling spline function was used.

Several mid-layer variables were calculated from these raw data: coordinate velocities, accelerations, and angles of head markers, which were later used to compute our metrics.

Velocity calculation

The total velocity is the norm of the coordinate velocity vector that is if we note by $P(t) = [x(t), y(t), z(t)]$ the position of a marker at the time t, then the coordinate velocities are

$$\left[\frac{dx}{dt}, \frac{dy}{dt}, \frac{dz}{dt}\right] \text{ and total velocity}$$

$$v(t) = \sqrt{\left(\frac{dx}{dt}\right)^2 + \left(\frac{dy}{dt}\right)^2 + \left(\frac{dz}{dt}\right)^2}$$

The issue with raw velocities is that the anthropometric data influence their calculation. Therefore, we normalised the data before metric calculation. In this experiment, the participants formed a triangle. Each triangle angle was indicated with a special spot on the ground of the laboratory, indicating a specific place for participant one, two and three. Each participant was always occupying the same physical place in all trials. We used three reflective markers placed on the floor, one for each participant, before the start of data acquisition. By keeping the setup consistent across different triads, we were able to use the position of three markers placed on the ground as reference points for the local coordinates of three participants. Then, for each participant, we shifted and rotated each of them to a particular point in space. Then their limb movements were normalised. The maximal distance between the head and hand marker was calculated for each person. Then all position data were multiplied in order to bring this maximal distance to the same value for all three participants. This allowed neglecting the anthropometric differences between individuals.

Firstly, the original velocities (**Figure 5A**) were extracted for each trial. Secondly, local detrending was performed to detect the oscillations by bringing the inflexion points to 0. When we compare the velocity variation between individuals, it is not the amplitude of that variation that counts but the oscillatory part. In simpler terms, a large movement of a particular oscillation would be similar to a small movement of the same oscillations. In order to extract the oscillatory part of the movement, we were inspired by the detrending techniques that we adapted to local levels. Schematically, for a given signal $s(t)$ we first calculate the inflection points $(t(k), s(t(k))$ that is such as $s''(t(k)) = 0$. In other words, we detect instances where a second derivative of the position time series equals 0. Then, we create a piecewise linear curve $L(t)$ by joining successive $(t(k), s(t(k))$ by linear interpolation. This permits calculating the detrended signal $S(t) = s(t) - L(t)$. This operation brings the inflexion points to 0 (**Figure 5B**).

The next step was to bring the local maxima of $S(t)$ to 1 and the local minima of $S(t)$ to -1. These successive new maxima and minima were connected by a local sine-like function (**Figure 5C**). The phases of these oscillatory signals were extracted with the Hilbert transform (**Figure 5D**). Finally, we calculated the Order Parameter of Kuramoto (**Figure 5E**), which quantifies the proximity of phases. Let $\theta_1(t),\ \theta_2(t),\ \theta_3(t)$ be the phases of 3 individuals at time t. The vectors $p_k(t) = exp\,(i \times \theta_k(t))\,,\quad k = 1,\ 2,\ 3$ have modulus 1. The Order Parameter at time t is the modulus of the mean vector.

$$opmt\ (t) = \left| \frac{1}{3} \sum_{k=1}^{3} p_k\ (t) \right|$$

Our metrics of interest—time in synchrony (TIS)—were computed from the phase data. A significant duration threshold of 3 s (10% of trial duration) was used to consider that TIS were valid. Another important point is the thresholds of TIS values. We calculated the probability distribution of Order Parameter values for a given triad through all its trials. Then, the TIS of order parameter was extracted according to the IQR principle, where Q1 represented the lower threshold for the weak synchronisation (less than or equal to 75% of pdf data), Q2—medium synchronisation (50% of data), and Q3— strong synchronisation (25% of data). In this study, we analysed the three levels of synchronisation, and prioritising, however, the results obtained with the weak level. The first reason is based upon the exploratory nature of using the Kuramoto model for the identification of affective information. The second reason relates to the non-linear dynamics literature on human synchronisation, in which humans are often regarded as weakly coupled oscillators (Pikovsky et al., 2001) as opposed to mediumly coupled (e.g., humans with haptic contact such as walking hand in hand) or strongly coupled oscillators (e.g., car wheels connected by the car axle).

In order to verify whether the effect found was not due to chance, we randomly generated new fake triads, or

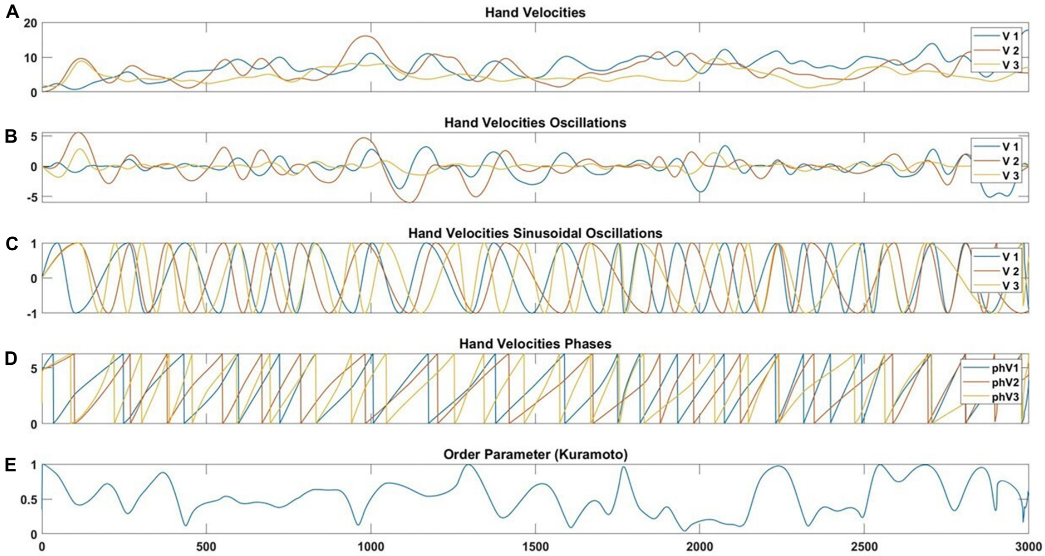


FIGURE 5
Illustration of the velocity pre-processing steps. Taking the raw signal **(A)**, implementing local detrending **(B)**, and the undulatory part of the signal **(C)** are used to extract phases with the Hilbert Transform **(D)** and implementation of the Kuramoto order parameter **(E)**. Within the graph legend, the V1, V2, and V3 correspond to the velocity of participant 1 (V1), participant 2 (V2), and participant 3 (V3). In addition, the phV1, phV2, and phV3 correspond to the we extracted phase velocities of participant 1 (phV1), participant 2 (phV2), and participant 3 (phV3).

pseudogroups, and compared them with the experimentally obtained data. Pseudo groups were organised by shuffling velocity time series from all triads and all trials and then randomly pairing them. For instance, one pseudo trial could be organised by pairing velocity time series from Participant (1) Triad (1) Trial (1) with Participant (3) Triad (11) Trial (9) and Participant (3) Triad (4) Trial (15). Afterwards, the other velocity time series were shuffled and paired until all the pseudo trials were generated.

Finally, to control that the task was executed correctly and that the participants were paying attention to each other, we dynamically built a triangle out of the head data for each individual. First, the centre point between each pair of LFHD and RFHD was found. The left-head to right-head points define a parallel to face vector f. Then a perpendicular vector to f was derived to detect the facing direction (head orientation). For each pair of participants (i, j) there were two numbers extracted. Pair i-j means participant i is facing participant j and pair j-i means that participant j is facing participant i. There were six pairs of numbers, two for each participant (e.g., for participant one: pair 1-2 and pair 1-3). The angles were calculated for each participant's directedness into the triangle. For the clarity of calculation, the angles were transformed into percentages. For example, the value of 0.5 means that the head orientation was exactly in the centre of the triangle. For a dynamical triangle for this specific angle with an angle of 80°, the 0.5 value means that the facing angle is 40°. The closer the value is to 0 for one pair, the more this first participant orients their head toward the second person. If the value is 1 or above, it means that the person is looking at the opposite person or even further outside the triangle. Negative values are not possible. We arbitrarily chose the value of 0.6 as a threshold for head orientation inside the dynamical triangle.

Psychological data

To detect how successful was the induction, we used Self-Assessment Manikin (SAM) scale (Bradley and Lang, 1994). It is a graphical and non-verbal procedure that portrays human-like figures with different faces and sizes for two different scales: pleasure and arousal. For the valance scale, figures range from unhappy to happy and for the arousal scale, figures range from calm to excited. Participants were instructed to identify themselves corresponding to their place on the continuums. The values for both scales ranged from −4 to 4. In addition, given a number of outcomes to which leads synchronisation, we included a scale for social consequences to investigate the impact of emotional induction and movement in unison on the desire to be engaged with the same individuals in the same activity in the future. The question ranged from 1 to 9 and participants needed to choose a score corresponding to their desire at the moment of being engaged with the same individuals (see **Figure 3**).

Physiological data

We obtained the ECG data with wireless Trigno Avanti Delsys biosensors. Participants placed the electrodes on disinfected skin for better electrical connectivity using the Delsys manual in a modified 3-lead ECG configuration. Electrode V− was placed on the left side below pectoral muscles on the lower edge of the left rib cage. Electrode V+ electrode was placed on the right side below the pectoral muscles on the lower edge of the right rib cage. The sensor body was placed under the positive electrode. R waves are the highest peaks seen on the ECG making them the easiest waves to detect. To be able to analyse heart data, we implemented sym4 wavelet transform to identify the R waves within the QRS complex. Given that individuals vary with regard to their resistance to the current flow as well as slight differences in electrode placements, the obtained ECG signal was of varying amplitude between different people. This caused the peak height to vary between the individuals that do not allow a one-size-fits-all parameter (i.e., the height of the peak and the distance between two successive peaks). To deal with this, as well as with artefacts for pre-processing of the data, we followed a series of steps: firstly, we automatically implemented wavelet transform on all the trials on all the people automatically in a loop. Then, we identified the physiologically implausible values for a moving person with an additional margin (i.e., less than 60 bpm or more than 120 bpm). If the chosen amplitude threshold is too high for a given individual, that will cause not identified peaks leading to a strongly decreased bpm rate. If on the other side the chosen amplitude threshold is too low for a given individual, that would identify by mistake not only the R wave leading to a strongly increased bpm rate. Afterward, these peaks were manually adjusted for each 30-s trial for each individual and compared visually with the raw ECG signal to ensure the correct detection.

Once the R peaks were accurately detected, they were modified into millisecond intervals between two successive heartbeats (i.e., RR intervals). To prepare such a non-stationary signal for phase detection, we transformed the signal. We created a new time series where we allocated number 1 for the time points of identified peaks. Next, we identified the midpoints between each pair of two successive heartbeats and allocated the number −1. This allowed deriving a sinusoidal-like time-series signal prepared for the Hilbert transform implementation. While this transformation brings to the artificial +1 value the heart peaks, it keeps absolutely all information about heart beat intervals and variability identical. It has the advantage that the transformed signal can be processed with continuous signal processing tools (FFT analyses, Hilbert transform method) in order to extract the phase modulation, and allows to interpret results from different levels of analysis (e.g., behavioural, physiological) in the same "language."

Separate one-way repeated measure ANOVAs were run on each of the metrics of interest, with appropriate *post hoc* comparisons to clarify significant differences between conditions. For this, we averaged different trial values per each emotion nested within each triad (i.e., an average of five trials for each of three emotional conditions). Statistical analyses were performed in the JASP software.

Results

Emotion effect on movement synchronisation

To investigate the impact of emotion, our independent variable, on spontaneous time spent in synchronisation, our dependent variable, we used the TIS metric of the *weak* level. This value was obtained per each trial as a cumulative score for the three participants. The possible range of values is between 0 s (e.g., no attained synchronisation) and 30 s (e.g., synchronisation during the whole duration of the trial). There was a statistically significant main effect of emotion on TIS behavioural scores suggesting that there was a difference between at least two experimental conditions, $F(2, 24) = 61.65$ ($p < 0.001$), $\eta_p{}^2 = 0.84$. The measures of central tendency and dispersion are as follows: negative emotion (mean = 19.84, SD = 0.41), neutral state (mean = 20.08, SD = 0.67) and positive emotion (mean = 22.28, SD = 0.54). *Post hoc* pairwise *t*-test comparisons with Bonferroni correction revealed that positive emotion was statistically significantly different from negative ($p_{bonf} < 0.001$, 95% CI = [−3.06, −1.82]) and neutral state ($p_{bonf} < 0.001$, 95% CI = [−2.81, −1.57]) no significant difference between negative emotion and neutral state ($p_{bonf} = 0.952$, 95% CI = [−0.87, 3.75]). This indicates that participants spontaneously spent more time in synchrony when they were positively emotionally induced (**Figure 6**). The effect was non-significant for medium level of TIS $F(2, 24) = 3.27$ ($p = 0.055$), $\eta_p{}^2 = 0.21$ and remained significant for high level of TIS $F(2, 24) = 5.87$ ($p = 0.008$), $\eta_p{}^2 = 0.33$.

To test whether this result was due to chance, we carried out pseudo synchrony measures. This approach consists of random reorganisation of individual trials from different triads and computing of the TIS scores. This pseudo behavioural synchrony measure was not significant for any pair of emotions [$F(2, 24) = 0.14$ ($p = 0.870$), $\eta_p{}^2 = 0.01$], suggesting that the effects of emotion on movement behaviour are not due to chance. With respect to controlling the head orientation, we have arbitrarily chosen a threshold of 0.6 of the values within the dynamic triangle, and we obtained less than 15% of data points larger than the threshold. Given the approximative nature of the threshold, this amount of data is inconsequential and therefore we can conclude that participants complied with the instructions for executing the task and were paying attention to each other.

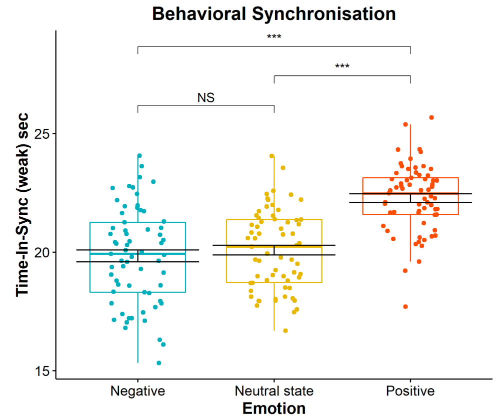


FIGURE 6
Time in synchrony (s) pairwise comparison for each of the three emotional conditions (negative emotion, neutral state, and positive emotions). Each dot represents a score of one 30 s trial. Significance levels 0.001, 0.01, or 0.05 are indicated with *, **, and *, respectively.

Emotion effect on pleasure, arousal, and social consequences

Right after every emotional induction and before the execution of the movement in the next trial, participants reported scores on the Self-Assessment Manikin (SAM) scale. There were two 9-item scales, pleasure and arousal, ranging from −4 to 4. In addition, there was a social consequence on 9 item scale ranging from 1 to 9. The scores for the SAM questionnaire as well as the social consequences item are the dependent variables.

For the SAM pleasure score, there was a statistically significant main effect of emotion on SAM pleasure scores suggesting that there were differences between at least two experimental conditions [$F(2, 24) = 3.85$, $p = 0.035$, $\eta_p{}^2 = 0.24$]. The measures of central tendency and dispersion are as follows: negative emotion (mean = 1.75, SD = 1.17), neutral state (mean = 2.05, SD = 0.85) and positive emotion (mean = 2.22, SD = 0.86). *Post hoc* pairwise *t*-test comparison revealed significant difference only between negative and positive emotional conditions ($p_{bonf} = 0.034$, 95% CI = [−0.92, −0.03]) but not negative and neutral ($p_{bonf} = 0.282$, 95% CI = [−0.75, 0.14]) nor neutral and positive ($p_{bonf} = 0.982$, 95% CI = [−0.62, 0.27]). The results indicate that positive emotional induction generated perceived higher valence scores and negative emotional induction caused a decline and lowered valence score.

For the SAM arousal scores, the sphericity assumption was violated and therefore the Greenhouse-Geisser correction was implemented. There was no statistically significant difference [$F(1.38, 16.76) = 2.80$, $p = 0.103$, $\eta_p{}^2 = 0.19$].

For the social consequences scores, there was a statistically significant main effect indicating that there was a difference between at least two experimental conditions [$F(2, 24) = 13.95$, $p < 0.001$, $\eta_p{}^2 = 0.54$]. The measures of central tendency and dispersion are as follows: negative emotion (mean = 6.28, SD = 1.54), neutral state (mean = 6.64, SD = 1.34) and positive emotion (mean = 6.90, SD = 1.30). *Post hoc* pairwise *t*-test comparisons were significant for negative and neutral ($p_{bonf} = 0.017$, 95% CI = [–0.66, –0.05]) and negative and positive ($p_{bonf} < 0.001$, 95% CI = [–0.92, –0.32]) but was not different between neutral and positive inductions ($p_{bonf} = 0.105$, 95% CI = [–0.56, –0.04]). Negative emotion had the weakest social consequences and positive having the strongest ones.

Emotion effect on physiology

We transformed the raw inter-beat interval time series into an oscillatory-like time series. This allowed the implementation of Kuramoto analysis and specifically the time series of the order parameter TIS, the dependent variable, per each executed trial as a function of induced emotion, the independent variable. The main effect of emotion on the physiological rhythm entrainment (dependent variable is TIS scores of RR intervals) was also investigated using the one-way repeated measures ANOVA. The results were not significant [$F(2, 24) = 0.53$, $p = 0.594$, $\eta_p{}^2 = 0.04$]. The effect was neither significant for medium level of TIS [$F(2, 24) = 1.14$, $p = 0.336$, $\eta_p{}^2 = 0.09$] nor for the high level of TIS [$F(2, 24) = 0.57$, $p = 0.576$, $\eta_p{}^2 = 0.05$].

Discussion

The aim of the present study was to investigate the effect of naturalistically induced emotion on synchronisation occurring across behavioural, psychological, and physiological modalities, with positive emotion expected to facilitated the beat in unison between interactants and negative emotion to disrupt it.

Behavioural modality

We confirmed our hypothesis that individuals induced with positive emotion would spend more time in spontaneous synchronisation than when they were induced with a neutral state and negative emotion conditions. Nevertheless, the negative emotion was not significantly different from the neutral state. These results confirm earlier findings (for instance, Tschacher et al., 2014) and suggest that positive affect is positively correlated to interpersonal movement synchronisation. At the same time, the observed asymmetry between positive and negative inductions contradicts the well-established negativity bias in psychological research (Rozin and Royzman, 2001) that humans are more efficiently induced by negative emotions than by positive ones. It is possible that moving together and just the mere sharing of a physical space facilitate interaction and help people bind together. Presumably, the improvisational type of interaction affords individuals with a drive towards social "likes" to develop strong social ties. There were no significant differences in TIS scores between negative emotion and neutral state. In fact, we have built the neutral condition in such a way that the ambiguity of possibly being the best and the worst at the same time would result in a more neutral induction. It is possible that this would have induced a positive valence in some participants and negative valence in others. However, as differences were found between neutral and non-neutral conditions for some variables (for instance, the social consequence score, see below), this possibility is not entirely convincing.

Psychological modality

We obtained a significant effect of emotion on pleasure scores but not arousal scores. As mentioned in the introduction, human emotions are not just changes in valence (pleasure scale) but involve a delicate combination between valence, arousal, behaviour and physiology. Given that there were emotional effects not only at the behavioural modality but also at the psychological level, we can conclude that the emotion induction was successful. As for the social consequences, the positive induction increased personal will to engage in a task with the same group members and this was decreased with the negative induction. This is rather a straightforward finding, as it suggests that our social consequences variable can determine the potential benefits of synchrony. What is not yet clear is whether this effect is due to emotional induction, movement synchrony, or both. This is important because it can be used as a tool for developing synergies and strengthening the cohesion levels of a group to attain higher performances.

Physiological modality

We did not find any significant main effect of emotions on the cardiac activity of the triad. What can be the reason(s) for the absence of an experimental effect on the physiological synchrony, an effect that was found before (e.g., Konvalinka et al., 2011)? One reason may relate to the different metrics used in different studies. For instance, Konvalinka et al. (2011) used a recurrence quantification analysis on cardiac activity, whereas we transformed the signal into a sinusoidal-like signal in order to homogenise our analyses between behavioural and physiological modalities. Another reason relates to the possible impact of physical activity on the Autonomic Nervous System (ANS), which is perhaps larger than the impact of emotion on ANS and could have dominated it. The possible solution is to adapt the task and adopt one that would reduce the movement components to their minimum.

Conclusion, limitations, and future work

From a theoretical standpoint, this study contributes to verifying whether ecological emotion elicitation can be manifested in human movement and interpersonal motor synchrony and provides a fundamental understanding of how different affective states result in human group synchronisation. From an applied perspective, these results can be used in the rehabilitation context, in which, based on the patient's movement, synchrony-based recovery interventions can be used to develop rapport (Fuchs and Koch, 2014) and facilitate, for instance, Autism Spectrum Disorder adaptations (Manders et al., 2021). They can also be used to improve human-machine interactions, for example, in adjusting behavioural interactions with human individuals based on their affective state and creating synergies within the group.

One limitation of our study is the possible blending of the effect of two different emotional induction procedures (i.e., deception based on social comparison and affective picture dataset). We cannot completely separate the part of emotion induction that relates to the naturalistic scenario of being evaluated in a personally valuable task by others and the part of emotion induction coming from emotionally inducing pictures. For this reason, a separate study might test each induction method in isolation and then together, preferably within a repeated-measures design to reduce the inter-individual differences. The goal of the present study was not to validate a specific and unique method of induction but rather to attain a high induction efficiency. In this light, the choice of reinforcing manipulated social feedback with an intuitive and fast mean appears justified. In post-experimental debrief, spontaneous feedback provided by a few participants was that they understood immediately from the pictures, without reading the text, whether they were getting a positive or a negative result. In such a manner, it seems that the pictures cued some participants to a specific emotion and helped make the induction instantaneous.

Another limitation of our study is the potential entanglement between emotion and motivation for the chosen experimental task. Indeed, after receiving evaluative social feedback with respect to their own performance, participants could have been more motivated in doing the task, creating a potential confound between emotion and motivation. Against this interpretation are the facts that emotion and motivation are not entirely stackable—the same negative emotion induction for the same individual can arouse anger and increased motivation on one occasion, and can cause sadness and decreased motivation on another occasion—and that a negative induction would have produced an increase in synchronisation, a result that was not found. More, we did tangentially control for the participants' motivation in our experiment, with the third question asked after each trial "Would you like to continue dancing with the members of this group?" We argue that this question embraces the motivation of individuals to engage in the task by exploring the fluctuations after each emotional induction. Answers to this question were significantly different between emotion conditions (i.e., lowest—negative, middle—neutral state, and highest—positive). Emotion is an emergent phenomenon that builds on motivation, and it is hard to separate them clearly. Emotions are intrinsic in individuals' achievement patterns (Nicholls, 1984; Dweck, 1986) and are approached as action tendencies (Frijda, 2007), suggesting that each experienced emotion guides and motivates individuals to engage in a specific action (e.g., anger to fight or fear to flight).

Due to the low sample size, care should be taken in generalising the presented findings. In addition, it is possible that emotional induction did not affect all triads and participants in the same way. Nevertheless, our statistical results related to the effect of emotion on behavioural TIS are strong (**Figure 6** demonstrates clustering of all data around mean values), indicating that despite interpersonal variability, there was a common and shared tendency toward spontaneous synchronisation.

This research focused on behaviour that combines naturalistic emotion induction and improvisational movements, with a trade-off between ecological validity of emotion induction and experimental control. This highlights the cardinal importance of selecting the best possible trade-off: Ecological validity shall not be sacrificed for the sake of high requirements for experimental control.

In future research, approaching emotion within a repeated-measures design seems a good strategy to be particularly cautious with the emotional aftereffects (Halovic et al., 2020), especially paying attention to the effect of emotions that can build up over time. Notably, emotions are non-linear in nature, meaning that one stimulus does not produce the same reaction between different individuals and even within the same individual on different occasions. Moreover, emotional induction is complicated for the repetitive type of experimental paradigms owing to a gradual individual's sensitisation to the same stimuli. This formulates a prominent line of research for mutually adapting human-computer and human-robot interaction systems that are occasion sensible and adjustable.

Another avenue when quantifying joint action in general, and synchronisation in particular, is to investigate different emotion entanglement in interpersonal adaptations (Burgoon et al., 1995; Hart et al., 2014). For instance, how much the interaction shapes the individual's behaviour reflects the degree of behavioural change, which could be informative for illustrating the strength of interaction as a function of emotion. Additionally, the direction of change, or its absence, could reflect leadership processes within group dynamics and whether some emotions overpower others when there are more representatives with one particular emotion rather than another.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://osf.io/d45t3/.

Ethics statement

The studies involving human participants were reviewed and approved by IRB 2002A of the EuroMov Digital Health in Motion. The patients/participants provided their written informed consent to participate in this study.

Author contributions

AS conceived the idea of the manuscript with the help of MB, SJ, and BB, collected the data with the assistance of SP, analysed the data under the supervision of SJ and BB, and wrote the first draft of the manuscript. MB, SJ, and BB contributed to manuscript revision, and read and approved the submitted version. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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Dyadic nonverbal synchrony during pre and post music therapy interventions and its relationship to self-reported therapy readiness

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Nonverbal interpersonal synchronization has been established as an important factor in therapeutic relationships, and the differentiation of who leads the interaction appears to provide further important information. We investigated nonverbal synchrony – quantified as the coordination of body movement between patient and therapist. This was observed in music therapy dyads, while engaged in verbal interaction before and after a music intervention in the session. We further examined associations with patients' self-reported therapy readiness at the beginning of the session. Eleven neurological in-patients participated in this study. Our results showed an increase in both nonverbal synchrony and patient leading after the music intervention. A significant negative correlation was found between self-reported therapy readiness and nonverbal synchrony after the music intervention. These findings point to the empathic ability of the music therapist to sense patients' therapy readiness. Higher patient leading in nonverbal synchrony after the music intervention may thus indicate that the music intervention may have allowed dyadic entrainment to take place, potentially increasing self-regulation and thus empowering patients.

KEYWORDS

neurological rehabilitation, therapy readiness, therapeutic relationship, motion energy analysis, nonverbal synchrony, music therapy

Introduction

Nonverbal synchrony plays an important role in the therapeutic relationship in psychological counseling and psychotherapy (Ramseyer and Tschacher, 2006, 2011; Altmann et al., 2020; Cohen et al., 2021). Music therapy is not only closely related to psychotherapy, but it also takes place within a therapeutic relationship (Österreichischer Berufsverband der MusiktherapeutInnen, 2022). Indeed, the therapeutic relationship is a crucial part of the therapeutic process, 30% of the client's improvement is accounted for by the therapeutic relationship (Asay and Lambert, 1999). Therefore, it is of great interest to music therapists to be able to capture nonverbal synchrony during their therapy sessions to deepen their understanding of their therapeutic relationships with patients. For this reason, we investigated the phenomenon of nonverbal synchrony during music therapy sessions between therapeutic dyads. Specifically, by comparing nonverbal synchrony, which we defined as quantified coordination of body movement between patient and therapist, while they engaged in verbal interaction before and after a music intervention, using a novel method in music therapy research such as Motion Energy Analysis. Our present study also sought to establish possible associations between nonverbal synchrony and patients' self-reported therapy readiness.

Conceptual background

Synchrony

The world we live in is fond of synchrony. In nature, we observe synchrony as we watch the wonderfully coordinated dance of swarms of birds returning to their nests at dusk. At night, by the tidal rivers of Southeast Asia, thousands of male fireflies congregate in trees, exhibiting in harmony their mating call; a mesmerizing silent concert of synchronized pulsating lights along the water (Strogatz and Stewart, 1993). Even deep inside our body, cells of our hearts generate an electrical rhythm in unison so as to command our hearts to beat, repeating this synchronized action for billions of times in our life time (Strogatz, 2015). In the 17th century, the Dutch astronomer and great inventor, Christiaan Huygens observed and described the phenomenon of the "Sympathy of two clocks". Forced to stay in bed due to illness, he observed the synchronization of two pendulum clocks which were hanging on a wooden beam. Even after he had disturbed them, they would eventually come to tick simultaneously again. Both clocks were apparently coupled to each other through a free medium, which was the flexible wooden beam, and therefore showed mutual synchronization (Pikovsky et al., 2001).

The word "synchrony" stems from the Ancient Greek words "chronos" (meaning time) and "syn" (meaning common). Taken together, synchrony translates to "occurring at the same time" or "sharing the common time"; an object adjusting its rhythm in conformity with the rhythm of other objects (Pikovsky et al., 2001). In music, "synchrony" could mean a period of phase-locking to an external referent, such as a metronome (Lindenberger et al., 2009). However, when two musicians play together, both interact and adjust toward each other to fit into the created or agreed tempo, creating a common phase which they both "lock in" to, synchronizing electrical brain activity as evidenced in dual EEG studies (Lindenberger et al., 2009). The process of getting "in synch" is described as "entrainment", it is a process in which two different rhythmic systems adjust to each other although the entraining rhythms do not match precisely (Clayton et al., 2004). Instead, their relationship with each other presents certain regularity (Bluedorn, 2002). The understanding and application of the terms "synchrony" and "entrainment" are not universal at all. Many terminologies have been applied to describe the interdependence behaviors of dyadic partners, such as the chameleon effect, mimicry, behavior matching, attunement, social resonance, synchrony, etc. (Delaherche et al., 2012; Chartrand and Lakin, 2013). The usage in therapy, anthropology, communication studies, etc., varies, depending on the context and the application in the different disciplines (Gill, 2012).

Nonverbal synchrony

Similar to the two clocks hanging on a single beam, when we observe another person or interact with them, we tend to adopt the physiology and behaviors matching his or her affective state (Stephens et al., 2010; Ebisch et al., 2012). The automatic mirroring of behaviors or the unconscious alignment of physiology during interactions is also called interpersonal synchronization (Feldman, 2007). Referring to Condon and Sander (1974) frame by frame analysis of mother–infant interaction, Aldridge discussed how talking and listening, co-creation and turn-taking find an analog nonverbal structure in music therapy improvisation (Aldridge, 1989).

This coordinative interaction helps us in our daily dealings and is integrated into multiple facets of our social lives (Kendon et al., 1975; Hu et al., 2022). It is a fundamental capacity, essential for us to be social (Cross, 2005). It existed as a main form of communication before language came into being and functions as a "social glue" (Lakin et al., 2003), bringing harmony to relationships and creating bonds. Infants engage in proto-conversation by using their congenital ability to synchronize with the impulses in the action of the parent's voice and gesture (Trevarthen, 2008). This skill is trained and honed while engaging in "motherese", an ability developing out of infant-directed speech synchronizing movement and nonverbal elements of vocalizing during "baby-talk" that would give the child a stronger bonding with the mother/carers and a higher likelihood of survival in adulthood. It seems that evolution has permanently engraved these nonverbal abilities to entrain and synchronize with others in us, making them instinctive and unconsciously coordinated when we interact with one another (Lakin et al., 2003; Gueguen et al., 2009; Gill, 2012).

Nonverbal interpersonal synchronization is regarded as an important factor in psychological counseling and psychotherapy related to building rapport and empathy (Kodama et al., 2018; Wiltshire et al., 2020). It plays a quintessential role in the development and maintenance of a positive therapeutic relationship (Ramseyer and Tschacher, 2006; Altmann et al., 2020; Cohen et al., 2021). Patients rate sessions with increased nonverbal synchrony as having higher relationship quality. Nonverbal synchrony is also higher with patients experiencing high self-efficacy and higher symptom reduction at the end of treatment (Ramseyer and Tschacher, 2011).

Music therapy research on nonverbal synchrony between dyads has focused predominantly on the population of autistic spectrum and neonatology. Indeed, nonverbal synchrony is an important indicator of the social and communication skills of children with Autism Spectrum Disorder and severe multiple disabilities (Neugebauer and Aldridge, 1998; Venuti et al., 2017; Johanne and Holck, 2020). It also plays a central role in music therapy with prematurely born infants to reduce stress (Haslbeck, 2014).

In a neurorehabilitation setting, Street et al. (2019) found indications that the auditory-motor pathway can be potentially fortified when the external auditory cues are internalized and patients are able to synchronize their movements independently. Other studies using Rhythmic Auditory Stimulation, which is also based on auditory-motor synchronization, have demonstrated its high success in gait training for various neuropathological gait disorders (Thaut and Abiru, 2010; Braun Janzen et al., 2022). Studies have also supported the efficacy of music therapy on mood, depressive syndromes, and the quality of life of neurological patients (Raglio, 2015). However, there has been so far no research in music therapy exploring nonverbal synchrony in the neurorehabilitation setting that uses state-of-the-art methods that are already established in current psychotherapy research.

Just as it is vital in psychotherapy, therapeutic relationship and alliance are also important factors in music therapy treatment (Silverman, 2019). Indeed, therapeutic relationships between music therapy dyads was found to be predictive of generalized clinical changes of symptom severity in children on the autism spectrum (Mössler et al., 2019). Therefore, this study applied methods already adopted in psychotherapy research to examine the nonverbal synchrony between patient and music therapist during verbal communication before and after the music intervention in a neurorehabilitation setting. The study expects to acquire a new perspective to examine therapeutic alliance and relationship in music therapy research to increase knowledge of effective factors in music therapy processes.

The effects of who is leading (driver) and who is following (driven) during synchrony are relevant to the association between nonverbal synchrony and therapeutic success (Altmann et al., 2020). Patient leading during nonverbal synchrony has been associated with patient's self-efficacy, whereas therapist leading has been associated with their therapeutic alliance (Ramseyer and Tschacher, 2011). Schoenherr et al. (2019a) found that it is crucial in the early phases of therapy for patients to be leading and therapists to be following, as this would indicate that the patient is speaking. This, in turn, was associated with a lower dropout rate. Therapist leading, on the other hand, influences the clinical outcome. Attention should also be given to what was happening in the session during the shifting of leadership (Schoenherr et al., 2019a). As music therapy is based on a process of mutual relation, the possible implications of leading and following are also of interest, although leading and following in a music therapy context can have reverse signs. The therapist may be leading the music therapy process while following the patient's play, and encouraging them to lead the musical activity (Brown and Pavlicevic, 1996). Based on their study with children with Autism Spectrum Disorder, Mössler et al. (2019) suggested that music therapists should be able to attune musically and emotionally to their client's way of communicating and relating, so that clients can develop meaningfully by giving them the opportunities to respond and relate.

Therapy readiness

Readiness can be defined as "patient's positive attitude and preparedness to enter into a therapeutic relationship for the purpose of resolving problems" (Ogrodniczuk et al., 2009, p. 427), and having therapy readiness indicates being motivated for therapy (Rapp et al., 2007). Constructs such as the five stages of change, taken from the transtheoretical model of change (Prochaska and DiClemente, 1983), or the readiness for therapy questionnaire by Ghomi et al. (2021), are used in mental health care to predict how likely a person is going to complete therapy or achieve their goals. Therapy readiness is closely related to common factors of psychotherapy such as "readiness to change" and "patient engagement", which are considered predictors of therapeutic success (Tschacher et al., 2014a).

Timing is an important factor for therapy readiness, and there is only one study that investigated when in the cancer treatment process should music therapy begin (von Allmen et al., 2004). However, timing also applies to the time of day and seasons. The effects of circadian patterns and seasonal changes are well known, for example, for people with depression (Germain and Kupfer, 2008; Wirz-Justice, 2008). Their mood is highest in summer and lowest in autumn and winter. Patients feel worst in the morning and get better as the day progresses. It is important to bear this in mind when scheduling music therapy sessions because daytime and our mood influences how we perceive music and also how we perceive ourselves (Brabant and Toiviainen, 2014). It affects our perception of musically-expressed emotions and also the recalling of memories from our lives, which has direct effects on our sense of self and our outlook on life (Fachner et al., 2017). Thus, the efficacy of music therapy could be increased if we can schedule music therapy sessions at the most suitable time. This information can also help music therapists to better interpret the events during a session, and a better understanding of chronopharmacology will also enhance the effect of medication and music therapy (Fachner et al., 2017). The chronobiological approach of considering temporal processes in biology is a holistic one (Balzer, 2009).

The first goal of this study was to analyse the change in nonverbal synchrony between patient and therapist quantified as the coordination of their body movement. We expected to find an increase in nonverbal synchrony after a music therapy intervention compared to synchrony prior to the intervention. Second, we explored the possible correlation between nonverbal synchrony and patients' self-reported therapy readiness as well as the leading characteristic of synchrony, to deepen our understanding of the meaning of nonverbal synchrony. We expected a positive correlation between pretalk nonverbal synchrony and therapy readiness.

Materials and methods

Sample

This nested study was embedded in a larger research project "Assessment of favorable therapy times for patients in neuro-rehabilitation" (Dür et al., 2022), focusing on developing evaluation methods to assess therapy readiness which involved $N = 60$ participants who were in-patients of a neurological rehabilitation facility in lower Austria. Music therapy was not in the standard treatment but it was offered to all participants in the larger project. The main study included an intensive data collection period of 4 days each. All participants in the nested study were recruited according to the inclusion criteria of the larger project: they had a principal neurological diagnosis, were able to verbalize, were able to give their written informed consent, and were between the ages of 18–99. Exclusion criteria were: pre-existing atrial fibrillation or atrial flutter or new onset of atrial fibrillation or flutter during the observation period, implanted pacemaker or defibrillator, contraindications for adhesive electrodes (e.g., allergy, severe psoriasis, etc.), limiting neuropsychological impairments, due to which keeping an activity log and scale-based self-assessment are not possible or the occurrence of a medical (life-threatening) crisis during the study.

Due to ethical and organizational constraints, we obtained a convenience sample of 11 dyads composed of 11 participants (seven females, four males) and one music therapist (female). The participants were between the ages of 39 and 60 (mean age 51 years, $SD = 6.48$), and the music therapist was 43 years old. None of the participants had physical impairments, such as hemiplegia, that would have impeded their movements. See **Table 1** for participants details.

Music therapy settings

The music therapy sessions were conducted in a therapy room. The patient and therapist sat facing each other at about 110° and after they were seated, patient proceeded to fill out a self-reported therapy readiness questionnaire. The music therapy session would start with a conversation (pretalk) to check in on the patient's condition and to decide on what they would do for the session. This was followed by the music intervention and a subsequent conversation (posttalk) to reflect on the process. As a pragmatic study, it was important to keep the clinical setting as authentic as possible. Thus, the type of music intervention was non-standardized, depending solely on the needs of the patients. It could be receptive music listening, improvisation, active music-making, singing, moving or dancing to music, etc. Likewise, the duration of the music interventions and the unstructured pretalk and posttalk segments during the session were also unrestricted to maintain the organic flow of the therapy sessions. **Figure 1** shows the schematic representation of the music therapy sessions. Although music therapy was not a standard treatment, all 11 participants received it during their stay at the hospital. Some continued with music therapy even after the data collection period, totaling between two and five music therapy sessions each. We examined one single session that was between the first and the third music therapy session. The music therapist was trained at IMC University of Applied Sciences Krems (Bachelor and Master) and had worked four years full time in neurology at the time of data collection. Shared moments of musical encounter and the principles of harmonizing psychological and physical states (regulation) are at the heart of the Krems approach

TABLE 1 Durations of pretalk, music intervention, posttalk, session, type of music intervention and diagnosis of participants.

ID	Pretalk duration hh:mm:ss	Intervention duration hh:mm:ss	Posttalk duration hh:mm:ss	Session duration minutes	Type of music interventions	Diagnosis ICD-10
P018	00:03:03	00:29:45	00:13:28	52.92	Active music making (drums) and receptive music (patient shared music).	M54.5
P019	00:08:51	00:29:08	00:08:24	48.68	Guided relaxation (sound bowls), song writing and performance.	I63.5
P025	00:05:38	00:26:03	00:04:00	40.13	Breath and voice work. Singing and active music playing (patient on drums and MT on ukulele).	M51.1
P028	00:07:46	00:23:59	00:06:46	54.67	Deep listening exercise (sound bowls) and improvisation on the theme "discovery" on harps.	M54.4
P031	00:04:45	00:35:01	00:02:58	47.52	Improvisation on theme “holidays” (patient on chimes and MT on harp) and active music making (drums).	M51.1
P032	00:24:40	00:11:29	00:05:50	53.97	Vocal improvisation (MT on voice and harp).	M51.1
P035	00:04:16	00:20:09	00:07:45	44.93	Improvisation on theme “under the stars” (harps) and free improvisation (harps and voices).	I63.9
P037	00:12:59	00:15:07	00:13:39	49.27	Improvisation “hands seperated and together” (patient on chimes an MT on harp).	M51.1
P047	00:04:44	00:34:32	00:06:28	52.15	Deep listening (sound bowls), voice work and improvisation (harps).	M51.1
P048	00:17:48	00:27:52	00:13:00	62.48	Improvisation on theme “taking time” (patient on sansula and MT on harp) and improvisation (patient with spoken words and MT on sansula).	M51.1
P057	00:12:46	00:28:14	00:09:54	55.32	Receptive music (patient’s choice) and singing (songs from patient’s native country).	M50.0
Mean	00:09:45	00:25:34	00:08:23	51.09		
Max	00:24:40	00:35:01	00:13:39	62.48		
Min	00:03:03	00:11:29	00:02:58	40.13		
SD	00:06:44	00:07:26	00:03:44	5.94		

to music therapy. In recent years, the anthropological approach in Krems focused on personalization of therapy, leading to the development of new models to facilitate authentic clinical research and abandoning the demand for standardization of therapeutic procedures (Tucek et al., 2021) (see **Table 1** for the type of music interventions and diagnoses of participants).

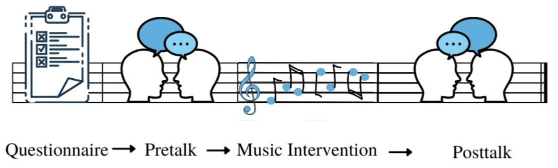

FIGURE 1
Music therapy session schematic.

Video material

The videos of the music therapy sessions were recorded on an iPhone 8 without auto focus at 30 frames per second. Light conditions were held constant, and as a technical demand of the Motion Energy Analysis, the chairs where the dyads were sitting were in fixed positions during pretalk, posttalk, and the music intervention. The camera position was fixed across all sessions. The videos were time-stamped after the recording in Adobe Premiere. The mean duration of the music therapy sessions was 51.09 min (*SD* = 5.94 min, range 40.13–62.48 min). Since the shortest available video was 2 min 58 s (see **Table 1** for individual durations), we used 2 min of the verbal interaction immediately before and after the music intervention for all dyads. In nonverbal research in the psychotherapy setting, synchrony tends to decrease over time (Ramseyer and Tschacher, 2011), therefore, we can reject the possibility of any bias in this choice. Furthermore, we explored a dataset with a similar nature, namely data from one single therapist across multiple patients: The author of MEA (Ramseyer, 2020) provides data of himself interacting with $N = 103$ patients during psychotherapy intake-interviews[1], and from this dataset, we calculated nonverbal synchrony with identical parameters used in the present study. We chose minutes 5–7 and 45–47, in order to gauge a potential temporal effect on nonverbal synchrony. Both 2-min segments had synchronies that did not differ from chance. Pseudosynchrony was equally high in these short time-segments. The comparison of initial minutes (5–7) versus final minutes (45–47) resulted in a significant decrease across time [$T(102) = 2.057$; $p = 0.04$].

Motion energy analysis

The Motion Energy Analysis (MEA; Ramseyer, 2020) is an automated application that quantifies movements from a video source. By comparing the changes in the pixel of each subsequent frame to its predecessor in predefined regions of interest (ROI), MEA is able to objectively generate time-series of pixel change within ROIs (for details see Ramseyer and Tschacher, 2011; Ramseyer, 2020). Six ROIs were firstly selected in MEA. ROI 1,2, 3, and ROI 4,5,6 were the predefined movement spaces for the head, upper body, and lower body of the music therapist and the patient, correspondingly (**Figure 2**). Since we are not discriminating movements from different areas of the body in our analysis, we have combined the 3 ROIs for each individual at the next step of analysis based on similar studies using MEA which employed full-body ROIs (Ramseyer and Tschacher, 2011; Erdös and Ramseyer, 2021).

Calculations of nonverbal synchrony

To calculate the nonverbal synchrony, the raw data generated by MEA (Ramseyer, 2020) was analyzed with the R package rMEA (R Studio Team, 2020; Kleinbub and Ramseyer, 2021). Using rMEA, the six ROIs were combined into two individual sets, creating two time series, one for the therapist and the other for the patient. Cross-correlation is the most commonly used method for the quantification of nonverbal synchrony in behavioral time series (Boker et al., 2002). The cross-correlations are windowed, i.e., calculated in separate segments, as our data contains human interaction, which is non-stationary. Although the optimal segment size is yet to be determined (Schoenherr et al., 2019b), previous research has used 30 s (Tschacher et al., 2014b) and 60 s (Ramseyer and Tschacher, 2014). Conversely, in another approach of "peak picking", a segment size of 4 s (Boker et al., 2002) was applied. It has also been suggested that the window width should be at least 50–70 values and about 4–5 times larger than the maximum time lag used (Cappella, 1996). Furthermore, since there is no one-size-fits-all solution, the length of the window is dependent on the processes occurring at different time scales (Moulder et al., 2018). In this study, the length of the selected data is 2 min long. Since we are interested in within-session phenomena, a segment size of 10 s was selected. This segment size is also the best mid value option after having examined the effect size of other segment sizes. **Figure 3** shows the comparison of our calculated synchrony to that of the pseudosynchrony. On the X-axis we show the Fisher's Z absolute mean cross correlation and the Y-axis provides the graphical representation of the distribution of these correlations.

Time series of two individuals are cross correlated at different time lags, thus allowing for possible delayed or lagged associations of movement activity. Similar to the segment size, the time lag is also largely at the discretion of the researcher (Schoenherr et al., 2019b). Previous studies have used ±5 s (Ramseyer and Tschacher, 2014; Tschacher et al., 2014b; Cohen et al., 2021; Erdös and Ramseyer, 2021). Using a lag of ±2 s was considered to be a conservative and suitable measure as real synchrony intercepted random synchrony at close to −0.5 and +2. Therefore, by choosing the value of ±2 s (**Figure 3**), more power was given to the pseudosynchrony derived from the surrogate test to be equally strong as the real signal, which increases the strength of the test. The windowed cross-correlation in our study was done without overlapping.

Pseudosynchrony

To ascertain that the synchrony we have observed was not merely a random coincidence, we compared the results to values of pseudosynchrony. Therefore, if actual synchrony is genuine, it should be higher than pseudosynchrony, with a greater effect size (Ramseyer and Tschacher, 2010). The pseudosynchrony was generated by bootstrapping, i.e., recombining one dyad's movement time series with another random movement time series from the pool of all observations, thus creating surrogate datasets. As suggested by Kleinbub and Ramseyer (2021), we used between subject shuffling, which was also better suited for the rather short duration

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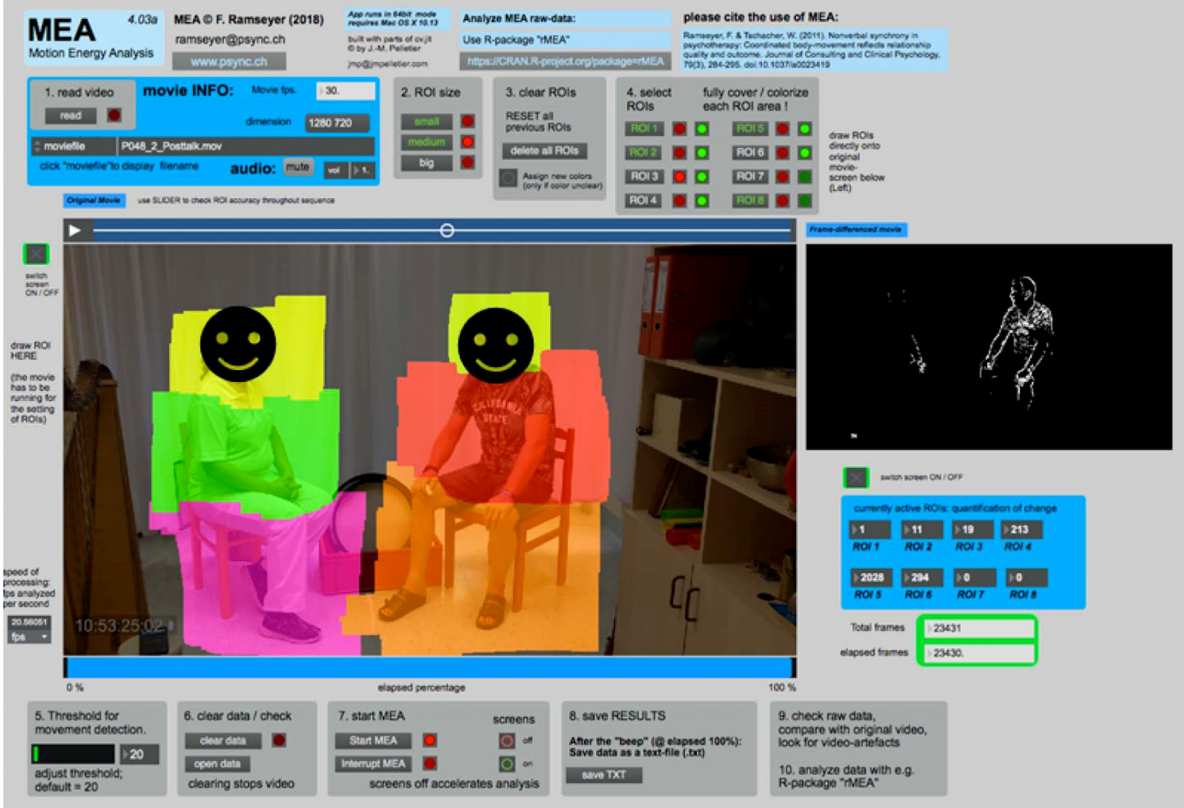
[1] https://osf.io/gkzs3/



MEA 4.03a
Motion Energy Analysis

MEA © F. Ramseyer (2018)
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App runs in 64bit mode requires Mac OS X 10.13
built with parts of cv.jit © by J.-M. Pelletier
jmp@jmpelletier.com

Analyze MEA raw-data:
Use R-package "rMEA"
https://CRAN.R-project.org/package=rMEA

please cite the use of MEA:
Ramseyer, F. & Tschacher, W. (2011). Nonverbal synchrony in psychotherapy: Coordinated body-movement reflects relationship quality and outcome. Journal of Consulting and Clinical Psychology, 79(3), 284-295. doi:10.1037/a0023419

1. read video

movie INFO: Movie fps. 30. dimension 1280 720

moviefile P048_2_Posttalk.mov

click "moviefile"to display filename

audio:

2. ROI size

3. clear ROIs
RESET all previous ROIs
Assign new colors (only if color unclear)

4. select ROIs — fully cover / colorize each ROI area !

draw ROIs directly onto original movie-screen below (Left)

use SLIDER to check ROI accuracy throughout sequence

switch screen ON / OFF

draw ROI HERE (the movie has to be running for the setting of ROIs)

speed of processing: fps analyzed per second 20.56051 fps

switch screen ON / OFF

currently active ROIs: quantification of change

ROI 1	ROI 2	ROI 3	ROI 4
1	11	19	213

ROI 5	ROI 6	ROI 7	ROI 8
2028	294	0	0

Total frames 23431
elapsed frames 23430.

0 % elapsed percentage 100 %

5. Threshold for movement detection.
20
adjust threshold; default = 20

6. clear data / check
clearing stops video

7. start MEA
screens off accelerates analysis

8. save RESULTS
After the "beep" (@ elapsed 100%): Save data as a text-file (.txt)

9. check raw data, compare with original video, look for video-artefacts

10. analyze data with e.g. R-package "rMEA"

FIGURE 2
Screenshot of the motion energy analysis (MEA, Version 4.03).

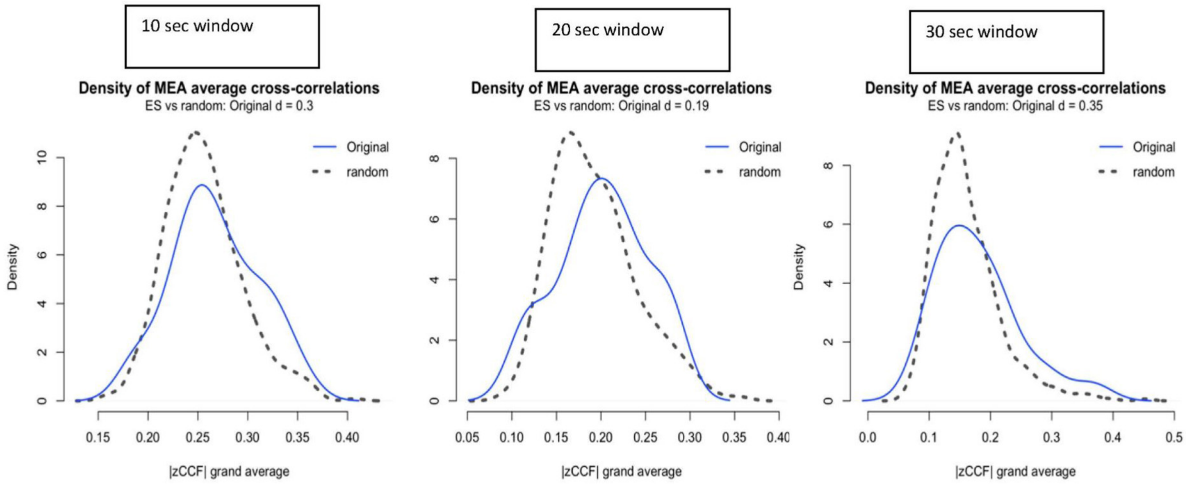

FIGURE 3
Effect size (ES) of synchrony above pseudosynchrony for window sizes of 10, 20, and 30 s. |zCCF|, Fisher's Z absolute mean cross-correlation.

of the analyzed segments in our sample. Within subject shuffling would have provided insufficient recombinations, if the segment size was kept identical in both real and pseudo interactions (Ramseyer and Tschacher, 2010; Moulder et al., 2018). Three pools of data were used for producing the surrogate datasets. For better results, each pool's sampling was done without replacement, since the sample size is small. Pool 1 consisted of all possible pretalk and posttalk

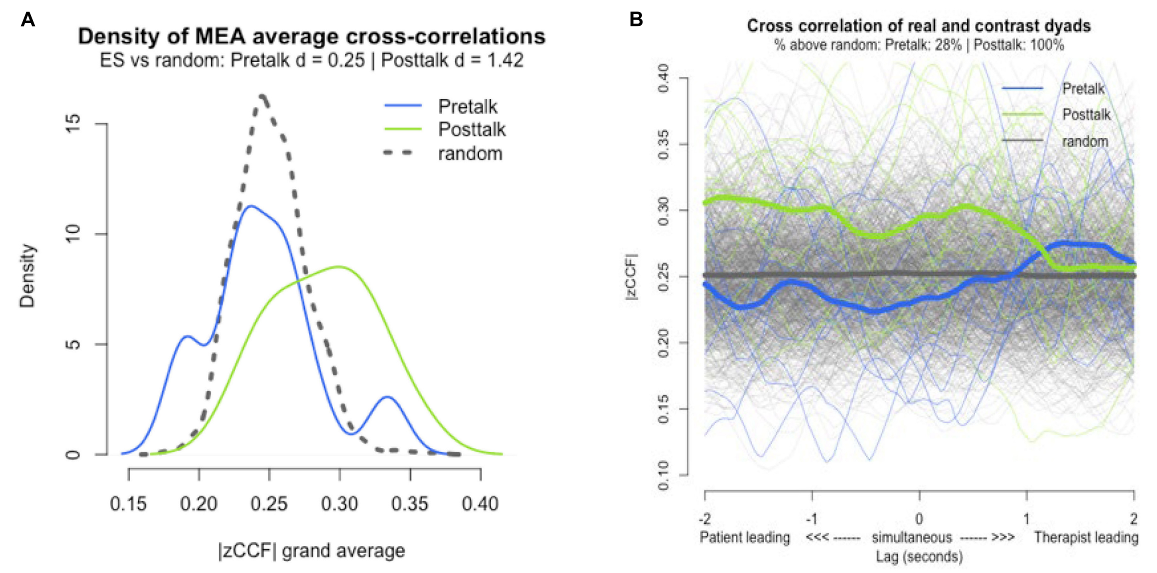

FIGURE 4

Synchrony vs pseudosynchrony. **(A)** Effect size of pretalk, posttalk, and pseudosynchrony. |zCCF|, Fisher's Z absolute mean cross-correlation. **(B)** Lag-plot of pretalk and posttalk synchrony. Gray line = pseudosynchrony (random).

data combinations for all members of any dyad ($N = 924$, i.e., 22 × 21 × 2), pool 2 consisted of all pretalk data ($N = 220$, i.e., 11 × 10 × 2), and pool 3 consisted of all posttalk data ($N = 220$, i.e., 11 × 10 × 2). The actual pretalk synchrony was compared to pseudosynchrony created by pools 1 and 2. The actual posttalk synchrony was compared to pseudosynchrony created by pools 1 and 3. Thus, the pseudosynchronies were produced by between-shuffling of interactions (Kleinbub and Ramseyer, 2021). Apart from calculating the nonverbal synchrony and comparing these to the pseudosynchrony, the roles of leader and follower were directly accessible through the differentiation into positive and negative lags. This distinction has been used in previous research (Ramseyer and Tschacher, 2011), and it is statistically implemented in the rMEA package (Kleinbub and Ramseyer, 2021). We thus ascertained the roles during the pretalk and posttalk using statistical procedures available in rMEA.

Correlation between nonverbal synchrony to visual analog scale of patients' self-reported therapy readiness

Before the commencement of the therapy session, patients were asked to complete a questionnaire regarding their therapy readiness. Their responses were unknown to the music therapist. This questionnaire consisted of 11 items, including a traditional visual analogue scale (VAS) (Dür et al., 2019). The VAS is a type of psychometric scale commonly used to quantify psychological phenomena such as satisfaction, well-being, mood, etc. VAS has been shown to have test-retest reliabilities of at least 80% across different constructs and contexts. In pain or quality of life studies, VAS is also comparable to the established gold standard of measurements (Nguyen and Fabrigar, 2018). The German instruction on the VAS can be translated as "Please use the following visual analog scale to indicate your estimation. Please mark the position on the bar with a vertical line that corresponds to your current therapy readiness". The left side of the VAS indicated an absolute readiness for therapy, and the right side indicate the contrary. Patients indicated their subjective assessments of their readiness for therapy by marking it on this 10 cm continuum. Items 1–10 of the questionnaire had very low variance, resulting in a ceiling effect. Therefore, only the VAS was used to make a statistical correlation with the nonverbal synchrony, using the application Jamovi 1.8.1.0 (The Jamovi Project, 2021).

Results

Nonverbal synchrony versus pseudosynchrony

We compared the nonverbal synchrony of the dyads during the pretalk and posttalk to pseudosynchronies. This revealed statistically significant differences between posttalk synchrony and pseudosynchrony derived from pool 1 (entire pretalk and posttalk data; $N = 924$, $p = 0.00976$; $d = 1.42$) as well as from pool

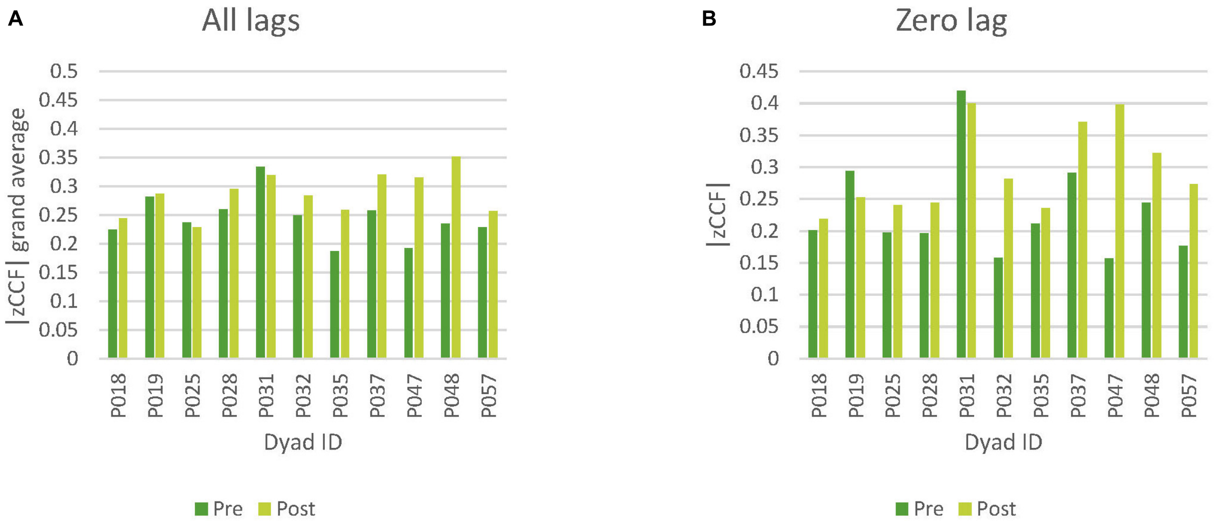

FIGURE 5
Comparison of pretalk and posttalk nonverbal synchrony. **(A)** Comparison based on all lags values (grand average). **(B)** Comparison based on lag zero values (only lag zero cross-correlations). |zCCF| Fisher's Z absolute mean cross-correlation.

3 (posttalk data only; $N = 220$, $p = 0.02046$; $d = 1.12$). Pretalk synchrony did not demonstrate a statistically significant value over the pseudosynchrony (**Figure 4**).

Nonverbal synchrony pretalk versus nonverbal synchrony posttalk

Comparing nonverbal synchrony in pretalk to nonverbal synchrony in posttalk, we found that nine out of eleven dyads showed an increase in nonverbal synchrony after music intervention for both all lags and lag zero (**Figure 5**).

Non-parametric test Wilcoxon Signed-Ranks Test indicated that nonverbal synchrony (all lags) was significantly higher in the posttalk ($Mdn = 0.29$) than the pretalk ($Mdn = 0.24$), $W = 5$, $p = 0.010$, $r = -0.85$. Significant increase was also found in the nonverbal synchrony (lag zero) for posttalk ($Mdn = 0.27$) than pretalk ($Mdn = 0.20$) $W = 6$, $p = 0.014$, $r = -0.82$ (**Tables 2**, **3**). For parametric test, please refer to **Table 4**.

Leading in pretalk and posttalk synchrony

Further inspections revealed that during pretalk, therapist leading was higher than patient leading in 9 out of 11 cases (**Figure 6**). However, in posttalk, patient was leading in 7 out of 11 cases.

A non-parametric test also showed that the increase in posttalk patient leading ($Mdn = 0.29$) from pretalk patient leading ($Mdn = 0.23$) was statistically significant $W = 0$, $p < 0.001$, $r = -1.00$. Pretalk therapist leading minus patient leading (Tlead-Plead) ($Mdn = 0.02$) was also significantly different to posttalk (Tlead-Plead) ($Mdn = -0.03$), $W = 59$, $p = 0.019$, $r = 0.788$ (**Tables 2**, **3**). For parametric test, please refer to **Table 4**.

Visual analog scale of patient's self-reported therapy readiness

Patients' therapy readiness ranged between 82 and 100% ($n = 10$, $M = 94.2\%$, $Mdn = 95.8\%$, $SD = 6.23$).

Association of nonverbal synchrony with patient's self-reported therapy readiness

Simple linear regression was calculated to predict pretalk and posttalk nonverbal synchrony as well as therapist leading and patient leading during pretalk and posttalk, based on patients' self-reported therapy readiness. A significant negative correlation was found between patients' self-reported therapy readiness and posttalk synchrony (all lags) [$F(1,8) = 5.32$, $p = 0.050$, with an $R^2 = 0.40$] as well as a trending negative correlation between patients' self-reported therapy readiness and patient leading during posttalk synchrony [$F(1,8) = 3.83$, $p = 0.086$), with an $R^2 = 0.324$]. Otherwise, no further associations were found (**Table 5**).

TABLE 2 Descriptive.

	Pretalk (all lags)	Posttalk (all lags)	Pretalk (lag zero)	Posttalk (lag zero)	Pretalk Therapist Lead	Pretalk Patient Lead	Pretalk Tlead -Plead	Posttalk Therapist Lead	Posttalk Patient Lead	Posttalk Tlead -Plead	VAS
N	11	11	11	11	11	11	11	11	11	11	10
Missing	0	0	0	0	0	0	0	0	0	0	1
Mean	0.245	0.288	0.233	0.295	0.258	0.233	0.0244	0.278	0.297	−0.02	94.2
Median	0.237	0.287	0.202	0.274	0.251	0.229	0.0172	0.291	0.291	−0.03	95.8
Standard deviation	0.041	0.0376	0.0768	0.0673	0.0317	0.0534	0.0322	0.0435	0.0518	0.0592	6.23
Minimum	0.187	0.229	0.157	0.219	0.227	0.147	−0.0188	0.166	0.21	−0.125	82
Maximum	0.334	0.352	0.419	0.4	0.324	0.343	0.0795	0.326	0.379	0.0985	100
Shapiro-Wilk W	0.942	0.97	0.836	0.863	0.882	0.939	0.944	0.817	0.973	0.979	0.871
Shapiro-Wilk p	0.544	0.884	0.028	0.063	0.111	0.507	0.57	0.016	0.917	0.959	0.103

TABLE 3 Results of paired samples Wilcoxon test.

		Statistic Wilcoxon W	p-value	Mean Difference	SE Difference	95% Confidence			Effect size
						Lower	Upper		
Pretalk (all lags)	Posttalk (all lags)	5	0.01	−0.037	0.014	−0.07350	−0.00780	Rank biserial correlation	−0.848
Pretalk (lag zero)	Posttalk (lag zero)	6	0.014	−0.0545	0.0229	−0.11090	−0.01425	Rank biserial correlation	−0.818
Pretalk therapist leading	Posttalk therapist leading	17	0.175	−0.0231	0.0152	−0.05900	0.01690	Rank biserial correlation	−0.485
Pretalk patient leading	Posttalk patient leading	0	<0.001	−0.0575	0.017	−0.11170	−0.02925	Rank biserial correlation	−0.1
Pretalk Tlead-Plead	Posttalk Tlead-Plead	59	0.019	0.0439	0.0158	0.00810	0.07945	Rank biserial correlation	0.788

Discussion

In summary, a statistically solid signal of synchrony with a large effect size ($d = 1.42$) only emerged in the posttalk, suggesting that nonverbal synchrony was only relevant during posttalk. Even though we cannot ascertain a level of synchrony beyond the level of coincidence in the pretalk, we have to bear in mind that the randomness of the pseudosynchrony concept itself has weaknesses: it works best in conditions where time series do not show specific, time-locked (repetitive) patterns. For example, if we were to compare the synchrony of two pendulums, pseudosynchrony would be equally high as genuine synchrony, because the different pendulums would still swing at the same frequencies (Ramseyer and Tschacher, 2010). In our study, all the sessions were conducted by the same music therapist, hence the potential for a certain degree of periodicity was embedded in the data, as her idiosyncratic movements would probably be constant across all sessions. Besides, due to the small sample size ($N = 11$), pseudosynchrony was expected to be rather close to the real synchrony, considering that only limited permutations were possible in the bootstrapping procedure due to the limited number of possible recombinations. Nevertheless, since the average pretalk synchrony (all lags) is 0.24 and the average posttalk synchrony (all lags) is 0.29, there is a strong case for the increase in synchrony even though nonverbal synchrony during pretalk was not beyond pseudosynchrony. Although there was no control group in this study, the observed synchrony was compared with pseudosynchrony ($N = 924$, $N = 220$), which indicated that the posttalk synchrony is beyond chance. A similar synchrony study using MEA revealed that dyads showed no increase in synchrony between two unstructured conversations of 6 mins each, with a filler task of watching a 6 mins film (Fujiwara et al., 2019).

In this study, the analysis of nonverbal synchrony within single music therapy sessions revealed a change in the level of nonverbal synchrony after music intervention. This increase in nonverbal synchrony during posttalk could suggest that the music intervention, akin to the flexible wooden beam in Huygen's observation, has served as a platform where entrainment took place. Entrainment is a delicate process and as shown by Huygen's clocks, the intensity of coupling should not be so strong that the individuality is lost (Bennett et al., 2002; Clayton et al., 2004). The music intervention seemed

TABLE 4 Results of parametric paired sample *T*-tests.

		Student's *t*	df	*p*
Pretalk (all lags)	Posttalk (all lags)	−3.03	10	0.013
Pretalk (lag zero)	Posttalk (lag zero)	−2.69	10	0.023
Pretalk therapist leading	Posttalk therapist leading	−1.33	10	0.212
Pretalk patient leading	Posttalk patient leading	−3.78	10	0.004
Pretalk Tlead-Plead	Posttalk Tlead-Plead	2.78	10	0.02

to have given enough space for the dyads to communicate with each other, reacting and moving to adapt to entrain to each other's rhythm as measured with motion energy during conversation. The increase in nonverbal synchrony after the music intervention may have been driven by increasing familiarity between the therapist and the patient, for having shared some time together. However, other studies point in the other direction, indicating that familiarity could also be causing a decrease of nonverbal synchrony (Erdös and Jansen, 2022).

With this study, we have also established a novel method in music therapy research, using Motion Energy Analysis in the pretalk and posttalk to capture and objectively quantify the process of entrainment in movement behaviors of patients and therapists.

Although our study has shown an increase in nonverbal synchrony after music intervention, the question of the meaning of this increase or whether this increase is necessarily beneficial still remains unanswered. It is important to look at nonverbal synchrony with a more differentiated view as recent research has shown that nonverbal synchrony is a multidimensional construct. Behaving synchronously has been strongly associated with positive aspects of social relationships (Chartrand and Lakin, 2013). Nonverbal synchrony has been associated with positive therapeutic relationships (Ramseyer and Tschacher, 2011; Altmann et al., 2020; Cohen et al., 2021), higher efficacy and higher symptom reduction at the end of treatment (Ramseyer and Tschacher, 2011), and low nonverbal synchrony has also predicted premature termination of therapy (Paulick et al., 2018). This is especially so with sessions at the beginning of the therapy process, as it may indicate low therapy alliance or an ill match between the therapeutic dyads (Schoenherr et al., 2019a). It has also been suggested that social interaction dynamics have a greater effect on our self-regulation than our own individual processes (Galbusera et al., 2019). Whilst these studies have shown that nonverbal synchrony is associated with positive benefits, others have found only marginally significant association (Schoenherr et al., 2019a) or even none at all. One interpretation of these conflicting results focuses on the varying methods for the statistical quantification of nonverbal synchrony (Paulick et al., 2018; Lutz et al., 2020; Ramseyer, 2020).

Beyond the method of analysis, higher levels of nonverbal synchrony may not be equatable to better therapy outcomes. A medium level of nonverbal synchrony between therapeutic dyads was associated with successful therapies where patients improved. Surprisingly, therapies were consensually terminated with no improvements for dyads with the highest level of nonverbal synchrony. At the same time, patients dropped out with no improvement for the lowest level of nonverbal synchrony (Paulick et al., 2018). In addition, a downward trend of nonverbal synchrony cannot be interpreted as a deterioration of therapeutic alliance, as one of the first studies employing MEA found a slight decrease in synchrony from the initial third of therapies to the final third (Ramseyer and Tschacher, 2011). An international coaching study with high level of client reported success (Erdös and Ramseyer, 2021) found that nonverbal synchrony showed a linear trend for a temporal decrease across ten sessions of coaching. It found no overall correlation between nonverbal synchrony and working alliance, affect balance, and goal attainment as such, but a temporal network analysis indicated differential associations in subgroups of higher or lower success. At the beginning of the entire group, synchrony was not indicative of a good coaching alliance. It appeared to be acting as a "corrective mechanism" in dyads with less stable working alliances. Thus, higher levels of nonverbal synchrony in these cases may be interpreted as emerging efforts to correct the process, to attain "the same wavelength with each other," which subsequently became less necessary when the progress was successful. Dyads do not maintain a constant level of synchrony, instead, they move in and out of interpersonal synchrony (Erdös and Ramseyer, 2021). This aspect of "effort" stands in line with another finding from the domain of psychotherapy, where so-called ruptures in the alliance were followed by higher synchrony (Deres-Cohen et al., 2021). A similar phenomenon has been found in physician-patient interactions in the oncology setting: dyads with a white physician and a black patient displayed significantly higher nonverbal synchrony in comparison with dyads comprised of racially-concordant members (Hamel et al., 2022).

Other factors, such as the pathology of the patients, the body responsiveness of the therapist, dyad type, and therapeutic approaches also appears to affect the level of nonverbal synchrony in session (Schoenherr et al., 2019a).

Finding on leading and following

Although it is not clear how this should be translated in the case of looking at processes occurring during a single

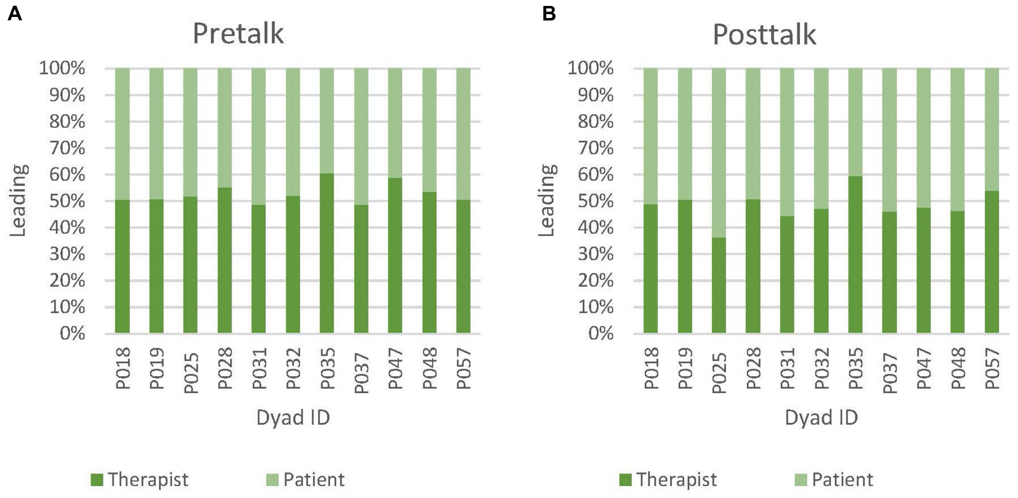

FIGURE 6

(A) Relative amounts (percentages) of therapist leading vs patient leading in pretalk nonverbal synchrony. **(B)** Relative amounts (percentages) of therapist leading vs patient leading in posttalk nonverbal synchrony.

session, such as what we are looking at in our study, we can infer that posttalk synchrony is most likely influenced by the music intervention. So, if we move to the discussion about changes in leading/following after the music intervention, we observed that patient leading in nonverbal synchrony increased significantly when comparing posttalk to pretalk. Another significant difference was found when comparing the difference between therapist leading and patient leading (Tlead – Plead) during pretalk (*Mdn* = 0.02) and posttalk (*Mdn* = −0.03).

Schoenherr et al. (2019a) found that in the early phases of therapy patients leading while therapists follow can affect drop-out rates. This would indicate that the patient is speaking, hence also moving. Therapist leading, on the other hand, influences the clinical outcome. The different leading and pacing appear to have influenced the outcomes in various ways (Altmann et al., 2020). Moreover, attention should also be given to what was happening in the session during the shifting of leadership (Schoenherr et al., 2019a). A recent study had found that different types of musical interaction influenced the subsequent dyadic interaction. Turn-taking music making behavior, for example, was manifested in the heightened attunement during the post music mirror game and more switching of leading/pacing (Buchkowski, 2018). This could be an explanation for the switch in leadership in our study. The significant increase in patient leading in nonverbal synchrony after the music intervention may indicate that dyadic entrainment during the music intervention had potentially increased self-regulation and empowered patients, which led to an increase in the patient leading in the nonverbal synchrony during the posttalk.

Finding on correlations between readiness and nonverbal synchrony

In this study, we were expecting a positive correlation between patients' self-reported therapy readiness and pretalk nonverbal synchrony. We did not find a positive significant correlation; instead, we found a non-significant negative correlation. Moreover, a significant negative correlation was shown between patients' self-reported therapy readiness and posttalk nonverbal synchrony (all lags), as well as a non-significant (p = 0.086) but trending correlation with patient leading during nonverbal synchrony in posttalk was shown.

These results are only counterintuitive so far as therapy readiness and nonverbal synchrony are conceptualized as favorable aspects: Therapy readiness may be driven by a high level of suffering or pathology, which could lead to a therapist's

TABLE 5 Correlations between nonverbal synchrony and patients' self-reported therapy readiness.

	F	df 1	df 2	p	R^2	t
Pretalk (all lags)	5.9	1	8	0.465	0.0686	−0.768
Pretalk (lag zero)	3.32	1	8	0.106	0.293	−1.82
Posttalk (all lags)	5.32	1	8	0.05	0.4	−2.31
Posttalk (lag zero)	1.22	1	8	0.302	0.132	−1.1
Posttalk minus pretalk (all lags)	1.11	1	8	0.323	0.122	−1.05
Posttalk minus pretalk (lag zero)	1.42	1	8	0.268	0.15	1.19
Pretalk therapist leading	0.28	1	8	0.611	0.0399	−0.529
Posttalk therapist leading	1.57	1	8	0.246	0.164	−1.25
Pretalk patient leading	0.701	1	8	0.427	0.0806	−0.837
Posttalk patient leading	3.83	1	8	0.086	0.324	−1.96

high level of mastery interventions, as shown in a psychotherapy context. Furthermore, nonverbal synchrony may be a sign of a high effort/engagement from the therapist (Deres-Cohen et al., 2021; Erdös and Ramseyer, 2021).

Regarding the negative correlation between patients' self-reported therapy readiness and posttalk nonverbal synchrony: the readiness data was collected at the beginning of the session, and we were not necessarily expecting a positive correlation because once the therapy was over, why should patients still be ready for therapy? The therapy has already passed, and thus decrease in therapy readiness was most likely being reflected in the negative correlation.

Another speculation could be that although the music therapist was unaware of the patients' self-reported therapy readiness, she was able to perceive the ambiguous attitude. This could influence the therapist to make extra cheerleading-like efforts to engage the patient during the pretalk, which may be reflected by higher therapist leading than patient leading. This cheerleading effort may not have been necessary any more during the posttalk, and that was subsequently reflected in the posttalk synchrony as an increase in patient leading.

We could also consider that patients' self-reported therapy readiness may have fluctuated during the session, or may be generally less connected with nonverbal synchrony than for example alliance. However, if patients' self-reported therapy readiness did have an influence on the level of nonverbal synchrony, we would expect to see a significant positive correlation to the pretalk synchrony and to the posttalk synchrony. This was not the case, probably because our sample size was not strong enough to allow for a conclusive relationship between the pretalk synchrony and patients' self-reported therapy readiness. Hence, at this point, our study does not reveal whether patients' self-reported therapy readiness was a good predictor of nonverbal synchrony.

Strengths and limitations

Since this is a convenience sample with a small sample size, the results should not be generalized, and the results should be cautiously interpreted as they are susceptible to bias. The sample size not only impeded any generalization of the findings but also lowered the possibility of more significant correlations. Pseudosynchrony was also closer to actual synchrony due to the small sample size and also because of the aforementioned weakness of having the same music therapist across all dyads.

Another limitation concerning the music therapist is that she may also have an experimenter bias in her dual role as the researcher as well. Nevertheless, the knowledge that nonverbal synchrony is being assessed need not necessarily increase the phenomenon. The assessment of nonverbal synchrony draws on an attribute that is outside conscious control as data presented in a recent study on the use of MEA has suggested. Knowing that synchrony is being assessed did not increase the amount of synchrony displayed, in fact, synchrony decreased as the therapist's professional experience augmented (Ramseyer, 2020).

Since the patients who participated in the study were highly motivated, we did not have any representation on the low end of the scale (patient was not ready for therapy). This ceiling effect resulted in less variance in our statistics.

Although patients were asked to indicate their level of therapy readiness, they may not have interpreted the meaning of "ready for therapy" in the same way. The VAS is a cognitive measure that may not be able to capture the difference between the bodily state of "being ready" for therapy and the cognitive appraisal of readiness. This could be a reason for the lack of correlation between patients' self-reported therapy readiness and the nonverbal synchrony and the leading characteristics. Patients themselves may not have known how ready they actually were at the beginning of the session. A patient's indication might be considered as low in this sample, but that could also be the highest value he or she would have given, compared to other therapies and at other times. There is no objective measurement of this variable. In addition, patients could have been "ready" for music therapy because they were exhausted and were looking forward to a relaxation exercise. They would perhaps have indicated to be less ready if they were going to another type of therapy session.

The MEA application is a simple, user-friendly tool that quantifies the dynamics of movement irrespective of movement quality. A recent study confirmed the similarity with more sophisticated measures such as OpenPose (Fujiwara and Yokomitsu, 2021). Still, MEA does not qualitatively assess the movements. It does not tell us if the movement was a smile or a roll of the eyes but these types of movements can be pivotal to the relationship. Furthermore, MEA does not measure nonverbal synchrony when there are no movements. This stillness could be actually more meaningful than moving. Nevertheless, MEA provides us an accessible objective, and quantifiable way to examine certain aspects of therapeutic interactions which can support and communicate the efficacy of the therapy. It is also an additional behavioral marker quantifying the observation of the therapeutic process.

Conclusion and future directions

This study presented a novel way to investigate nonverbal synchrony in music therapy in the neuro-rehabilitation setting. We found increased nonverbal synchrony and patient leading synchrony after the music intervention, which could indicate a growing bond between the dyads through the entrainment during music interventions. Further, this study reports a negative correlation between patients' self-reported therapy readiness and post music intervention nonverbal synchrony and its characteristics. Future studies should strive for a bigger sample size with different pairs of dyads so that it would be possible to make a generalization and remove possible bias. Data should be collected across multiple sessions across longer time to investigate possible temporal changes.

Different standardized assessments for symptom reduction, therapeutic relationship quality, or mood change could also be included to study what an increase in nonverbal synchrony in the music therapy settings with neuro-rehabilitation patients could indicate.

Sessions should also be scheduled at different times of the day for the individuals, to gather data from different states of therapy readiness, and to look deeper into the chronobiological effects.

This study utilized a combined ROI, but ROIs could also be separated between head and body, to examine nonverbal synchrony with more details. Future research could also look deeper into segments of the music interventions that had taken place to establish possible relation to nonverbal synchrony. Therapists' assessments of patients' readiness could also be compared to patients' self-reported therapy readiness to investigate the effects of therapists' expectations.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The studies involving human participants were reviewed and approved by Ethics Commission of Lower Austria GS1-EK-4/633-2020. The patients/participants provided their written informed consent to participate in this study.

Author contributions

SSY carried out the therapies, acquired, and prepared the data. SSY and FR performed the synchrony calculations and the initial analysis of the data. JF, CM, GT, and WT supervised the project. SSY drafted the manuscript. All authors conceptualized and designed the study, discussed the results, revised the manuscript critically, and approved the submitted version of the manuscript.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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Characterising the spatial and oscillatory unfolding of Theory of Mind in adults using fMRI and MEG

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Theory of Mind (ToM) is a core social cognitive skill that refers to the ability to attribute mental states to others. ToM involves understanding that others have beliefs, thoughts and desires that may be different from one's own and from reality. ToM is crucial to predict behaviour and navigate social interactions. This study employed the complementary methodological advantages of both functional MRI (fMRI) and magnetoencephalography (MEG) to examine the neural underpinnings of ToM in adults. Twenty healthy adults were first recruited to rate and describe 28 videos (15s long), each containing three moving shapes designed to depict either social interactions or random motion (control condition). The first sample of adults produced consistent narratives for 6 of those social videos and of those, 4 social videos and 4 control videos were chosen to include in the neuroimaging study. Another sample of twenty-five adults were then recruited to complete the neuroimaging in MEG and fMRI. In fMRI, we found increased activation in frontal-parietal regions in the social compared to the control condition corroborating previous fMRI findings. In MEG, we found recruitment of ToM networks in the social condition in theta, beta and gamma bands. The right supramarginal and angular gyri (right temporal parietal junction), right inferior parietal lobe and right temporal pole were recruited in the first 5s of the videos. Frontal regions such as the superior frontal gyrus were recruited in the second time window (5–10s). Brain regions such as the bilateral amygdalae were also recruited (5–10s), indicating that various social processes were integrated in understanding the social videos. Our study is one of the first to combine multi-modal neuroimaging to examine the neural networks underlying social cognitive processes, combining the strengths of the spatial resolution of fMRI and temporal resolution of MEG. Understanding this information from both modalities helped delineate the mechanism by which

ToM processing unfolds over time in healthy adults. This allows us to determine a benchmark against which clinical populations can be compared.

KEYWORDS

Theory of Mind (ToM), functional magnetic resonance imaging (fMRI), magnetoencephalography (MEG), social attribution, functional connectivity

Introduction

Humans have an advanced capacity to ascribe intentions to the minds of others. Premack and Woodruff (1978) coined the term "Theory of Mind" (ToM) to capture this ability to make inferences about the mental states of others including perspectives, desires and beliefs. During social interactions, ToM enables an individual to predict another person's behaviour. Explicit ToM is acquired between 3 and 5 years of age (Wellman et al., 2001, 2011; Callaghan et al., 2005), but ToM skills continue to improve throughout development (Blakemore, 2012; Lagattuta et al., 2015) and mastery of the subcomponents of ToM varies individually and cross-culturally (Shahaeian et al., 2011; Wang et al., 2016).

A debate remains ongoing regarding the mechanisms of ToM processing in part because it is hypothesised that ToM is not a singular skill and relies on multiple subprocesses including but not limited to self/other distinction, emotion processing, face recognition, cognitive flexibility, inhibition, working memory, moral reasoning, etc. as proposed by Schaafsma et al. (2015). Secondly, the term ToM remains unclearly operationalized across studies, with a range of paradigms that often focus on a single specific subtype of ToM such as inferring a character's perceptions, emotions or cognitive states, making it difficult to compare directly across studies. Despite these methodological constraints, fMRI investigations have furthered our understanding of a network of brain regions that is consistently activated across various ToM tasks (Carrington and Bailey, 2009; Schurz et al., 2014; Kliemann and Adolphs, 2018; Arioli et al., 2021). The right temporal-parietal junction (an area encompassing the angular and supramarginal gyri) is thought to be central to ToM processing due to its selective activation in mental state attribution conditions compared to social descriptions (Saxe and Wexler, 2005). Others have argued that the medial prefrontal cortex is most crucial, by serving a central role in social cognition, and specifically in thinking about oneself and others (Gallagher et al., 2000; Amodio and Frith, 2006). The right TPJ is associated with re-orienting to others and inferring their mental states (Saxe and Kanwisher, 2003; Rothmayr et al., 2011), and the medial prefrontal cortex is involved in decoupling thoughts about self from thoughts about others (Döhnel et al., 2012; Schuwerk et al., 2014).

Although the fMRI literature has advanced our knowledge of the key players in the ToM network, our understanding of how these regions *functionally* communicate remains unclear in the ToM neuroimaging literature. Other neuroimaging modalities such as EEG have provided some information about the timing of activation of these brain areas. For example, an early event-related potential (ERP) study using a subtype of ToM tasks known as false belief, showed increased late positive complex (LPC) over parietal regions (300–600ms) followed by a late slow wave divergence over anterior regions (600–900ms) in adults in the false belief compared to the true belief condition (Meinhardt et al., 2011). MEG (magnetoencephalography) can measure neuronal activation with far superior temporal resolution to fMRI, with access to information about the *timing* of activation (in ms), as well as *oscillatory* activity as it can directly quantify the brain's neural activity (Hari and Salmelin, 2012) and is not distorted by the skull or scalp, providing better spatial resolution than EEG. MEG allows the quantification of local and long-range oscillatory changes and their localisation in the brain (Hunt et al., 2019).

Previous MEG connectivity studies have shown that cognitive processes are modulated by specific frequency oscillations including theta (implicated in long-range communication in the brain), alpha (implicated in several cognitive processes including attention and memory), beta (implicated in top down processing) and gamma (implicated in visual attention, awareness, emotional processing) (Von Stein and Sarnthein, 2000; Engel and Fries, 2010; Palva et al., 2010; Klimesch, 2012; Mellem et al., 2013; Sherman et al., 2016; Solomon et al., 2017; Betti et al., 2018; Richter et al., 2018; Soto-Icaza et al., 2019). Although the current fMRI literature suggests that ToM is supported by a core ToM network, whether there are multiple independent networks which are temporally separate and modulated by different frequency bands remains a question. This is particularly important since ToM difficulties are common in several clinical populations such as autism spectrum disorder, schizophrenia, preterm birth and traumatic brain injury (Baron-Cohen et al., 1985; Penn et al., 2002; Hill and Frith, 2003; Brüne, 2005; Chertkoff Walz et al., 2010; Martín-Rodríguez and León-Carrión, 2010; Williamson and Jakobson, 2014; Bora and Berk, 2016; Mossad et al., 2017; d'Arma et al., 2021; Csulak et al., 2022) and access to information about ToM processing in typical development allows us to investigate the various aetiologies of these ToM deficits in clinical populations. A recent study on individuals with ASD highlighted that a multimodal neuroimaging approach would likely be more helpful to study ToM in ASD as their fMRI results did not point to clear differences in the ToM network that would relate to experienced social difficulties (Moessnang et al., 2020). An MEG functional connectivity analysis would therefore allow us to further characterise (1) which regions in the core ToM network are functionally connected, (2) the temporal sequence of these network dynamics, and (3) whether specific frequency bands support different ToM networks. Thus, using these two neuroimaging modalities (fMRI and MEG) allows us to pinpoint the stages of ToM processing. We do this by relying on fMRI which has excellent spatial localisation to assess whether our findings corroborate findings from previous source localisation studies, and by relying on MEG which has excellent temporal and oscillatory resolution to determine when these regions are functionally connected, as well as whether there are particular oscillatory characteristics that underlie these brain networks.

In this study, we measured ToM ability using a social attribution task, first introduced by Heider and Simmel (1944) and further developed by others (Castelli, 2002; Schultz et al., 2003; Gobbini et al., 2007). The social attribution task involves moving shapes designed to depict social interactions and invokes mental state attributions from the viewer. This task has been used in fMRI to interrogate ToM processing (Kana et al., 2015; Martin et al., 2016; Synn et al., 2017) as it has lower cognitive demands compared to classic false belief tasks. Using the social attribution task in this study therefore allows replication in other clinical populations using multi-modal neuroimaging. Although ceiling effects can occur in the behaviourally administered version of this task, we were interested mainly in the neural correlates of the ToM condition of the task.

We recruited two groups of healthy adults to complete this study. The first group ($n = 20$) watched a set of videos depicting either social interactions or random motion and provided their verbal descriptions of each scenario. Videos where all subjects attributed mental states to the shapes were categorised as the ToM condition and videos were all the subjects did not attribute mental states to the shapes were categorised as the non-ToM condition. The second group of healthy adults ($n = 25$) completed the social attribution task in the fMRI and MEG. The study had three main objectives: (1) to corroborate previous findings that the social attribution task recruits core ToM regions in fMRI, (2) to determine which frequency bands modulate ToM processing in the social attribution task, and (3) to establish which regions of the ToM network are functionally connected. We predicted greater recruitment of the ToM network in the social compared to the control condition and further that ToM processing would be coordinated by oscillatory activity in beta band based on previous EEG findings (Guan et al., 2018).

Methods

Participants

Forty-five adults were recruited by posting flyers in the Peter Gilgan Centre for Research and Learning at SickKids, Toronto, Canada. Twenty of those adults were recruited to provide descriptions for 28 videos designed by Klin (2000) and Schultz et al. (2003) that depict social interactions (16 videos) or random motion (12 videos). There was consensus among participant narratives for 6/16 social videos and 6/12 random motion videos. Of those, four videos depicting social interactions and four videos depicting random motion were included in the social attribution task.

A second sample of twenty-five adults (12 females, mean age: 26.7 ± 5.4 years) completed the social attribution task in MEG and fMRI. Exclusion criteria included intellectual impairment or any other language or vision issues preventing successful completion of tasks, as well as standard MEG/MRI contraindications. This study was approved by the SickKids research ethics board. Participants gave their written informed consent according to the declaration of Helsinki. All study components, intellectual testing, MEG and fMRI scans, were completed on the same day.

Intellectual testing

Participants completed two subtests (Vocabulary and Matrix Reasoning) of the Wechsler Abbreviated Scale of Intelligence (WASI, Wechsler, 1999) as an estimate of their Full-Scale IQ.

The social attribution task

The social attribution task is based on previous findings that adults attribute mental states (intentions, emotions, beliefs and personality traits) to moving geometric shapes based on their kinetic features (Heider and Simmel, 1944). These findings have been replicated in various behavioural studies and later in neuroimaging studies (Phelps and LeDoux, 2005; Amodio and Frith, 2006; Hynes et al., 2011).

The task consisted of eight 15-s videos which included three white shapes (square: 0.6 × 0.6 cm, circle: 1 cm diameter, and triangle: 1.4 × 1 × 1 cm) moving in and around a white fixed square frame (with one side that hinged open and shut). The frame was centred in the middle of the screen and the shapes were displayed against a black background. The task included two conditions: a social condition and a control condition. In the social condition, the videos depicted a non-verbal narrative—with a start, middle and resolution—which unfolded among the shapes. In the control condition, the three shapes were moving randomly (at varying speeds and angles) across the screen. The basic visual characteristics (speed, orientation of motion, etc.) were similar across the social and control conditions.

A 10 second baseline (black screen with a white centred fixation cross) was presented at the beginning of the task in both the MEG and fMRI scans, followed immediately by the first video, Figure 1. The eight videos were presented in pseudorandom order and each video was followed by a prompt for participants to choose whether the shapes were moving randomly ("Random") or were socially interacting ("Interacting"). This prompt included a fixation cross centred on the screen and the two words were displayed on either side of the fixation cross. Participants had 3 s to respond. Following this prompt, an interstimulus interval with only the fixation cross was presented (5 s in the MEG and 8 second in the fMRI). The task was run 3 times in both MEG and fMRI. The run time of the task was 3.3 min in the MEG and 3.7 min in the fMRI for each run.

Following the MEG and MRI scans, participants watched each video and provided verbal responses to the question "Tell me everything that is happening in this video". Their responses were recorded on an audio recorder, transcribed and then scored based on scoring criteria developed by Klin (2000). Participants' attributions were categorised into behaviour (e.g., triangle *chases* square), perceptions (e.g., square *sees* the circle), emotions (e.g., square is *happy*), cognitions (e.g., triangle *wants* to trick the circle), relationship/personality traits (e.g., square is circle's *friend* or square is a *bully*). Participants' use of symbolic descriptions (e.g., the square and circle leave their *house*) was also scored and the mean number of attributions in between conditions was compared using paired *t*-tests.

Data acquisition and pre-processing

fMRI

T1-weighed structural magnetic resonance images (MRIs) were collected on a 3T Siemens MAGNETOM Prisma Fit scanner with a 20-channel head and neck coil. A three-dimensional (3D) magnetisation-prepared rapid gradient-echo (MPRAGE) sequence (TR/TE/TI: 1870/3.14/945 ms; FA: 9°; FOV: 240 × 256 mm; number of slices: 192; resolution: 0.8 mm isotropic; scan time: 5:01 min) was used to collect the MR images.

fMRI data were acquired while participants completed the social attribution task using an echo planar imaging (EPI) sequence (TR/TE: 1,500/30 ms; FA: 70°; FOV: 222 × 222 mm; number of slices: 50; resolution: 3 mm isotropic). Participants responded using button press (on a 4-button Diamond Fibre Optic Response Pad by Current Designs).

All scanning took place at the Hospital for Sick Children (Toronto, Canada). Standard Analysis of Functional NeuroImages (AFNI, Cox, 1996; Cox and Hyde, 1997), FreeSurfer (Dale et al., 1999) and FMRIB Software Library (FSL, Jenkinson et al., 2012) tools were used to process fMRI data. T1-weighted images were skull stripped using FreeSurfer. Slice timing and motion correction were applied to the fMRI data and the 6 motion parameters (3 translations + 3 rotations) were estimated. We calculated frame-wise displacement (FD), and volumes with FD > 0.9 mm (Siegel et al., 2014) were removed from the data. We used a 6 mm FWHM Gaussian kernel to smooth data and then data were intensity normalised. White matter, CSF and whole-brain signal contributions along with the 6 motion parameters were regressed from the data. A 0.01–0.2Hz bandpass philtre was applied. FSL's FLIRT (Jenkinson and Smith, 2001) was used to register functional images to MNI standard space and FIX was used for ICA denoising (Griffanti et al., 2014; Salimi-Khorshidi et al., 2014).

MEG

Participants were scanned in a magnetically shielded room in supine position using a 151-channel CTF system (CTF MEG International Service LP, Coquitlam, BC, Canada). Data were recorded at a 600 Hz-sampling rate with third order noise cancellation and continuous head localisation throughout the recording. Stimuli were presented ~80 cm from the participant. Participants responded on a VPIXX 4 button pad (Visual Science Solutions, Saint-Bruno, Canada). Analyses and statistics were conducted in MATLAB implementing functions from the FieldTrip toolbox (Oostenveld et al., 2011), Network-Based Statistics (Zalesky et al., 2010), BrainNetViewer (Xia et al., 2013) and Marc's MEG Mart (MMM; https://gitlab.com/moo.marc/MMM).

"Social" and "Control" trials were epoched from −5 to 17s. Heartbeat and ocular artefacts were removed using ICA by author SIM. Trials where the signal exceeded 2,500 fT were also rejected. Head motion was calculated by fitting a rigid sphere to the average fiducial marker locations (right and left pre-auricular points and nasion) and tracking the motion (rotation and translation) of the sphere continuously using the HeadMotionTool from the M MM toolbox. Trials with >10 mm motion from the median head position were rejected.

MEG source analysis

Data were imported to MATLAB, mean-centred and then filtered with a 4th order Butterworth band-pass philtre from 1 to 150 Hz, as well as a discreet Fourier transform notch philtre at 60 and 120 Hz to remove line noise. Single shell head models based on each participant's MRI were computed using SPM12 through FieldTrip and template coordinates were non-linearly transformed into subject-specific coordinates. Linearly constrained minimum variance (LCMV) beamforming with 5% regularisation and projection of the activity to the dominant orientation was performed to estimate the neural activity index (NAI) at the centroid of each of the cortical and subcortical regions of the AAL atlas.

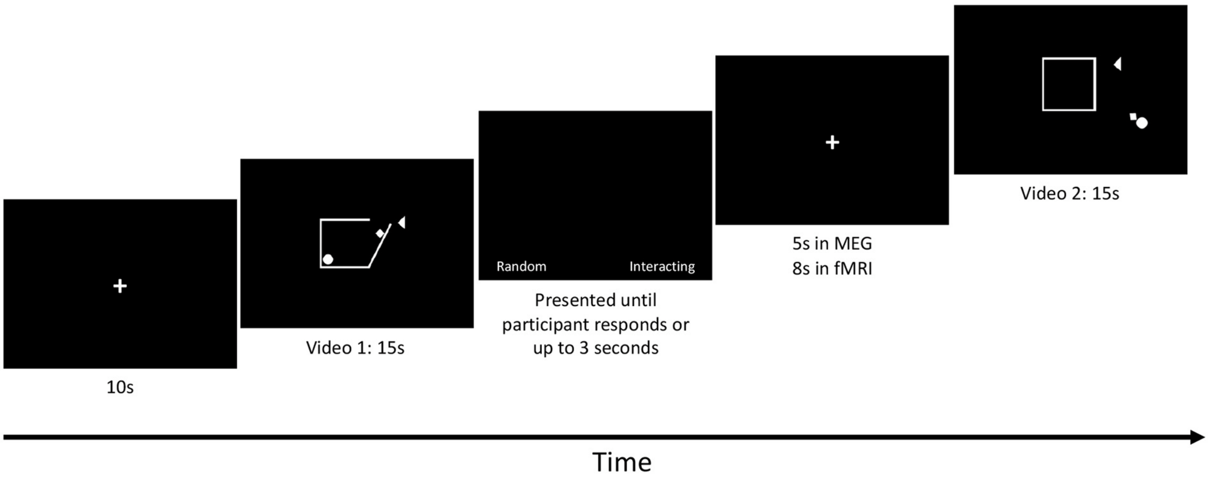

FIGURE 1
SAT protocol: Each run started with a 10-s baseline followed by a 15-s video. Each video was followed by a prompt for each subject to respond by button press to whether the shapes' movement was interpreted as Random (Control condition) or whether the movements were interpreted as Interacting (Social condition). The prompt was presented until each subject responded or up to 3 s elapsed. An inter-stimulus interval was then presented. The length of the inter-stimulus interval was 5 s in MEG and 8 s in fMRI. The videos were designed by Klin (2000) and Schultz et al. (2003).

MEG connectivity analysis

The NAI timeseries were then filtered into 4 canonical frequency bands: theta (4–7 Hz), alpha (8–12 Hz), beta (13–29 Hz), gamma (30–55 Hz), using FIR philtres (MATLAB's fir1). Filtered NAI time series were orthogonalized (using the symmetric orthogonalization procedure from Colclough et al., 2015) to remove effects of signal leakage.

Connectivity was estimated using amplitude envelope correlations (AEC). Amplitude envelopes were computed using the absolute value of the Hilbert transform (Brookes et al., 2011; Hipp et al., 2012). To obtain the AEC, the Pearson correlation coefficient was computed for amplitude envelopes from each pair of nodes. The AEC time series were then baseline corrected by calculating the fractional change from the mean baseline AEC (−5 to 0 s).

Statistical analysis

fMRI

First-level analyses using the task conditions (social, control, baseline and response) were used as explanatory variables and convolved with a double-gamma hemodynamic response function using FMRIB's Improved Linear Model (FILM; Woolrich et al., 2001). The model included nuisance regressors for the 6 motion parameters and motion-scrubbed volumes and investigated contrasts between the social and control conditions. Second-level analysis was performed to average contrast estimates over runs within each subject using FSL's FMRI Expert Analysis Tool (FEAT) with fixed effects (Woolrich et al., 2004). Finally, the across-condition effects of the social vs. control contrast were examined using FMRIB's Local Analysis of Mixed Effects (FLAME; Woolrich et al., 2004). Multiple comparisons correction was performed with Gaussian random field theory at the cluster level ($Z > 2.3$), holding significance at $p_{\text{corr}} < 0.05$. The cluster size threshold as calculated by FEAT was at least 225 voxels.

MEG

Whole brain network connectivity in the social condition (Social > Baseline) was identified in Network Based Statistics (NBS) (Zalesky et al., 2010). First, NBS applies mass univariate testing to test the null hypothesis at each connexion between two nodes across the whole brain. For each connexion, a strict t-value threshold of 2.75 was applied, allowing only connexions with a t-value of 2.75 and above to be included. Next, NBS examines the topology among the connexions which passed suprathreshold connexions using cluster-based statistics. Therefore, each surviving cluster was composed of supra-threshold connexions, with a path connecting any two nodes. Finally, permutation testing (permutations were repeated 5,000 times) was used to compute a family wise error corrected p-value for each network. Networks passing the significant threshold ($p_{\text{corr}} < 0.05$) are reported for the time windows of interest (0–5, 5–10, 10–15 s).

Results

Intellectual testing

Participants who completed the neuroimaging component had an average IQ of 117.1 ± 10.5.

SAT descriptions

Participants made significantly more attributions overall to the shapes in the Social compared to Control condition including more behavioural, emotional and cognitive state attributions (all $ps < 0.05$, Figure 2).

Neuroimaging results

fMRI results

Scenarios depicting social interactions (Social condition) elicited fMRI activity in parietal regions: the bilateral superior and inferior parietal lobules, the bilateral supramarginal gyri and the precuneus. Increased activity in the Social condition was also seen in frontal regions: bilateral inferior frontal gyri, bilateral middle frontal gyri and bilateral orbital frontal gyri (Figure 3). The list of significant activations can be found in Supplementary Table S1.

MEG results

MEG results confirmed involvement of several regions found in the fMRI analysis but also suggest that parietal and frontal regions are involved in a sequential order rather than in concert in ToM processing (Figure 4). In the earlier time window: from 0 to 5 s, two temporal-parietal networks were involved, one in theta band (4–7 Hz) and one in gamma band (30–55 Hz). In theta band, the network was comprised of the right supramarginal gyrus, right superior parietal gyrus, right inferior parietal lobule as well as right temporal pole and left insula. Other regions which are not classically involved in ToM were also found in this network including the left post central gyrus and left supplementary motor area. In gamma band, the network included the right angular gyrus and posterior cingulate gyrus.

From 5 to 10 s, a beta band network involving mainly frontal parietal regions as well as subcortical structures was found in the Social condition. Regions in this network included the right angular gyrus and the right inferior parietal lobule and the bilateral amygdalae as well as the superior frontal gyrus and bilateral orbital frontal gyri. There were no significant networks found in alpha band or the last time window (10–15 s).

Discussion

A large body of research suggests that humans have an intrinsic ability to attribute human experiences such as personality traits, relationships and thoughts to moving shapes based on their kinetic features (Heider and Simmel, 1944; Castelli et al., 2000; Schultz et al., 2003). Consistent with prior research, we found that adults made significantly more behavioural, perceptual, emotional and cognitive attributions in the Social compared to the Control condition. During the Social condition, we found recruitment with fMRI of the classic ToM network including the TPJ, superior temporal sulcus and precuneus, consistent with other studies using a similar experimental paradigm (Castelli et al., 2000; Osaka et al., 2012). These regions are also commonly involved in other ToM tasks such as those invoking false belief and social storey protocols (Carrington and Bailey, 2009). Our MEG results complemented the fMRI data by offering novel insights into the timing of the involvement of these regions, as well as the oscillatory frequencies that support these networks, adding exciting new information about the mechanisms of ToM processing. Specifically, our study extends the previous literature by suggesting that ToM is supported by processing first in a network comprised mainly of temporal-parietal regions followed by a network comprised of frontal-parietal regions. Based on the previously documented functions of regions that comprise these two networks, social attribution tasks involve an initial shifting of attention to the agent to which attribution is made (temporal-parietal connexions) followed by self/other delineation (frontal-parietal connexions). We also found that ToM processing is supported by neural oscillations in theta, beta and gamma. The current study highlights the complex interplay between neural activity, neural oscillations and specific timing of these activations to support ToM processing in healthy adults.

ToM involves distinct temporal-parietal and frontal-parietal connectivity networks

Over the last few decades, several fMRI studies have tried to delineate the role of regions that comprise the ToM network. This network consists of the medial prefrontal cortex (*mPFC*), medial orbital frontal cortex (*mOFC*), the anterior cingulate cortex (*ACC*), the precuneus, bilateral temporal poles (TP), posterior superior temporal gyri (*STG*), bilateral temporal parietal junctions (*TPJ*), and bilateral inferior frontal gyri (*IFG*) (Molenberghs et al., 2016). Our MEG results help address this issue of priority of these brain areas. We found that networks from 0 to 5 s in the Social condition involved the right TPJ, right temporal pole, right parahippocampal gyrus and left insula.

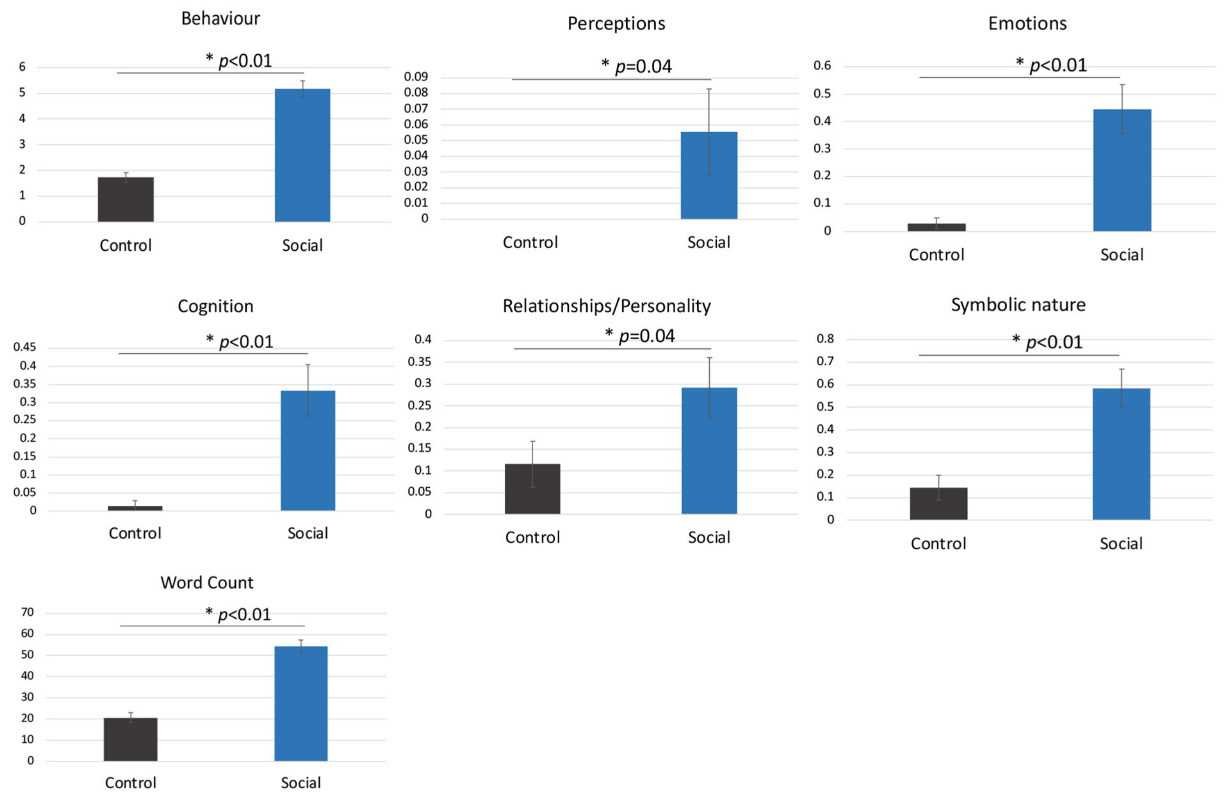

FIGURE 2
The mean number of attributions per video in the Social compared to Control condition (± standard error). Asterisks represent a statistically significant difference. Participants did not make perceptual attributions in the Control condition.

Similarly, a previous study using MEG, found that during false belief processing (ToM task), the right TPJ was recruited from 150 to 225 ms, followed by activation in the precuneus, the right inferior frontal gyrus (200–375 ms) and the superior frontal gyrus (300–400 ms) (Mossad et al., 2016). These findings corroborate previous suggestions that the right TPJ is one of the key regions involved in ToM processing to facilitate orienting to socially relevant stimuli. We also found that the TPJ was functionally connected with the insula, which would facilitate detection of salience of the socially relevant events in the videos. Parietal-temporal connexions were also found between the right TPJ and the right parahippocampal gyrus. Connexions between parietal to medial temporal structures support the hypothesis that previous knowledge stored in memory is accessed during ToM processing to help explain the relation between the mental state attribution and the action to be predicted (Frith and Frith, 2003).

In the second time window (5–10 s), a network with dense frontal-parietal connexions was found. The main frontal structures involved were the superior frontal gyrus and the right orbital frontal cortex, concordant with previous literature on the importance of medial frontal areas in ToM. The fact that this frontal region was seen at 5–10 s but not 0–5 s suggests that it follows the TPJ and the temporal-parietal networks. The fact however, that the TPJ and the prefrontal regions were functionally connected during ToM processing supports the integration of these key structures in the concerted processes of inferring the mental states of others and decoupling one's own mental state from others' mental states.

ToM is supported by theta, gamma and beta oscillatory frequencies

The ToM networks we found were supported by theta and beta frequency bands in addition to a focal network in gamma band. Theta (4–7Hz) classically underlies long-range communication in the brain and facilitates complex cognitive processing (Mellem et al., 2013; Kaplan et al., 2017). The largest network we found was in the 0–5s time window in theta and indicated the early activation and integration of the temporal-parietal brain areas involved in ToM. Consistent with this, an EEG study using an animated videos paradigm showed that theta frequency oscillations were modulated by varying the complexity of the presented

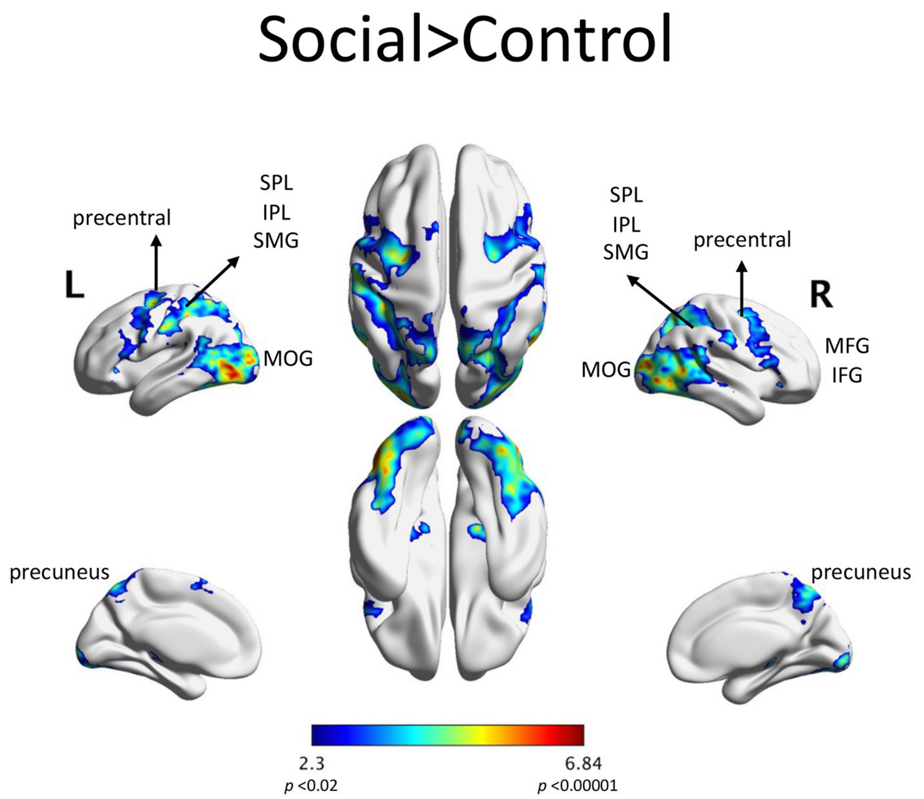

FIGURE 3
fMRI activations in the Social > Control contrast included: SPL: superior parietal lobule, IPL: inferior parietal lobule, SMG: supramarginal gyrus, MFG: middle frontal gyrus, IFG: inferior frontal gyrus, MOG: middle occipital gyrus. This activation was composed of largely one contiguous set of regions, with the highest activation in the left visual area. AAL regions with at least 1% of the cluster's volume are listed in Supplemental Table S1.

social interactions (Blume et al., 2015). In the same time window, there was a focal network in the right temporal-parietal region, in gamma. Gamma band activity is related to visual attention and awareness (Tallon-Baudry, 2009) and is central to the binding of perceptual representations with emotional meaning (Garcia-Garcia et al., 2010; Martini et al., 2012; Safar et al., 2020). This gamma band network thus suggests that the detailed attentional processing of the social, emotional aspects of the videos were being processed in this small, discrete network in the first few seconds of the video.

In the following 5 s (5–10 s), the third network was seen in beta band, anchored in the orbital, medial frontal areas. Frontal beta oscillations play a key role in top-down attentional control of information (Richter et al., 2018; Riddle et al., 2019; Kajal et al., 2020) and are associated as well with processing of visual, emotional stimuli (Güntekin and Başar, 2010; Luckhardt et al., 2017). This suggests that this beta network, underpinned the attentional processing of the social and emotional aspects of the videos. The fact that it involved the frontal regions, unlike the networks at 5–10 ms, strongly suggests that the medial prefrontal activation seen in fMRI *follows* the activity in the TPJ and other temporal parietal areas. Interestingly, however, this network included the right TPJ areas and amygdalae, thus linking the processing of the self vs. others, seen in these frontal areas, with the inferences of mental and emotional states, that may rely more on the TPJ and amygdalae. This also further highlights the hypothesis that ToM is not a singular process (Schaafsma et al., 2015) but rather is based on multiple cognitive subprocesses. We add to this by showing the sequence of these processes.

We had also predicted involvement of alpha band in the current paradigm as it was previously implicated in ToM processing (Perry et al., 2010, 2011) and was also found to be involved in the social attribution task in MEG in typically developing children ($n = 43$) (Mossad et al., 2017) but a reason why we may have failed to make this findings is the relatively small ($n = 25$) sample size in this study.

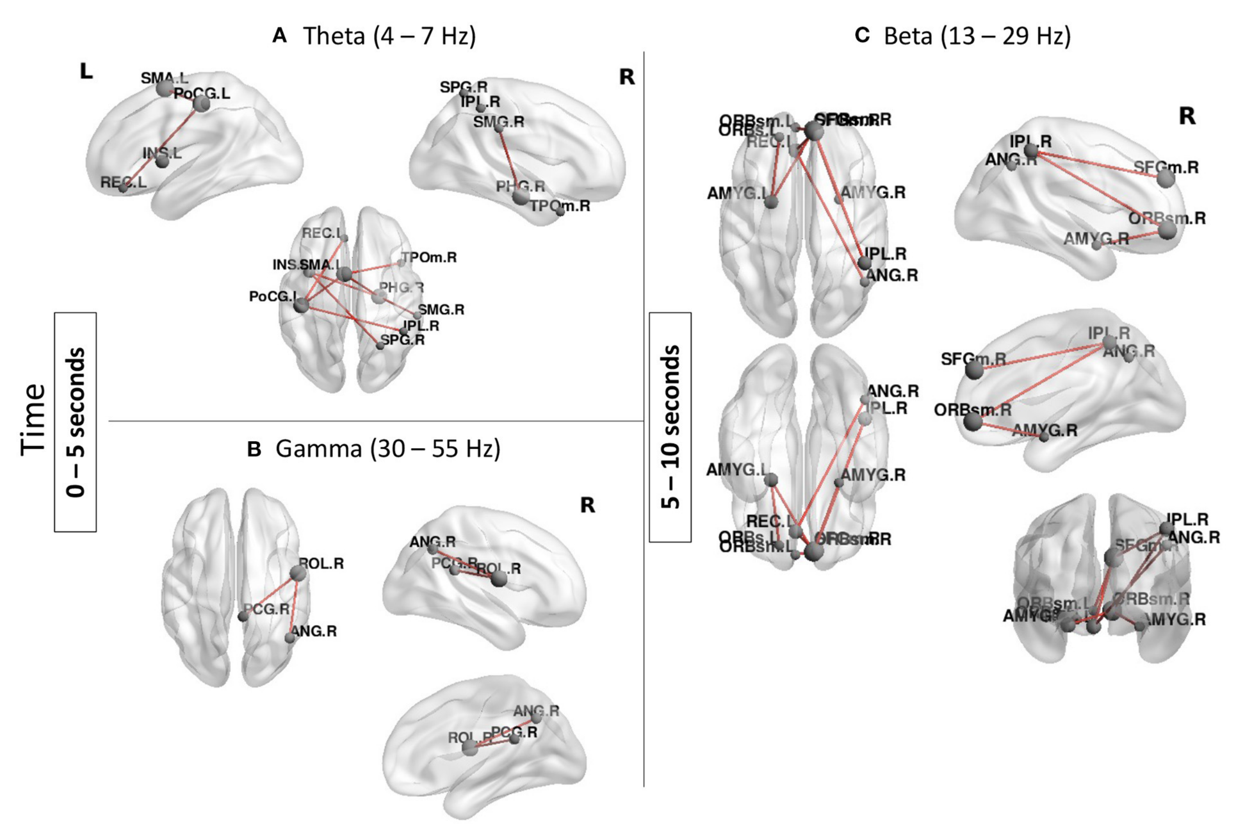

FIGURE 4
Functional connectivity results during the Social condition (Social > Baseline). **(A,B)** A temporal-parietal network was found in theta and gamma bands from 0 to 5 s. **(C)** A frontal-parietal network was found in beta band from 5 to 10 s. Node size represents the number of connexions each node has with other regions of the network, larger nodes indicate more connexions. Networks shown are reported at $p_{\mathrm{FWER}} < 0.05$.

fMRI source localisation vs. MEG functional connectivity analyses

Based on previous fMRI findings, it is known that there is an overlap across ToM study paradigms in core brain activations. In this study, the temporal-parietal junction, medial prefrontal cortex, inferior parietal lobule and the precuneus were found to be more highly activated in the social compared to the physical (control) condition in the source localisation fMRI analysis, which was previously reported in several ToM paradigms (see meta-analysis by Schurz et al., 2014). In the social animations paradigm, there is overlap with regions found in previous studies in the precuneus, medial prefrontal cortex, temporoparietal junction, superior temporal sulcus and occipital gyrus (Castelli et al., 2000; Moessnang et al., 2020; Schurz et al., 2021).

One of the unique aspects of this study design was the use of two neuroimaging modalities: fMRI and MEG. Since the focus of the analyses were different in each modality, a direct comparison is not supported; however, some conclusions can be drawn from each analysis. For example, we found regions that were recruited both in the spatial localisation analysis (done in fMRI) and the functional connectivity analysis (done in MEG). These regions included the right supramarginal gyrus (region in the right TPJ), the right superior parietal lobule and the right inferior parietal lobule. The consistent involvement of these regions in spatial localisation and functional connectivity highlights the previously hypothesised role of this right parietal region as being central to ToM. Damage to the right parietal cortex may therefore have the greatest impact on ToM processing, as our findings suggest that this region is not only recruited for ToM but is also communicating with other regions to process information about others. In a recent study investigating ToM skills in tumour patients, Campanella et al. (2022) found that patients with right superior parietal damage had the highest selective impairments in intention attribution compared to patients with temporal or frontal lesions both before and after surgery.

Importantly, the fMRI activations were largely bilaterally symmetrical, whereas the MEG hubs were right-dominant.

Considerable research has suggested that the ToM, social-cognition network is right lateralised (Saxe and Kanwisher, 2003; Saxe and Wexler, 2005), consistent with the MEG findings. Since fMRI and MEG capture different processes (Hall et al., 2014), these differences in lateralization are unsurprising. Because fMRI relies on the slow hemodynamic response, it is biassed towards long-lasting processes (or neural activations) that occur in the very slow oscillatory frequency ranges, whereas, MEG will capture fast-occurring and high frequency activity. For this reason, differences in localizations including laterality can differ. The bilateral effects seen in fMRI suggest that with time, homologous brain areas are also activated, but the MEG results suggest that only the right lateralized parietal regions are functionally connected with other ToM regions during processing the social information in the videos.

It is also significant to note that some regions were found in the functional connectivity analysis in MEG but not in the spatial localisation analysis in fMRI such as the superior frontal gyrus, right temporal pole, left insula, bilateral amygdalae. This is not surprising as key structures, which may activate only for short periods of time, would be missed by fMRI. As some previous fMRI studies have shown involvement of these frontal and subcortical regions (Gallagher et al., 2000; Phelps and LeDoux, 2005; Gobbini et al., 2007), this suggests that their activation may also be task dependent. These data would suggest that the greater temporal resolution of MEG allows for greater sensitivity in identifying key hub regions implicated in ToM which are more transiently active, which would be not uniformly present in fMRI results.

Future directions and limitations

A methodological advantage of this task is that does not require language proficiency and therefore the paradigm can be studied across developmental groups and clinical populations. For example, in a recent MEG study using this paradigm, we found a similar frontal-parietal network in beta band in healthy full-term born, 8-year-old children compared to preterm born children (Mossad et al., 2021), suggesting that this network may be recruited across typical development. We have also shown that this protocol can distinguish types of social interactions portrayed in the video in children with and without neurodevelopmental disorders (Vandewouw et al., 2021). However, a methodological limitation of this task is that given the length of each trial, fewer scenarios overall can be used in the social attribution task and therefore the results of this study are limited to the scenarios presented. Future studies can aim to compile a database of social attribution videos and investigate mental state attribution across various social interactions to allow presentation of a more standardised set of stimuli. Twenty-five participants completed the paradigm in both the MEG and the fMRI. A potential limitation is that there may have been practise effects in the fMRI due to the stimuli having been presented already in MEG. Activation in ToM regions were found in the fMRI but future studies should include measures such as eye tracking to ensure that the participants focus on the scenarios or use slightly different scenarios that are known to elicit similar descriptions. An important point for this study is that we have demonstrated that this protocol is adaptable to both neurophysiological and hemodynamic neuroimaging approaches. Clearly the MEG provides richer data and offers advanced options in understanding the timing and frequencies associated with various aspects of ToM processing.

Conclusions

In this study, we found that ToM processing was supported by three networks in MEG in theta, beta and gamma bands. These networks included regions that are classically involved in ToM studies (Carrington and Bailey, 2009). The right TPJ was involved in all three networks, further highlighting its role as a key player in ToM processing, while medial prefrontal cortex and subcortical connexions were found only in beta band. The specificity of the findings was greater in MEG than fMRI; fMRI results showed bilateral, classic areas of activation only. Information about the temporal and oscillatory properties of these network dynamics through MEG allowed us to conceptualise a sequence for ToM processing, providing rich information against which atypically developing populations can be compared.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The studies involving human participants were reviewed and approved by SickKids Research Ethics Board, Hospital for Sick Children, Toronto, Canada. The participants provided their written informed consent to participate in this study.

Author contributions

SM collected and analysed the data and wrote the manuscript. MV and KV helped analyze the data and contributed to manuscript development. EP and MT contributed to the design of the study and manuscript development. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fnhum.2022.921347/full#supplementary-material

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Interpersonal sensorimotor communication shapes intrapersonal coordination in a musical ensemble

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Social behaviors rely on the coordination of multiple effectors within one's own body as well as between the interacting bodies. However, little is known about how coupling at the interpersonal level impacts coordination among body parts at the intrapersonal level, especially in ecological, complex, situations. Here, we perturbed interpersonal sensorimotor communication in violin players of an orchestra and investigated how this impacted musicians' intrapersonal movements coordination. More precisely, first section violinists were asked to turn their back to the conductor and to face the second section of violinists, who still faced the conductor. Motion capture of head and bow kinematics showed that altering the usual interpersonal coupling scheme increased intrapersonal coordination. Our perturbation also induced smaller yet more complex head movements, which spanned multiple, faster timescales that closely matched the metrical levels of the musical score. Importantly, perturbation differentially increased intrapersonal coordination across these timescales. We interpret this behavioral shift as a sensorimotor strategy that exploits periodical movements to effectively tune sensory processing in time and allows coping with the disruption in the interpersonal coupling scheme. As such, head movements, which are usually deemed to fulfill communicative functions, may possibly be adapted to help regulate own performance in time.

KEYWORDS

interpersonal coordination, intrapersonal coordination, embodied music cognition, music ensemble performance, multiple timescale

Introduction

We adapt to complex and changing environments by finely coordinating multiple body parts at the same time. Doing so "in concert" with others enables very subtle forms of collaboration, such as playing together in a sport team or in a musical ensemble. However, coordinating the self and coordinating with others are most often investigated separately. In effect, motor coordination has long been studied in the sole context of individual actions, while a growing number of studies have recently focused on coordination at the interpersonal level (Sebanz et al., 2006; Schmidt and Richardson, 2008; Laroche et al., 2014; Cornejo et al., 2017; Wiltshire et al., 2020; Dean et al., 2021).

Indeed, similar laws of coordination have been observed in tasks that can be performed by either one or two individuals (e.g., arm movement coordination within or between participants; Amazeen et al., 1995; Schmidt et al., 1998; Schmidt and Richardson, 2008; Fine and Amazeen, 2011). Patterns of coordination emerge even when participants hold opposite intentions or when they are not even aware of their mutual interactions (Issartel et al., 2007; Auvray et al., 2009). In return, patterns at the macro-level constrain the activity of the body parts at the micro-level, inducing synergy among them (Kelso and Engstrom, 2006; Riley et al., 2011).

From this perspective, intrapersonal motor coordination has been hypothesized to be "nested" within higher-order processes of interpersonal coordination (Ramenzoni et al., 2011). A few experiments have testified of the effect of interpersonal processes on intrapersonal coordination. For instance, synchronously walking with another person improved individual gait coordination (Nessler et al., 2015). On the contrary, synchronizing finger tapping with a partner impaired bimanual coordination at the intrapersonal level (Lorås et al., 2019). Most often, interpersonal visual coupling stabilized postural equilibrium (Varlet et al., 2011, 2014; Athreya et al., 2014; Gueugnon et al., 2016). In fact, postural equilibrium can be affected by both intra and interpersonal constraints, with a modulatory effect of task difficulty (Stoffregen et al., 2013).

Earlier studies have found interpersonal coordination to be stronger than intrapersonal coordination when studying them with similar tasks but in separate trials (Schmidt et al., 1998; Black et al., 2007). However, Romero et al. (2015) studied both kinds of coordination simultaneously using a task where one participant had to bring a pointer at the center of a target held by her partner, and observed that interpersonal coupling was stronger than intrapersonal coupling. All in all, these results highlight that intrapersonal coordination can be flexibly subordinated to interpersonal task goals (Bosga et al., 2010). For instance, Aikido experts (but not novices) whom natural movements were artificially perturbed decreased their intrapersonal coordination between sternum, wrist, and elbow in order to strengthen their interpersonal coupling (Caron et al., 2017). To sum up, interpersonal roles and task constraints can thus elicit distinct and complementary modes of intrapersonal coordination (Ramenzoni et al., 2012).

However, previous studies only involved postural or bodily symmetric tasks (ankles during gait, fingers during tapping, arms during precision tasks). Most importantly, they all tackled this issue in dyadic contexts – most often visuomotor tasks – where goals predominantly targeted one level of coordination (either intra- or interpersonal) at the expense of the other. Yet, collaborative activities often involve different body parts (on top of postural demands) that move at distinct paces (unlike synchronized tapping or walking), and they can take place in larger groups of multi-modally coupled individuals whose performances are critical at both intra- and interpersonal levels. More complex and ecological experimental settings are thus required to understand whether and how intrapersonal coordination dynamically adjusts based on changes in interpersonal coupling demands.

A conducted musical ensemble is probably one of the best scenarios to tackle this issue (D'Ausilio et al., 2015; Volpe et al., 2016). Performers coordinate several body parts that move at multiple timescales to play complex musical patterns, and they aim at an exquisite temporal accuracy at both the individual and collective levels of coordination. Coupling between musicians is multimodal (auditory, but also visual, especially with a conductor), and body parts can serve different purposes, from instrumental gestures (those contributing to sound production) to so-called ancillary gestures (such as head movements, which communicate structure and convey expressivity; Nusseck and Wanderley, 2009; Demos et al., 2014).

So far, studies on orchestral ensembles have focused on interpersonal processes (Volpe et al., 2016; Palmer and Zamm, 2017; Wöllner and Keller, 2017; Fadiga et al., 2021). They looked at the coordination between musicians and conductors (D'Ausilio et al., 2012; Meals, 2020), or among musicians, as a function of task difficulty (Badino et al., 2014), leadership (Timmers et al., 2014; Wing et al., 2014; Varni et al., 2019), interpersonal network properties (Shahal et al., 2020), visual communication (Bishop et al., 2021), emotional expression (Chang et al., 2019), or instructions of interactions (Proksch et al., 2022). Solo and collective performances have been compared to quantify behavioral interdependence between players of an ensemble (Papiotis et al., 2014). Such comparisons also helped revealing differences in head motion patterns and functionality across these contexts (Glowinski et al., 2013). In effect, when a player was asked to produce unexpected tempo changes, head movements became more coordinated and asymmetries related to leadership decreased (Badino et al., 2014). The structure of leadership also got weakened together with a decrease in body sway coordination when visual coupling between musicians was removed (Chang et al., 2017). Finally, simply changing the network of visual coupling among players differently affected sensorimotor communication channeled through ancillary (head) and instrumental (bow) movements (Hilt et al., 2019).

Despite providing a relevant context, none of these studies has examined how the interpersonal coupling scheme within a musical ensemble affects the intrapersonal coordination of multiple body parts that music performance involves. To study this, we perturbed the network of sensorimotor communication of an orchestra: the visual coupling of first-section violinists with the conductor (normal condition) was replaced by visual coupling with the second section of violinists (perturbed condition). Because the conductor plays a crucial role in regulating the timing of the players (Luck and Sloboda, 2008; D'Ausilio et al., 2012), preventing vision of his gestures makes it harder for musicians to correctly adjust the timing of their instrumental performance. Given the lack of collectively shared temporal cues provided by the conductor, we expected that violin players would enhance their intrapersonal coordination between ancillary (head) and instrumental (bow) movements to better focus on and regulate the timing of their own instrumental performance.

Materials and methods

Participants

A 17-piece orchestral ensemble, with two sections of violinists composed by four players each, and two different conductors were recruited for the experiment. The study was approved by the SIEMPRE Project Management Committee in respect with the standards of the Declaration of Helsinki, and participants gave written informed consent prior to the experimentation. The data set was recorded in the context of the SIEMPRE EU-FP7-FET[1] project and partially used in a previous publication (Hilt et al., 2019). Here we performed a different pre-processing of the raw data, we computed a different collection of motion features, and we performed different analyses to tackle new research questions.

Procedure

The members of the orchestra were invited to perform at Casa Paganini in Genova, Italy. This is a research center endowed with a 250-seats auditorium that can be configured to serve as an ecological environment resembling a concert hall. The stage at Casa Paganini is fully equipped with a motion capture system and with professional devices for audiovisual recordings. The orchestra played a familiar excerpt from its repertoire - the opening of "Signor Bruschino" (1813) by Gioacchino Rossini – which eschewed learning effects during the experiment. Furthermore, several features make the piece interesting to study interpersonal coupling processes, as well as their effects on intrapersonal coordination. First, the elevated tempo (near 230 bpm; see Section "Results") and the speed of execution of passages requiring the bow to revert direction every eighth note place high demands on the fine rhythmical coordination of the players. Second, the important rhythmical differences between the scores of V1 and V2 suits the purpose of evaluating the impact of the presence or absence of a visual coupling between the two sections. Third, the recurrent pauses between the different running passages impose that players pay close attention to their peers and to the conductor in order to finely control their timing when their instrument re-enters the piece. This suits well the goal of studying how changes in visual cues impact the coordination of players' movement.

To allow the repetition of several takes while avoiding accumulating fatigue over these multiple trials, the chosen excerpt was about 1 min long (i.e., the 55 first bars of the piece). This constitutes a good trade-off between the ecological context of the orchestra and an empirical format where different conditions are examined over repeated measures.

Importantly, none of the two conductors had practiced with this orchestra before, and they were not given any particular indication regarding their interpretation of the score (e.g., in terms of tempo). Participants completed two experimental conditions: a control condition (NORM) where all performers set at their normal position in the orchestra, and a perturbed condition (PERT) where first-section violinists (V1) turned their back on the conductor and faced the second-section violinists (V2) instead (see **Figure 1**). This manipulation allowed us to probe the sensitivity of V1's intrapersonal movement coordination, on which we focus here, to the constraints of their interpersonal coupling[2]. Three takes were recorded with each of the 2 conductors and for each of the 2 conditions (NORM/PERT), leading to a total of 12 takes. To avoid changing the spatial configuration of the orchestra too often and to let the players concentrate on the takes, the experiment was blocked by conductor. More precisely, the first conductor led the orchestra during 3 takes in NORM and then 3 takes in PERT, before the second conductor did the same.

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[1] http://www.siempre.infomus.org

[2] Although interpersonal coupling changed for V2 as well, the perturbation was more intense for V1, who completely lost sight of the crucial timing cues of the conductor in the process and gained an unprecedented visual access to V2's motion. On the contrary, V2 already had access to V1 head and bow motion in the normal condition, although from a reverse angle. Moreover, V2's score was sparser: they alternated short sequences where they played with sequences where they paused, making the assessment of their intrapersonal coordination non-suitable.

Apparatus and set-up

Movement data were collected with a Qualisys motion capture system equipped with seven cameras. Violinists and conductors each wore a cap with three passive markers of the Qualisys motion capture system (positioned at Pz, F3, and F4 in the 10–20 electroencephalographic system), and another marker was placed on the tip of their bow and the conductors' baton. The stability of the cap and the bow was ensured prior to the experimentation. Data tracking was done by the Qualisys Track Manager software, with a sampling rate of 100 Hz. An audio recording of the ensemble was also collected to provide the motor performances with a musical timeline of reference. Synchronized recording and storing of audio and motion capture data was performed by the EyesWeb XMI platform.

Musical and audio analysis

We analyzed the content of the musical score of V1 as well as V2 in two respects: the articulation techniques being used and the presence of a musical content to be played (as opposed to pauses). The analysis of techniques allowed us to exclude portions of data where performers did not use the bow or used it in an unusual fashion (e.g., a kind of "col legno" where they hit the stand of the desk with the bow, leading to important data losses as the markers got masked in the process). Using video recordings, we also excluded portions where some violinists had to turn the pages of the sheet music. Analyzing the musical content allowed us to exclude from the analysis the portions of data where V1 was not playing. To do so, we segmented the score in steps equivalent to a half-note (or two beats, representing a duration of about 500 ms in this up-tempo piece), and we excluded the steps during which players paused all along. This procedure allowed us to extract four passages of the score in which data could be properly analyzed, and whose duration ranged from 3.5 to 17 s approximately (from bar 1 to the first half of bar 5, from the second half of bar 7 to the first half of bar 11, from the second half of bar 13 to the first half of bar 27, and from bar 39 to bar 55). To extract these passages from the overall time series, we used the audio recordings of the ensemble as referents. Guided by the segmented score, we identified in each trial the starting location of each step by looking for corresponding attack events in the audio signal waveform. To identify the attack portion of a note, we used the software Ableton Live 10, which enables visualization of audio signals at a temporal resolution that is well below the millisecond scale (this task has been performed by the first author who is formally trained and highly experienced in audio micro-editing). Since performances are naturally fluctuating in tempo, this manual annotation also allowed us to estimate tempo locally (for each half-note steps). This will help us relate analysis conducted in the frequency domain to the ongoing tempo of each performance.

Data pre-processing

Data analyses were performed with custom-made MATLAB codes. We extracted the velocity time series of the head and the bow by computing the Euclidean distance between the successive positions of their associated markers and taking its derivative. The data of the three markers on the cap were averaged to simplify analysis and avoid redundancy. Windows of missing data shorter than 50 ms were cubically interpolated. Longer portions of missing data were considered as absent values ($<$1% of the data, for the bow motion only). Data of each of the four selected passages were normalized to z-scores and filtered with a zero-phase second-order Butterworth bandpass filter between 0.5 and 12 Hz. The filter bandpass frequencies were chosen based on the main rhythmical values played with the bow and on the minimum length of the passages which prevented from capturing lower frequency components.

Analysis

Musical timing information

To better understand the musical timing of the performances, we used the data of the manual segmentation of the audio waveform of the performances. First, we computed the length of each take as the time interval between the beginning of the first half-note segment and the end of the last one. Then, we computed the average tempo of each take. To do this, we computed the average duration of the half-note segments of each take. We divided the results by 2 to obtain the average inter-beat interval duration of each take. Finally, we assessed tempo variability within each take by computing the coefficient of variation (i.e., the ratio of the standard deviation to the mean) of the series of inter-beat interval duration.

Windowed cross-correlation

To gauge V1's overall intrapersonal coordination, we looked at the extent to which head and bow motion varied together. To do so, we performed windowed cross-correlations between their respective velocity time series (Boker et al., 2002). We used 1,000 ms windows (approximately four beats, which form a bar in this piece), with a 50% overlap between contiguous windows. Cross-correlation coefficients were computed at up to (±) 60-ms lags. Since the musical score contains eighth notes whose

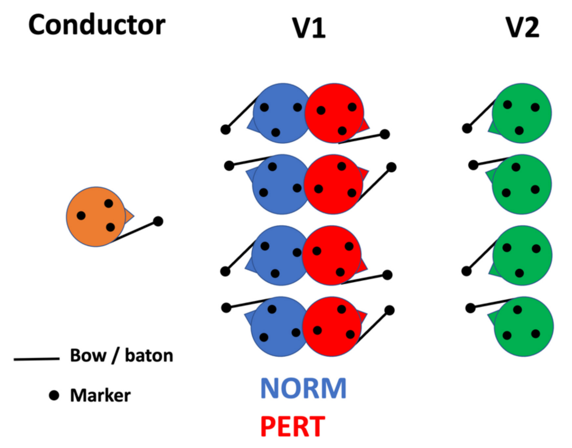

FIGURE 1
Position of the violinists whose motion has been recorded in normal (NORM) and perturbed (PERT) conditions. The experimental manipulation consisted in changing the arrangement of V1 with respect to the conductor and V2, preventing V1 from seeing the conductor and instead making them face V2.

performed rate could be as fast as 120 ms lags larger than half this length would introduce the risk of correlating head and bow motions spanning different notes instead of the same note. Windows were slidden within each of the four selected musical passages separately, and the resulting functions obtained were collapsed for each take of each V1 violinist.

The cross-correlation functions obtained in each 1-s window allowed us to compute 4 statistical indices about the amount of correlation and the lags at which correlation was maximally observed. First, since head and bow motion could have been coordinated with a (variable) delay, we considered the peak correlation across all lags (from −60 to +60 ms in steps of 10 ms). This quantifies coordination strength irrespective of delay. Importantly, Fisher z-transformation was applied to all coefficients before performing any averaging and further statistical analysis. To numerically and graphically present the results, we used hyperbolic tangent transformation to revert the values back to the scale of correlation coefficients. Second, we computed the lags at which peak correlation was observed. This indicates the specific time relationship between head and bow (i.e., whether the head lags ahead or behind the bow). Next, we considered the absolute lag at which peak correlation was observed (independently from its sign). Finally, we estimated lag variability by computing the standard deviation across 1-s windows of the lags corresponding to peak correlation. This was taken as an index of the stability in the coordination pattern between head and bow. These indices were averaged for each take of each V1 violinist before they were submitted to statistical analysis.

Movement amplitude and spatial dispersion

To better understand the factors that underlie a potential change in the intrapersonal coordination of head and bow, we gauged the amplitude of their displacements. To do so, we first measured the spatial dispersion and the volume these displacements covered in each 1-s windows of analysis and averaged these indices for each take of each V1 violinist (these windows were slidden within each of the 4 selected musical passages separately, before collapsing the results across all windows for each take of each V1 violinist). Spatial dispersion was estimated by computing the mean (Euclidean) distance between all positional datapoints (i.e., all the distances between any two positions in space that head and bow, respectively, visited during each 1-s window). We then computed the volume contained by the 3D convex hull of head and bow spatial trajectories (i.e., the volume of the smallest possible polyhedron that contained all data positions). This indicates the amount of space covered by head and bow motion trajectories.

Power spectral density

To investigate the temporal structure of bow and head motions, we examined them separately in the frequency domain by computing their respective power spectral density (PSD, using the pwelch function in Matlab). Since the rhythmical content of the musical score is changing over time, and since tempo fluctuates over the course of the performance (with a notable shift toward acceleration in the last portion), we proceeded by short windows. This helped us focusing on the frequency range within which instrumental motion was prominent (between 1 and 8 Hz approximately, which roughly correspond to whole and eighth notes, respectively). We used windows of 3 s (i.e., 300 data points, corresponding to 3 cycles at 1 Hz – the lowest estimated frequency component) within each selected musical passage and with no temporal overlap. To avoid discarding data at the edge of the selected passages due to the windowing procedure, all residual data points not amounting to a 3-s long segment were included in the preceding data window. All windows were then zero-padded to 512 points before estimating PSD.

To verify that spectral content of head and bow motion was meaningfully related to the musical performance, we related the main spectral peaks to the frequencies at which various rhythmical values or metrical levels were performed (whole, half, quarter, and eighth notes). To this end, we took the average tempo at which the piece was performed and computed the relevant harmonics and subharmonics. This helped us to relate peaks observed in the power spectrum with the metrical levels embedded in the performed score (see Section "Results"). Since tempo naturally fluctuates within and between performances, different windows of analysis and trials may yield (slightly) different frequency peaks. Instead of comparing power at fixed frequencies across conditions, we therefore selected the frequencies that corresponded to the similar metrical levels (e.g., the frequencies that corresponded to quarter notes, even though the exact frequencies might slightly differ across trials and windows of analysis). To identify the frequencies that matched metrical levels in each window of analysis and each trial, we relied on manual segmentation of the audio files (see above). Specifically, we averaged the length of the inter-beat intervals that were contained in the corresponding window of analysis, and converted it in a frequency value (i.e., by taking the invert of the interval length expressed in seconds). This gave us an estimate of the frequency associated to the ongoing tempo of the performance. From there, estimates of the frequency associated to other metrical levels could be easily derived (e.g., dividing the frequency value by 4 to obtain the frequency associated to the level of whole notes). Power was then extracted at the frequency bins that locally matched the metrical levels of the performance.

Power correlation

To verify whether changes in head motion frequency composition could reflect the mirroring of the rhythmical (instrumental) movements of the bow, we constructed time series of the power estimated at each metrical timescale for both head and bow motion. To do so, we took the power estimated at the relevant frequency for each window of PSD analysis (exact frequencies could change across windows; see above). Then, we computed the correlation coefficient between the series of power values obtained across the windows of all four selected musical passages for the head and the bow. Such correlation indicates the extent to which the head and bow motion covaried at each metrical timescale.

To evaluate whether changes in head motion frequency composition could be due to V1 being visually coupled with V2 during PERT, we performed a similar power correlation analysis between V1 head and V2 head or bow motion. To this end, we first computed PSD for V2's head and bow motion. Then, we repeated the above-described procedure to construct series of power values of V2's head and bow motion at each metrical timescale. Finally, for each relevant timescale, we computed the power correlation between the head of each V1 performer and the head and bow of the V2 performer each V1 performer was facing. This indicates the extent to which V1's head motion and V2's head and bow motion evolved similarly, quantifying the degree of informational coupling between the two sections of violinists.

Consistency in relative phase

We also evaluated the phase coupling between head and bow across the multiple timescales at which their individual motion was organized. To do so, we apply band-pass filtering (two-pass Butterworth, second order) on 512-points zero-padded data windows (same as used to estimate PSD; see above) with frequency bands defined as ±0.5 Hz relative to each of the musically relevant frequencies (same as defined above). We then applied the Hilbert transform and derived two time series describing the instantaneous phase angle of the head and bow at each relevant timescale. We then took the difference in phase angle between the head and bow (relative phase, RP). By averaging the RP across windows and trials (for each performer separately) we estimated: (1) the vector length (VL) which gauges the stability or consistency of the head-bow phase relationship, (2) the mean angle (MA), which quantifies their mean phase difference, and (3) the mean absolute angle (MAA) which captures the mean phase difference regardless of its directionality (i.e., which series precedes which).

Statistical analysis

Criteria such as the normality of the distribution and the homoscedasticity of the data could generally not be assumed. Therefore, we used non-parametric Friedman 2-way analyses of variance tests for statistically evaluating differences between conditions (NORM vs. PERT). Given the relatively small sample size (four violinists) which is inherent both to the ecological context of the experiment and to the actual composition of a (chamber) orchestra, Friedman test offers the opportunity to directly address the difference between our two conditions of interest (NORM and PERT) at the level of the section while controlling for the effects linked to the subjects' factor. For all analyses, the data obtained for the two different conductors were collapsed. We checked that the conductor type did not introduce major differences in the main findings (i.e., the overall intrapersonal coordination measured with windowed cross-correlations). Since we observed some differences for other analyses, we also report the comparisons between conductors for all variables and for each experimental condition in the **Supplementary material**. For the main analyses, collapsing data across conductors resulted in matrices of four blocks (corresponding to four violinists) that each contained six repeated measures, and two experimental conditions (NORM vs. PERT) as the column effect to be tested.

Results

Similar musical timing across conditions

The average length of the excerpt was 57.8 ± 1.5 s and was similar across conditions (NORM: 57.8 ± 1.8 s; PERT: 57.8 ± 1.2 s). The average inter-beat interval duration was 263 ± 7 ms, which is equivalent to 229 bpm, and was similar across conditions (NORM: 263 ± 8 ms; PERT:

263 ± 6 ms). The coefficient of variation of inter-beat interval duration was 0.062 (±0.011). It was slightly higher in NORM (0.064 ± 0.015) than in PERT (0.0596 ± 0.005). Using a Friedman test with the two conductors as subject factor with three takes each, this difference was not significant (chi2 = 0.38; *p* = 0.53). Overall, musical timing information such as average tempo and tempo variability did not differ across conditions.

Head and bow show enhanced (intrapersonal) coordination during perturbation

To gauge V1's overall intrapersonal coordination, we performed windowed cross-correlations on head and bow velocity time series (average cross-correlation functions are presented in **Figure 2**, and representative examples of velocity time series are presented in **Figure 3**). Peak coefficients were significantly higher in PERT (*r* = 0.42, ±0.07) than in NORM (*r* = 0.36, ±0.05; chi2 = 12.41; *p* = 0.0004). Head and bow thus tended to move more similarly during PERT, irrespectively of the lag difference between the two time series. On average, peak correlations were observed near, yet slightly before lag-0 (NORM: −3.19 ± 9.57 ms; PERT: −7.08 ± 8.29 ms), indicating that performers tended to synchronize their head and bow movements, yet head movements slightly preceded bow movements. Lags associated to peak correlations did not significantly differ across conditions (chi2 = 0.41, *p* = 0.52). However, there was a marginal tendency for absolute lags to be smaller in PERT (32.92 ± 9.90 ms) than in NORM (38.89 ± 8.33 ms; chi = 3.41; *p* = 0.0647). Thus, head and bow tended to move more synchronously during PERT than NORM. Finally, the lag at which peak correlations occurred was less variable in PERT (33.63 ± 11.62 ms) than in NORM (42.09 ± 8.65 ms; chi2 = 5.77; *p* = 0.0163). The temporal coordination between head and bow motion was thus more stable (i.e., less variable) during PERT. In sum, head and bow overall intrapersonal coordination was stronger (higher peak correlation coefficients), more in phase (closer to lag-0) and more stable (less variability in the lags of peak correlations) during PERT. However, these results only provide us with hints about the overall similarity of variations between head and bow velocity at the 1-s window scale. Finer-grained analyses are required to parse the effects of the different timescales at which periodical variations were observed (see **Figure 3**). This issue is treated further below, with the study of the frequency composition of the movement and the analyses of phase relationships at the different frequency components it highlighted.

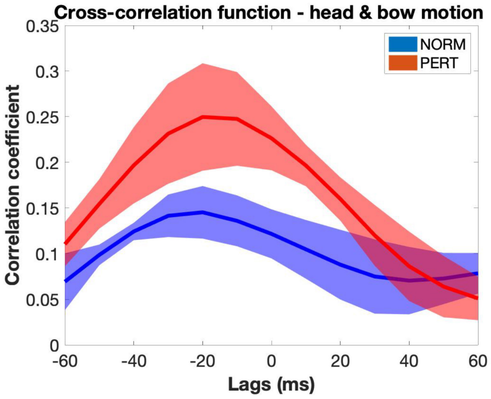

FIGURE 2
Average cross-correlation functions between head and bow motion across takes and violinists in the NORM and PERT conditions (shaded areas represent standard errors of the mean). Correlation coefficients were higher in the PERT condition than in the NORM condition, suggesting that head and bow were more strongly coupled during PERT. In both conditions, average functions peak at negative lags, indicating that head movements slightly preceded bow movements. Note that this figure represents all cross-correlation functions computed for each 1-s window averaged across participants and then across takes. The amplitude of the peaks of these average functions and the lag at which they are observed can thus differ from the values of the indices obtained by extracting only the peak correlation value and the associated lag in each 1-s window.

Head (but not bow) motion is reduced in amplitude during perturbation

To investigate the kinematic changes that underlie differences in intrapersonal coordination, we gauged movements amplitude by measuring their spatial dispersion (mean inter-distance between all datapoint positions) and the volume covered by head and bow motion (convex hull).

Mean inter-distances did not differ across conditions for the bow [chi-2 = 2.91(*10e-30); *p* = 1] but they were significantly larger in NORM than in PERT for the head (chi-2 = 23.08; *p* = 0.000002; see **Table 1** and **Figure 4**). Differences in variance across conditions are important, but individual comparisons confirmed that the reduction of spatial dispersion during PERT was observed for all players (with differences ranging from a decrease of 8% for the player that moved with the least amount of spatial dispersion to a decrease of more than 50%). Head (but not bow) motion trajectory thus visited positions that were less spread in space during PERT.

The volume contained in the convex hull of bow trajectories did not differ between conditions (chi-2 = 0.06; *p* = 0.81), but it was significantly smaller in PERT than in NORM for head trajectories (chi-2 = 25.44; *p* = 0.0000005; see **Table 1** and **Figure 4**). Motion of the head, but not of the bow, covered

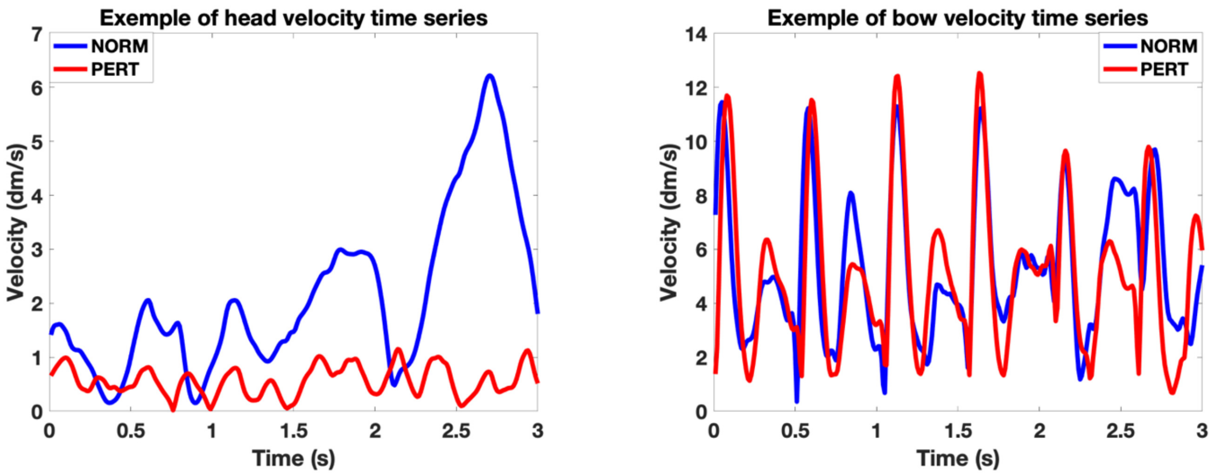

FIGURE 3
Representative examples of head **(Left)** and bow **(Right)** velocity time series. The examples correspond to a 3-s window of the movement of the first violinist of V1, during the third take in NORM and the third take in PERT with the first conductor, starting at bar 18. In these examples, we can appreciate the periodical nature of both head and bow motion, the similarity of bow motion across conditions and the differences in amplitude and frequency composition of head motion across those conditions. Notice that the Y-scales of the examples of head and bow motion differ, as the possible range of head motion is physiologically restricted compared to the amplitude required by the execution of bow motion.

TABLE 1 Mean inter-distance (in mm) between positional datapoint and convex hull volume (in cm^3) indicating head and bow trajectories, compared across experimental conditions.

	Mean inter-distance		Convex hull	
	Bow	**Head**	**Bow**	**Head**
NORM mean (std.)	101.86 (16.11)	43.00 (24.15)	1162.69 (764.14)	45.727 (53.95)
PERT mean (std.)	96.52 (2.52)	25.62 (10.15)	916.47 (106.23)	9.308 (7.27)
Chi-2	2.9127e-30	23.08	0.06	25.44
P-value	1.00	**0.000002**	0.8102	**0.0000005**

P-values in bold indicate significant differences.

smaller portions of space during PERT. Interestingly, mean inter-distances and convex hull of both the head and the bow were more variable across performers in NORM than in PERT (see **Figure 4**). Individual motor strategies were thus sparser in NORM and more commonly shared in PERT. However, smaller convex hulls during PERT were observed for all players, with decreases ranging from 28 to 82%. In sum, movement amplitude and dispersion of the head were smaller in PERT than in NORM, but they did not vary across conditions for the bow (the representative examples of head and bow velocity time series in **Figure 3** illustrate these differences – or lack thereof – well).

Frequency composition of head motion matches the score metrical hierarchy during perturbation

The average spectrum of the bow velocity showed multiple peaks around 1, 2, 4, and 8 Hz (peaks observed at these frequency components will henceforth be designated as P1, P2, P3, and P4, respectively; see **Figure 5**). According to the segmentation we performed on audio tracks, whole, half, quarter, and eighth notes were performed at rates of 0.96, 1.93, 3.85, and 7.70 Hz, respectively. The overall spectral composition of bow motion thus reflected the rhythmical organization of the performance well, with multiple frequency components corresponding to the different metrical timescales of the score.

To compare frequency peaks across conditions, we extracted power at the frequency bins corresponding to each of the four metrical timescales described above. No difference was found across conditions for any of the peaks in the bow motion (**Table 2**). In other words, the bow movements closely mirrored the metrical organization of the score rather than being affected by the nature of interpersonal coupling.

In contrast to bow movements, head movements clearly differ between NORM and PERT. In NORM, the frequency composition of head movements was much simpler than for bow movements (**Figure 5**). The spectrum is dominated by a

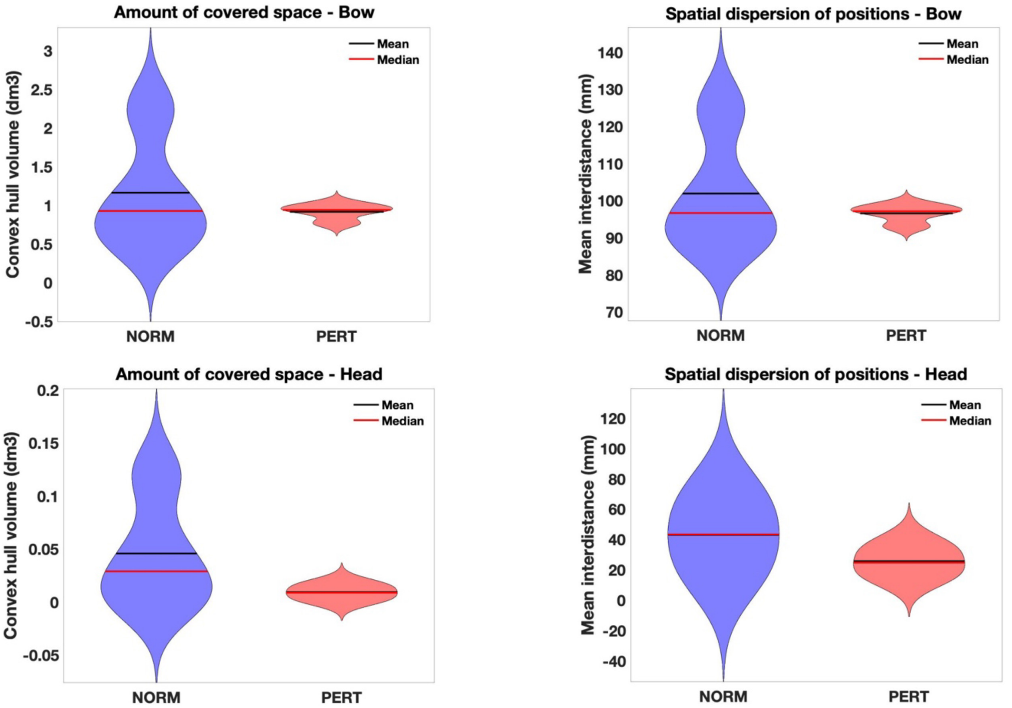

FIGURE 4
Violin plots of the amount of covered space (convex hull volume – **Left**) and spatial dispersion (mean inter-distance – **Right**) of bow **(Upper)** and head **(Lower)** positions in each experimental condition. Head (but not bow) motion was drastically reduced in amplitude during perturbation. This partly explains the reduced variability in that condition, although it might also reflect more stable and shared movement strategies. In effect, while these variables didn't differ in magnitude across conditions for the bow motion, variability among players was also drastically reduced during perturbation. Notice that the Y-scales for head and bow motion differ, because the possible range of head motion is physiologically restricted compared to the amplitude required by the execution of bow motion.

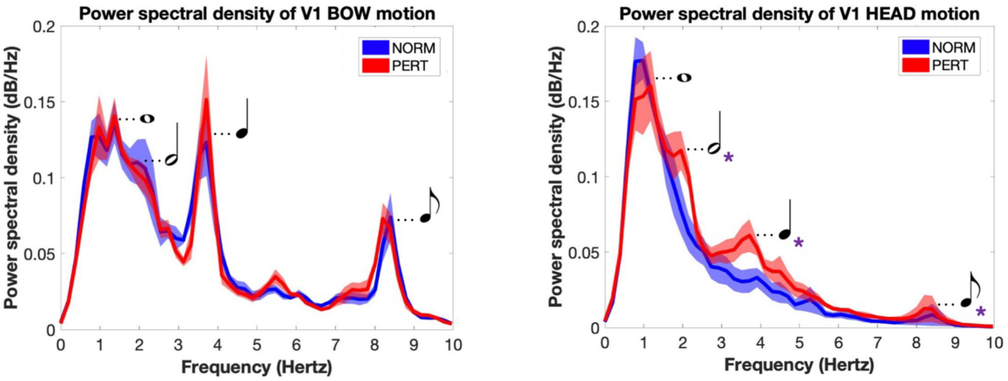

FIGURE 5
Power spectral density of V1's bow **(Left)** and head **(Right)** motions for each experimental condition. Main frequency peaks are associated with the rhythmical values they corresponded to in the performed piece (and represented here as musical notations). Bow motion was characterized by multiple periodicities that reflected the metrical organization of the score. Head motion shift from simple patterns dominated by one frequency peak near 1 Hz in NORM to more complex patterns of motion in PERT, where multiple, faster periodicities appeared and matched those found in the bow motion. Shaded areas represent standard errors of the mean; violet asterisks denote the metrical scales where power was significantly different across conditions.

main component centered around 1 Hz (P1) – i.e., the frequency that corresponded to the average periodicity of the bar, or whole note, during the performances. During PERT, this peak persisted (although peak frequency shifted slightly higher to 1.2 Hz), but other peaks appeared around 2.0 Hz (P2), 3.7 Hz (P3), and 8.2 Hz (P4). Just like those of the bow motion, these

TABLE 2 Power values (db/Hz) extracted from the power spectral density spectra at the four frequency bins that corresponded to musical metrical levels (P1 – P4), compared across experimental conditions for the motion of the bow.

BOW	P1	P2	P3	P4
NORM mean (std.)	0.125 (0.031)	0.109 (0.027)	0.152 (0.065)	0.079 (0.026)
PERT mean (std.)	0.133 (0.043)	0.108 (0.013)	0.147 (0.067)	0.094 (0.022)
Chi-2	1.64	0.16	0.03	2.83
P-value	0.2002	0.6889	0.8728	0.0927

TABLE 3 Power values (in db/Hz) extracted from the power spectral density spectra at the four frequency bins that corresponded to musical metrical levels (P1 – P4), compared across experimental conditions for the motion of the head.

HEAD	P1	P2	P3	P4
NORM mean (std.)	0.173 (0.024)	0.096 (0.047)	0.033 (0.017)	0.007 (0.010)
PERT mean (std.)	0.153 (0.051)	0.117 (0.033)	0.060 (0.014)	0.013 (0.018)
Chi-2	2.83	5.77	14.16	12.98
P-value	0.0927	**0.0163**	**0.0002**	**0.0003**

Bolded *P*-values indicate significance ($p < 0.05$).

additional peaks matched the average frequency of the metrical timescales of the performed piece well (half, quarter, and eighth notes). Power observed at these additional peaks (i.e., P2, P3, P4, but not P1) was significantly higher during PERT compared to NORM (Table 3). During PERT, head motion thus became more complex, displaying activity at multiple and faster metrical timescales than during NORM (see Figure 3 for a representative example of changes in the rhythmical patterns of head motion). Further, in PERT more than in NORM, the overall frequency composition of head motion resembled that of the bow motion.

Spectral power does not show local intra- (head-bow) and inter- (V1–V2) personal correlation

To check whether the frequency composition of head motion during PERT reflected the mirroring of the bow rhythmical movements, we computed the correlation between power observed in head and bow of V1 at each relevant metrical timescale. Correlation coefficients were very small, and no significant difference was found between conditions for any of the timescales (Table 4). Whereas multiscale head motion patterns reflected the overall metrical structure of the score more during PERT, they did not match local rhythmic variations of the bow.

To verify whether the changes in head motion frequency composition observed during PERT were due to the visual coupling with V2, we first computed the PSD of V2's head and bow motion, and then we computed the correlation between power observed in V1's head motion and V2's head as well as bow motion at each relevant metrical timescale. In both conditions, the average spectrum of V2's bow motion mainly featured peaks close to 1 and 2 Hz (whole and half-notes, or P1 and P2), with additional small peaks around 4 Hz (quarter-note level, P3) and 6 Hz (dotted eighth notes; see Figure 6). V2's head motion was dominated by a frequency component close to 1 Hz (P1), with a smaller peak around 2 Hz (P2) and a small hump around 4 Hz (P3). Besides P2, which was present in V2's motion and enhanced during PERT in V1's head motion, the frequency composition of V2's head and bow motion hardly reflected the overall changes observed in V1's head motion during PERT, where the two sections faced each other. Correlation coefficients between V1 and V2 power time series were also very small, and no difference was observed between conditions for any of the peaks (Table 5). Therefore, the evolution of the frequency composition of V1's head motion does not seem to be informed by V2's head or bow motion.

TABLE 4 Correlation coefficients representing the co-evolution of V1's head and bow power spectral density at the four frequency bins that corresponded to the piece metrical levels (P1 – P4), compared across experimental conditions.

	P1	P2	P3	P4
NORM mean (std.)	−0.01 (0.13)	−0.1 (0.24)	0.06 (0.16)	0.44 (0.25)
PERT mean (std.)	−0.03 (0.08)	0.03 (0.28)	0.19 (0.28)	0.55 (0.33)
Chi-2	0.1	4.01	1.26	2.08
P-value	0.7488	**0.0453**	0.2623	0.1495

Bolded *P*-values indicate significance ($p < 0.05$).

Intrapersonal coordination increased differentially at multiple timescales

To evaluate head and bow coupling with respect to the multiscale nature of their movements, we analyzed their phase relationships at each metrical timescale (see Figure 7). Consistency in the phase relationship was higher in PERT than in NORM at all timescales, and significantly so at the level of the bar (P1: Chi2 = 8.31, p = 0.0039) and the beat (P3: Chi2 = 5.3, p = 0.025; see Table 6). However, the difference at P3 was mainly driven by the performance with conductor 2 (see **Supplementary material**). There was also a marginal trend for vector length to be higher in PERT than in NORM at P2 for conductor 1 only (see **Supplementary material**). All in all, the coordination between head and bow motion was therefore more stable in PERT but at selective metrical levels that dominated bow motion frequency composition the most. Mean phase differences were close to zero degree (i.e., in-phase) for P1 and P2 and slightly negative for P3 and P4 (i.e., head motion shortly preceded the bow motion). Mean phase differences were comparable between NORM and PERT except that for P4 (Chi2 = 4.33, p = 0.0374; see Table 6). This indicates that, at

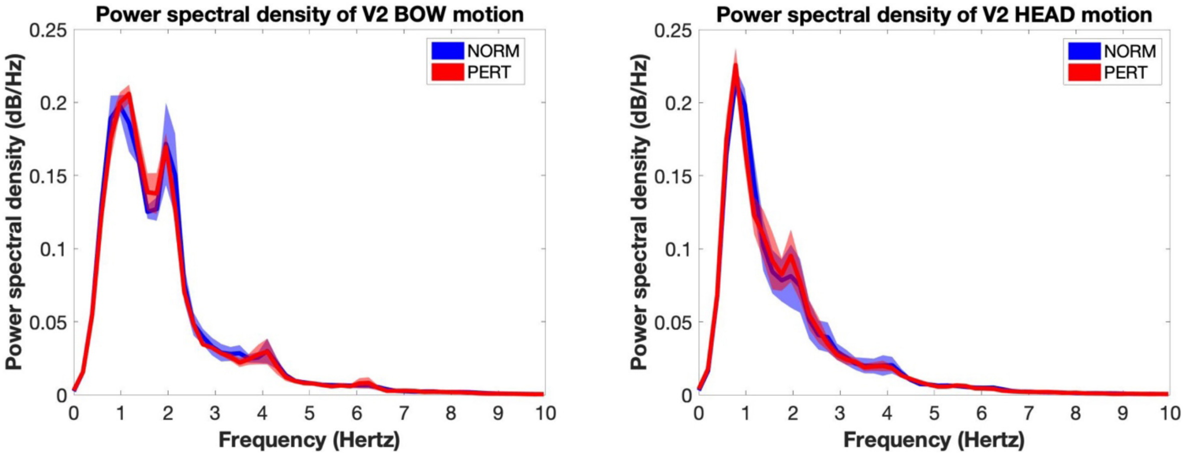

FIGURE 6
Power spectral density of the motion of the bow **(Left)** and the head **(Right)** of V2 for each experimental condition (shaded areas represent inter-subject standard error). The frequency composition of the bow motion was concentrated around 1 and 2 Hz (reflecting whole and half notes) with peaks near 4 and 8 Hz (quarter and eighth notes). The motion of the head as dominated by a component situated near 1 Hz, with an important secondary component near 2 Hz and a tiny peak near 4 Hz. No change was observed across conditions. Importantly, this frequency composition hardly explains the shift observed in V1 during perturbation, when they were facing V2.

the eighth-note level, head and bow motion were more in-phase during PERT. Mean absolute phase differences were smaller in PERT than in NORM, and the difference was significant for P2, P3, and P4 (P2: Chi2 = 4.33, $p = 0.0374$; P3: Chi2 = 9.75, $p = 0.0018$; P4: Chi2 = 10.78, $p = 0.001$; see Table 6, middle). Head and bow were thus moving more in-phase during PERT at all metrical timescales except that at the whole-note level (P1).

Discussion

During sensorimotor interactions, people tend to coordinate their movements interpersonally and beyond intention or awareness (Issartel et al., 2007; Auvray et al., 2009). Interpersonal interactions can thus constrain and shape individual behavior (De Jaegher et al., 2010). Yet, little is known about how sensitive the intrapersonal coordination of multiple body parts is to interpersonal coupling constraints, especially in complex ecological settings. To study it, we chose to make a trade-off between the ecological context of an orchestra playing an excerpt of a familiar piece of its repertoire and an empirical format where different conditions were observed across repeated measures. Specifically, we replaced the visual coupling of first-section violinists with the conductor (normal condition) by a visual coupling with the second section of violinists (perturbed condition). Focusing the analysis on the intrapersonal coordination of head and bow movements allowed us to gauge its sensitivity to varying interpersonal coupling constraints.

TABLE 5 Correlation coefficients representing the co-evolution of V1's and V2's head (upper table) and V1's head and V2's bow (lower table) power spectral density at the four frequency bins that corresponded to the piece metrical levels (P1 – P4), compared across experimental conditions.

	P1	P2	P3	P4
HEAD				
NORM mean (std.)	0.05 (0.23)	0.08 (0.09)	0.22 (0.21)	−0.03 (0.06)
PERT mean (std.)	−0.08 (0.15)	−0.09 (0.03)	−0.03 (0.11)	0.06 (0.11)
Chi-2	1.44	1.08	1.44	0.16
P-value	0.2298	0.2980	0.2298	0.6889
BOW				
NORM mean (std.)	0.03 (0.23)	−0.07 (0.17)	0.18 (0.38)	0.10 (0.14)
PERT mean (std.)	0.08 (0.14)	−0.10 (0.07)	0.02 (0.18)	0.30 (0.37)
Chi-2	1.26	0.03	0.1	2.56
P-value	0.2623	0.8728	0.7488	0.1093

We observed three main effects in first-section violinists: (1) as expected, the overall intrapersonal coordination of head and bow motion increased, (2) qualitative shifts occurred in head (but not bow) movements: they diminished in amplitude but increased in spectral complexity, to reflect more closely the metrical structure of the score, and (3) the intrapersonal coordination of head and bow movements increased differentially at multiple timescales. We will discuss each of these results in the following.

In both conditions, first-section violinists' head and bow motion were weakly but non-randomly coupled, illustrating the soft entrainment of ancillary movements to instrumental gestures (Colley et al., 2020). Interpersonal coupling constraints, however, affected head and bow intrapersonal coordination. Perturbation of first-section violinists' visual coupling network

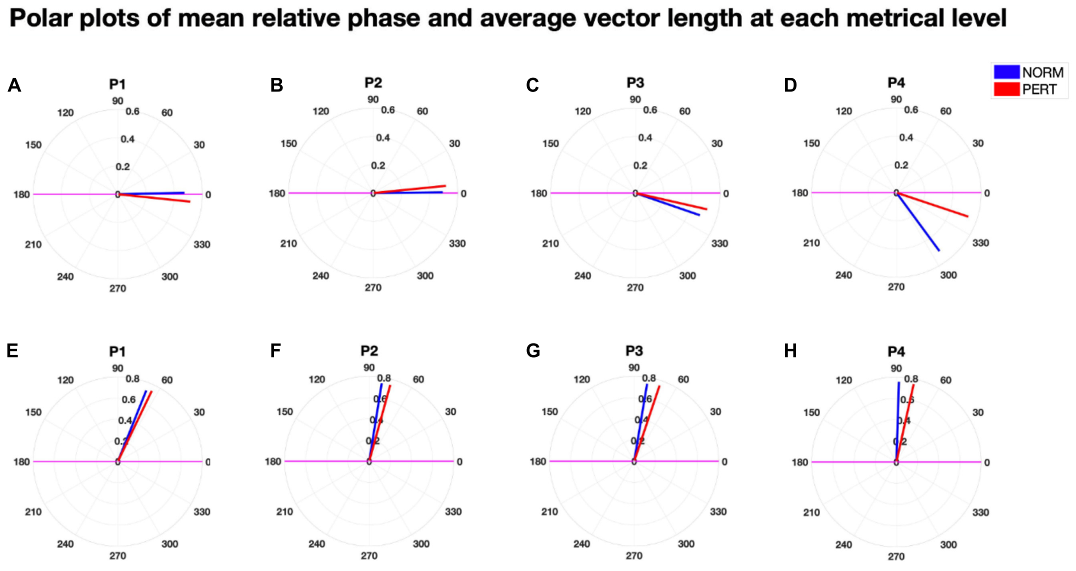

FIGURE 7

Polar plots of the (signed) mean relative phase **(A–D)** and the mean absolute relative phase **(E–H)** as well as their associated vector length, for each experimental condition and at each metrical timescale. The size of the vector length of the (signed) mean relative phase was higher in PERT than in NORM, and significantly so for P1 and P3. The (signed) mean relative phase was significantly shorter (i.e., closer to 0°, that is, synchrony) in PERT than in NORM for P4. The mean absolute relative phase was also shorter in PERT than in NORM for P2, P3, and P4. Overall, phase relationships were thus slightly but significantly more stable and closer to synchrony at several metrical timescales in PERT than in NORM.

TABLE 6 Vector length (upper table), mean relative angle (in radians, middle table) and mean absolute angle (in radians, lower table) of the relative phase between head and bow motion, computed at each metrical timescale (P1 – P4), compared across experimental conditions.

	P1	P2	P3	P4
Vector length				
NORM mean (std.)	0.473 (0.039)	0.493 (0.057)	0.482 (0.023)	0.514 (0.076)
PERT mean (std.)	0.517 (0.046)	0.518 (0.037)	0.521 (0.014)	0.537 (0.091)
Chi-2	8.31	1.85	5.3	1.85
P-value	**0.0039**	0.1735	**0.025**	0.1735
Mean angle				
NORM mean (std.)	0.022 (0.258)	0.011 (1.350)	−0.331 (0.560)	−0.937 (1.088)
PERT mean (std.)	−0.102 (0.343)	0.098 (0.931)	−0.223 (0.448)	−0.323 (0.866)
Chi-2	1.85	2.56	0.01	4.33
P-value	0.1735	0.1093	0.9362	**0.0374**
Mean absolute angle				
NORM mean (std.)	1.190 (0.062)	1.411 (0.141)	1.405 (0.109)	1.539 (0.090)
PERT mean (std.)	1.123 (0.112)	1.300 (0.160)	1.246 (0.106)	1.352 (0.179)
Chi-2	2.08	4.33	9.75	10.78
P-value	0.1495	**0.0374**	**0.0018**	**0.001**

Bolded *P*-values indicate significance ($p < 0.05$).

increased the coordination between their own head and bow in terms of strength (larger peak correlation values), temporal tightness (shorter lags at which peak correlations were observed), and stability (increased consistency in the lags at which peak correlations occurred). This resonates with studies on joint-precision tasks showing that intrapersonal coordination increases with task difficulty (Ramenzoni et al., 2011; Davis et al., 2017). In contrast, Aikido experts decreased their intrapersonal coordination to strengthen their interpersonal coupling (Caron et al., 2017). In the latter experiment, however, and differently from the present study, perturbation was applied to individual properties of movement (using arm weights), while the task-goal was interpersonal in nature (coordinating defense and attack moves). What is common to all these observations is the apparent flexibility with which participants can modulate their intrapersonal coordination when they have to cope with changes in interpersonal task constrains.

What is new here is that the effect of perturbation was not merely quantitative (in contrast to differences in variability reported previously, or to the overall increase in intrapersonal coordination in the present study). Rather, a shift toward a different, more complex pattern of coordination occurred during perturbation. In the normal condition, head motion was dominated by a single frequency component at the level of the bar (or whole note). This reflects the tendency of postural sways (which are embedded into head motion) to embody the temporal structure of musical performances (Nusseck and Wanderley, 2009; MacRitchie et al., 2013; Demos et al., 2018; same as during music listening: Burger et al., 2018). During perturbation, however, head movements shifted toward a more complex regime, introducing multiple and faster frequency components. These components were situated at harmonic ratios (near 2, 4, and 8 Hz) of the fundamental frequency observed in normal condition (near 1 Hz). Appearances of harmonic peaks have previously been reported in expert motor learning (Cordier et al., 1996) as well as in power spectra of phase relationships during simple bimanual coordination (Fuchs and Kelso, 1994). These changes were attributed to modifications in the intrinsic dynamics governing movement and might not necessarily reflect a genuine periodical activity at these frequency bands. However, the visual inspection of the time series (see **Figure 3** for a representative example) seems to indicate the genuine presence of faster periodical components in head motion. Importantly, these additional components were also observed in the bow motion regardless of the condition, and they well reflected the metrical organization of the musical score (half, quarter and eighth notes). This suggests that these frequency components resulted from changes in the rhythmical patterns with which V1 players moved their head during perturbation: patterns that more closely matched the metrical hierarchy of the piece.

Changes in head motion could reflect a communicative strategy aiming at fostering interpersonal coordination during perturbation (Davidson and Good, 2002; Glowinski et al., 2013). Indeed, visual coupling suffices to induce interpersonal coordination (Richardson et al., 2007). More generally, expressive gestures enhance visuomotor entrainment (Coorevits et al., 2020). A familiar musical example is players nodding their head to cue the beat (Bishop and Goebl, 2018). Thus, musicians synchronize head movements more during unstable moments or when the auditory feedback of their partner is compromised (Goebl and Palmer, 2009; Badino et al., 2014; Bishop et al., 2019; see also Hadley and Ward, 2021 for similar observations in the context of conversations). Importantly, players move more when they seek more interaction with their partners but move their head less when visuomotor communication is reduced or hindered (Bishop et al., 2019, 2021). Here, the amplitude of V1 head motion decreased drastically during perturbation. This is unlikely to indicate an attempt to increase visuomotor communication with V2. However, the reduction in amplitude might be a consequence of the changes in the frequency composition of head motion. Indeed, the addition of periodic motion at higher frequencies requires more direction reversals and acceleration breakpoint, drastically reducing the possible range of movement amplitude.

Changes in head motion could also reflect interpersonal entrainment to the second section of violinists (Hilt et al., 2019). However, the frequency composition of the second section's movement did not vary across conditions in the same way as it did for the first section, ruling out the possibility that spectral changes in V1 are the effect of entrainment to V2. One could also question the role of the vision of the conductor and its absence during perturbation. The frequency composition of the conductors' motion barely changed across conditions and poorly matched the pattern of V1 head motion, even in normal condition (see **Supplementary material**). In effect, for both the conductors' baton and head motion, the dominant frequency component was situated near 2 Hz. An important peak was also observed at 1 Hz in the conductors' head motion, as well as a clear peak near 4 Hz in the baton motion, but only in one of the two conductors. Plus, differences in the frequency composition of movement across conductors did not affect the frequency composition of V1 head motion: only the experimental manipulation did. More generally, differences across conductors were small. Each conductor having led the orchestra in two separate, consecutive blocks, this indicates that motor performances and differences across conditions were rather stable across time, and that the coupling with the conductor (or its absence) hardly accounts for the frequency composition of V1 head motion.

Increased intrapersonal coordination and changes in head motion might rather reflect individual strategies to cope with the introduction of challenging interpersonal coupling constraints. In line with this interpretation, similar effects have been observed in solo string players during various forms of perturbations. First, enhanced metrical coupling between head and bow motion, reduced head motion and shifts toward movements at faster metrical timescales all occurred spontaneously and without much change in bow motion properties when cellists had their posture constrained (Rozé et al., 2017, 2019, 2020). Next, violists' head motion changed (and most often diminished) when their bow strokes were constrained as well (Visi et al., 2014). Furthermore, adapting to a metronome also decreased the upper-body movements of violinists, but increased motion in their sacrum, whose usual stability supports upper-body expressivity (Glowinski et al., 2014). Spontaneous compensation between body parts thus seems to help string players to flexibly shift motor strategies (Shan et al., 2012; Verrel et al., 2014). In short, the reorganization of movements across body parts allowed players to cope with intrapersonal constraints in previous studies, and therefore probably helped to cope with interpersonal ones in the present study.

According to our initial hypothesis, enhanced head and bow coupling could reflect an attempt to stabilize motor coordination. This is coherent with the observation that during perturbation, head motion matched bow motion more closely from a metrical point of view. Nonetheless, this required head motion to increase in complexity. In line with this observation, it has previously been reported that greater intrapersonal coupling can be accompanied by more complexity when a joint task increases in difficulty (Davis et al., 2017). In effect, stabilizing interpersonal coordination sometimes requires the recruitment of additional degrees of freedom (Fine et al., 2013; Fine and Amazeen, 2014). However, the frequency composition of head motion only reflected bow motion at the scale of the whole excerpt. In effect, when examined at a finer-grained scale through power correlations, head and bow motion frequency composition appeared to fluctuate independently across the piece. This suggests that during perturbation, head movements were marking the metrical organization of the score rather than (anticipatively) mirroring the rhythmical performance of the bow. This argues against a purely, and rigid, synergistic motor strategy.

To interpret these results, we probably need to consider the tight link between action and perception and the role that the former plays for the latter (Varela et al., 1991; O'Regan and Noë, 2001). While head movements can express the perception of musical forms (Colley et al., 2020), body movements also actively contribute to perceptual experiences (Noë, 2004; Di Paolo et al., 2017; Benedetto et al., 2020). Especially, motor activity and auditory processes hold strong links (D'Ausilio et al., 2006; Zatorre et al., 2007; Morillon and Baillet, 2017; Froese and González-Grandón, 2020). For instance, movements can entrain to auditory rhythms with clear benefits on rhythm perception (Todd et al., 1999; Su and Pöppel, 2012). In particular, head motion stimulates the vestibular system which knowingly contributes to beat and meter perception (Phillips-Silver and Trainor, 2005, 2008). This phenomenon can be modeled as an oscillatory motor network that is entrained to the musical rhythm, and entrains, in turn, an auditory network, eventually improving the processing of incoming acoustic information (Tichko et al., 2021). Head movements can thus help to appropriately tune the auditory system to the ongoing rhythmical and metrical structures, playing a role in the very perception of musical events (and not merely expressing or reflecting such perceptual process).

The temporal coordination between movements and auditory processes is rather fine-grained: for example, fluctuations in auditory sensitivity are phase-aligned to simple periodical movements (Morillon and Baillet, 2017; Zalta et al., 2020). This resonates with the Dynamic Attending Theory which holds that attention is tuned to the temporal structure of sensory events, thereby enhancing sensory processing at specific points in time when salient/relevant events are expected (Large and Jones, 1999). If overt movement improves the tuning of attentional fluctuations over time, then V1 head movements may aid in framing auditory processing in accordance with the musical structure they mark. Miyata et al. (2017, 2018, 2021) have shown that interpersonal visual coupling with others affect individual audio-motor coordination, but that interpersonal auditory coupling had compensatory effects when vision degraded individual audio-motor performances. In our study, V1 players might thus have exploited the link between head motion and auditory processes in order to focus their perceptual activity on the auditory stream, thereby compensating for the perturbation of their habitual visual coupling with the conductor. This would explain the increased strength and synchronicity of intrapersonal temporal coordination during perturbation. Moving the head more in phase with the bow would help focusing on note onsets and locating them more accurately in time. Faster periodicities of head movement should increase the frequency and saliency of attentional checkpoints, while smaller movements should sharpen the temporal focus of attentional pick-ups. In effect, smaller movements reflect a deeper focus on note playing accuracy, shifting the attention away from the interaction with co-performers (Bishop et al., 2019). This would explain why the shortening of the phase lag between head and bow motion was most visible at the highest frequency component (around 8 Hz, where not only the absolute but also the relative phase lag decreased significantly during perturbation). Interestingly, head and bow motion frequency composition evolved most similarly at that one particular metrical level. Moving the head at the highest frequency thus accompanied musically dense passages, probably enabling a narrower focus of attention that fits rapid changes of notes.

During perturbation, however, head movements did not just increase in frequency: they became more complex as multiple frequency components appeared. Similarly, musical events are not merely periodical but rather organized at multiple timescales, forming a structure that span several metrical levels. The perception of this metrical framework can be modeled as an entrainment of neural oscillations to auditory events at multiple timescales (Large and Snyder, 2009), and provides a prism through which music can be flexibly attended to (Keller, 2001). This flexibility allows to shift the focus of attention between different timescales of organization of auditory events (Nolden and Koch, 2017). Musicians can then exploit this ability by mentally foregrounding those metrical levels that best help to cope with momentary goals or constraints – for instance, concentrating on the quarter-note level when the group lacks coordination (Berger, 1997).

The metrical framework through which we attend to music is reflected in body movements as well: we spontaneously move at timescales that match those of the metrical organization of music we interact with, whether as listeners

(Toiviainen et al., 2010), dancers (Leman and Naveda, 2010), or performers (Walton et al., 2015; Eerola et al., 2018). However, these patterns of movement are not the mere expression of music perception, but they rather seem to play an active role in the constitution of perceptual experiences. For instance, shifting movements across metrical levels impacts how time is perceived in return (Hammerschmidt and Wöllner, 2020; Wöllner and Hammerschmidt, 2021). Body movements thus actively tune the metrical framework through which we attend to music (Large et al., 2015; Kozak, 2021). In violinists, the link between body kinematics and focus of attention has been demonstrated as well (Allingham et al., 2021). More particularly, shifts in head motion patterns during perturbation of solo string players have been interpreted as reflecting attentional changes (Visi et al., 2014; Rozé et al., 2020). Interestingly, cellists too moved their head more frequently and with more energy at several timescales (especially at half and quarter-notes levels) when they played a melody by focusing their attention on shorter rather than longer groupings of notes (Huberth and Fujioka, 2018). In fact, even spectators sense that the timescales at which musicians move their body reflect the way they attend to their own performance: they attribute slower body sways to communicative intents, and faster head nods to pulse perception (Eerola et al., 2018).

In our experiment, changes in head motion during perturbation might thus not only reflect an increase in perceptual focus but also a qualitative reframing of its temporal organization. This reorganization consisted of bringing more diverse and higher-frequency metrical levels into focus, possibly to concentrate on and regulate the short-term timing of the performance. This would explain why head and bow motion were more synchronous at multiple timescales during perturbation. This would also explain why the stability of head and bow coordination increased at the functionally most relevant timescales, namely, the metrical levels of the bar and the beat that dominated bow motion (although, in the case of the beat, this was true with only one of the conductors). In short, shifting toward patterns where the head moves at multiple timescales should have allowed players to frame, hierarchize and shift the temporal organization of perceptual focus across metrical levels. This reframing could then have been used as a background perspective against which coordination of incoming sensory events (the performance of the self and others) was accurately monitored, gauged and ultimately regulated, allowing violinists to better cope with the lack of timing cues from the conductor during perturbation.

Conclusive remarks, limits and future directions

When their network of interpersonal sensorimotor communication was perturbed, first-section violinists increased their intrapersonal coordination and changed their head motion patterns. The present study thus highlights the sensitivity of intrapersonal body coordination to interpersonal coupling constraints in the complex and ecological context of a musical ensemble. By showing how flexible the coordination between body parts is, our results also underscore the (multi-)functional role of non-instrumental gestures such as head movement. This questions the conceptual segregation between ancillary and instrumental movements. In effect, posture and head movements seem to offer support for the control of instrumental gestures (Rozé et al., 2020). By shaping attention, framing sensory processing, and thereby honing musicians' sense of timing, ancillary movements might directly participate to the fine-grained motor coordination of instrumental gestures (Colley et al., 2020). This echoes the fact that the control of such movements and musical learning co-develop (Rodger et al., 2013). Head movements would thus not only constitute a way to communicate with others, but also a strategy to inform the very self. This highlights the importance of studying intrapersonal and interpersonal coordination processes in the context of each other, and at multiple timescales.

An important limitation of these results is that they have been observed in one peculiar context: a short excerpt of one particular piece, which in the perturbation condition was performed in an unusual configuration. First, the short duration of the excerpt is a clear limitation because interpersonal coordination processes can evolve over time and can take time to fully form. In return, longer periods of interpersonal coupling might change the way intrapersonal coordination is impacted. Nonetheless, this short duration simultaneously provided us with an opportunity to zoom in the moments where interpersonal coordination had yet to be established, and where intrapersonal coordination could particularly support this endeavor and/or to compensate for the perturbation of the habitual visual coupling.

Second, it is possible that the specific musical demands of the piece encouraged the behavioral phenomena we observed. The tight control of the timing required by the speed of execution, the repeated need to re-enter the piece, and the large differentiation with the rhythmical content of the score of V2 might have played an important role in the changes observed in V1. Slower pieces with more similar scores between the two sections could have led to different outcomes. Similarly, passages with less interruption could impact intrapersonal strategies differently. On the contrary, it would be interesting in future studies to explicitly assess the role of body movement in inter- and intra-personal coordination processes during moments where performers do not play yet need to track the subtle timing of their peers to re-enter the piece accurately. Furthermore, we could question the generalizability of the results regarding not only the choice of the piece, but also the choice of the instrument and the musical genre. However, the reports of Berger (1997) on the shifts of focus between different metrical timescales in heavy-metal drumming as a support of different perceptual and motor coordination goals resonate deeply with our results and interpretation.

Third, our trade-off between a complex ecological context and an empirical format constitutes a limit to the generalization of the results, since the phenomena of interest have emerged from a non-habitual situation. However, the fact that a single modification in interpersonal coupling suffices to induce important shifts in intrapersonal coordination is revealing. While the perturbation method literally "sat" participants in unusual conditions, it highlighted how body movements can be used to cope with and make sense of a variety of uncertain situations (Dotov and Chemero, 2014). Such perturbation methods thus allow us to reveal the relevant functional variables that can be exploited and the patterns that can be spontaneously reorganized during interactions, especially when facing changes in environmental constraints (Glowinski et al., 2016). Therefore, the sort of generalization this kind of work permits is precisely the vicariousness and the situatedness of complex motor coordination. Furthermore, our interpretation of the present pattern of results encourages further investigation that could take the form of confirmatory studies. In particular, one could test if head motion at multiple scales frame auditory perception to support the coupling with instrumental action in properly ecological contexts (i.e., pieces performed in usual conditions only). Passages with differentiated demands in terms of timing control or dependance on other sections could be contrasted to verify if the patterns of head motion and interpersonal coordination change accordingly. Otherwise, experimental procedures where perturbations (e.g., unanticipated tempo changes and altered perception of peers) are applied only momentary could be used. This would allow to verify if players cope with the perturbation with similar changes in intrapersonal coordination and head motion as we observed here. In such contexts, longer excerpts could be used to enhance the ecological validity of the studies.

Another limitation of this study is the restricted focus on the analysis of movement (although musical information was taken into account to segment the data). Future studies should take musical information more closely into account. Separate audio recordings of the players would allow to investigate the potential acoustic correlates of the changes observed in motor behaviors, as they might affect the pressure of the bow for instance, and have consequences on the expressivity, the intensity and timbral features such as the harshness of the sonic outputs (Rozé et al., 2020). Similarly, more markers could be used for the motion capture. This would particularly help to parse postural fluctuations and genuine head motion. In the current study, we restricted the investigation of frequency composition to a range that corresponded to what was observable in bow motion and fitted the size of our windows of analysis. Yet periodicities at lower frequencies could probably be observed in head motion, in particular as consequences of torso movements. This would allow us to expand our understanding of intrapersonal coordination at multiple timescales and its relationship with interpersonal coupling.

Finally, future studies should integrate first-person inquiries about the strategies skilled experts use to cope with changes in complex and ecological situations. This would enable investigating whether changes in intrapersonal coupling and in head motion more particularly emerged from the coupling situation and from a tacit bodily know-how, or whether they rather reflect conscious, explicit strategies.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation, to any qualified researcher.

Ethics statement

The studies involving human participants were reviewed and approved by SIEMPRE Project Management Committee. The patients/participants provided their written informed consent to participate in this study.

Author contributions

GV, AC, LF, and AD'A designed the study and collected the data. JL analyzed the results with the support of AT and AD'A. JL wrote the first draft of the manuscript. AT, GV, AC, LF, and AD'A contributed to the final manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fnhum.2022.899676/full#supplementary-material

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Follow the sound of my violin: Granger causality reflects information flow in sound

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Recent research into how musicians coordinate their expressive timing, phrasing, articulation, dynamics, and other stylistic characteristics during performances has highlighted the role of predictive processes, as musicians must anticipate how their partners will play in order to be together. Several studies have used information flow techniques such as Granger causality to show that upcoming movements of a musician can be predicted from immediate past movements of fellow musicians. Although musicians must move to play their instruments, a major goal of music making is to create a joint interpretation through the sounds they produce. Yet, information flow techniques have not been applied previously to examine the role that fellow musicians' sound output plays in these predictive processes and whether this changes as they learn to play together. In the present experiment, we asked professional violinists to play along with recordings of two folk pieces, each eight times in succession, and compared the amplitude envelopes of their performances with those of the recordings using Granger causality to measure information flow and cross-correlation to measure similarity and synchronization. In line with our hypotheses, our measure of information flow was higher from the recordings to the performances than vice versa, and decreased as the violinists became more familiar with the recordings over trials. This decline in information flow is consistent with a gradual shift from relying on auditory cues to predict the recording to relying on an internally-based (learned) model built through repetition. There was also evidence that violinists became more synchronized with the recordings over trials. These results shed light on the planning and learning processes involved in the aligning of expressive intentions in group music performance and lay the groundwork for the application of Granger causality to investigate information flow through sound in more complex musical interactions.

KEYWORDS

Granger causality, cross-correlation, amplitude envelopes, information flow, music performance, expressivity, synchrony

1. Introduction

Coordination through social interaction, including the ability to coordinate movements with others in time and space (joint action) underpins many complex, cooperative tasks that are unfeasible for individuals acting alone (Sebanz et al., 2006). In humans, action synchronization can increase cooperation, trust and prosocial behavior (Hove and Risen, 2009; Marsh et al., 2009), even in infants (Cirelli et al., 2014). Acting in concert with one another has enabled many cultural and technological advancements that would have been impossible otherwise (Cosmides et al., 2010; Tomasello, 2014). Benefits conferred by successful coordination in the challenges of everyday life may explain how these abilities developed in humans, and why group activities such as team sports and ensemble music performance are ubiquitous across cultures and throughout history (Axelrod and Hamilton, 1981; Morley, 2002).

Group music performance is a unique form of social interaction in that it requires a high degree of coordination among individuals. Typically, ensemble musicians share (or evolve) a common aesthetic goal that requires communicating the musical structure and their expressive intentions to each other and to their audience (Keller, 2014). Often this is achieved through the coordination of multiple distinct musical parts played simultaneously. At least in the Western classical musical tradition, to achieve a cohesive musical product, musicians must continually agree on or negotiate a set of shared expressive intentions and coordinate their actions to communicate them. This requires an awareness on the part of each performer of how and what their co-performers are playing—they must agree on or negotiate (often non-verbally) the character of the music they wish to convey because no individual part is heard in isolation. In the Western tradition, a collective musical expression from multiple separate parts requires temporal alignment of both note onsets (the precise timing of when notes are to be played), and the expressivity or character with which a piece is played. Expert musicians exert a large degree of control over the sound of any one note or sequence of notes by making continual adjustments to how they play their instruments. On the level of the performance, this translates to phrasing and articulation, dynamics (intensity), expressive timing, the use of vibratos, caesuras, and fermatas, and many other stylistic features of a performance—all of which unfold over time but are not strictly aligned with the musical beat.

While the musical context, as well as complexity, familiarity, and the musicians' expertise, can affect how alignment of expressive intentions takes place (Keller, 2014), it fundamentally entails a type of non-verbal communication in which musicians sense each others' actions to infer their musical intentions. By analogy, when two friends move a couch together, they communicate when and where they intend to move it through a *haptic* channel (the couch itself). Musicians, on the other hand, communicate their intentions largely through auditory and visual channels by watching and listening to each other play (even if the notes themselves are predetermined). Musicians' ancillary body movements—those not related to the *functional* purpose of producing the notes themselves—can serve a *communicative* purpose, signaling visually how and when to play (Wanderley et al., 2005; Pezzulo et al., 2019). Gestural motion, eye-gaze, facial expressions, head motion, and body sway (movements not directly related to producing sound) have all been shown to play communicative and expressive roles in group performances (Wanderley et al., 2005; Davidson, 2012; Chang et al., 2017; Bishop et al., 2019a). One study of qualitative observations from video recordings found that a piano duo increased their eye-contact and gestural cues (hand movement and torso-swaying) during "musically important" periods of performances (Williamon and Davidson, 2002), and another showed that gestural cues in leading violinists and pianists indicated tempo and beat positions (Bishop and Goebl, 2018). Noticing and interpreting micro-variations in the sounds and movements produced by fellow musicians—and indeed acting to produce them—is necessary for ensemble members to coordinate their actions in the pursuit of their shared aesthetic goals.

This automatic interpretation of sensory signals from other performers makes ensemble performance a valuable context within which to study non-verbal communication and the group coordination that it makes possible (D'Ausilio et al., 2015). Ensemble musicians exchange sensory information within a set of physical constraints (those inherent to playing an instrument) and rule-based constraints of the musical conventions, style, and genre. These conditions allow for tightly controlled experiments within naturalistic settings that are easily repeatable and can be adapted for different size groups, from duets, quartets, and jazz bands to full symphony orchestras.

While large orchestras usually benefit from an external timekeeper (a conductor who communicates tempo, dynamics, and other stylistic aspects of a performance to all the musicians simultaneously), smaller ensembles such as string quartets function as self-managed teams wherein each member contributes and group cohesion is particularly important for success (Murnighan and Conlon, 1991; Cohen et al., 1996; Davidson and Good, 2002; Luck and Toiviainen, 2006). Although the four members in a standard string quartet (first violin, second violin, viola, and cello) generally occupy different roles (the first violin most frequently functions as the "leader"), they are all responsible for arriving at a shared interpretation of the score and coordinating their playing to convey it. This means not only negotiating the expressive characteristics of the music, but also aligning their notes in time. One way musicians can accomplish this is by setting up explicit leader-follower relationships. This places more responsibility on one of the performers at any one time to set the tempo and convey dynamic changes and other expressive characteristics. Indeed, when a member of a string quartet is assigned as leader, they tend to exaggerate their bow movements (Timmers et al., 2014) and, compared to followers, leaders' head movement acceleration better indicates the beat (Bishop and Goebl, 2018). Even brain activity differs between leaders and followers (Novembre et al., 2014; Vanzella et al., 2019). To some extent, the other musicians may react to the sounds and movements of the leader once they hear and see them, but because it takes time to plan motor movements, relying on a reactive strategy such as this would leave the musicians out of sync with the leader. A more effective strategy for playing synchronously would be to anticipate fellow musicians' actions and sounds before they occur, and to plan their own in accordance with how they predict their partners will play (Sebanz and Knoblich, 2009; Moore and Chen, 2010).

Leadership dynamics in string quartets and orchestras have been studied in the context of how musicians use the sway of each other's bodies to predict how they will move next using Granger causality (e.g., D'Ausilio et al., 2012; Chang et al., 2017; Hilt et al., 2019). Granger causality (GC) is a measure of directed functional connectivity that quantifies how well information contained within the past of one time series (e.g., body sway of one musician) helps predict the current value of another (e.g., body sway of a second musician) based on vector-autoregressive (VAR) modeling (Granger, 1969). One time series is said to "Granger-cause" another if its history helps predict the time series' current value above and beyond prediction based on that time series' own history. When this is the case, information is said to flow from one time series to another. While such a measure cannot rule out the existence of a hidden variable that is driving the "causality," it is a useful tool for examining prediction, and is sometimes referred to as "Granger prediction" to avoid the implication that causality is necessarily involved (Cohen, 2014). Nevertheless, the ability of one time series to predict another implies some form of communication must have taken place, an area of inquiry to which GC has been successfully applied. GC has proven to be a useful tool for quantifying the communicative capacities of body motion among skilled musicians in several studies of string quartets. Badino et al. (2014) measured GC between head movement time series of all four members of a string quartet while introducing perturbations known only to the leader. The total inter-group communication, as measured using GC between all the members, increased during periods following the perturbations, and when playing more complex pieces. Chang et al. (2017) found that the body sway of secretly assigned leaders in a string quartet influenced that of followers more than vice versa, and more than followers influenced each other. Assigning different members of the quartet as leader changed their relative predictive influences on the other members.

The cognitive processes that underlie inferring and predicting a partner's goals and actions have been proposed to stem from "common coding" (see Prinz, 1990), which hypothesizes a functional relationship between the perceptual and motor systems (Prinz, 1997; Schütz-Bosbach and Prinz, 2007). Perceiving another's actions can affect the performance of one's own related actions. For instance, reaction times of participants making perceptual judgments in a dual-choice button-press task show a similar compatibility effect compared to a those for a go-nogo task in the presence of a partner making complementary button presses, suggesting that one's own actions and the complementary actions of another are similarly represented (Sebanz et al., 2003). In a study comparing solo and duo conditions in a dot-stimulus tracking task, Knoblich and Jordan (2003) found that the presence of auditory cues regarding a partner's actions enhanced group performance. The ability for musicians to continually arrive at shared musical goals may rest on such perception-action links whereby partners simulate each other's intentions (Knoblich and Sebanz, 2008; Keller et al., 2014). In essence, they rely on or evolve shared musical (sound-based) goals to develop a dynamic internal representation of their partner's actions that can be used to make predictions about their partners' musical goals (Sebanz and Knoblich, 2009).

The ability to make predictions based on sound alone has been shown to be important for coordinating precisely during performances. One study of piano duos found that the ability to imagine sounds produced by others before hearing them (anticipatory auditory imagery) correlated with body movement coordination quality measured using motion capture (Keller and Appel, 2010). Another study found that individual differences in auditory prediction abilities modulated accuracy in an interpersonal sensorimotor synchronization task involving tapping with a partner (Pecenka and Keller, 2011).

Most examinations of sound-based prediction and synchronization in ensembles have focused on how musicians precisely synchronize the timing of their notes (e.g., by measuring the interval between note onsets of two or more musicians). This approach is particularly well-suited to percussive instruments such as pianos for which note-timing information is easily accessible (e.g., *via* MIDI recordings). Note onset asynchronies between two pianists have been used to show that decreasing auditory feedback decreases interpersonal synchronization (Goebl and Palmer, 2009), and that familiarity with a co-performer's part affects synchronization on short time-scales (keystrokes) and long time-scales (body movements) differently (Ragert et al., 2013). MacRitchie et al. (2018) used mean absolute asynchronies between pianists' notes to tease apart how incongruencies between individual and joint goals differentially affect synchrony. However, with non-percussive instruments, musicians can continuously vary the sound of their instrument, including on time scales shorter than single notes. For example, in stringed instruments, pitch and dynamics (loudness) can change markedly within the duration of one bow stroke, and wind instruments can expressively vary sound characteristics including timbre and vibrato on a continuous basis. Despite this, few studies have examined how musicians make predictions based on the continuous sounds produced by their fellow musicians, and fewer still have used measures of information flow. Granger causality (GC) (Chang et al., 2017) and mutual information (Ragert et al., 2013) have been applied to body movements, but information flow between the continuous sounds of performing musicians remains essentially unstudied. To our knowledge, GC has not been used to date to study information flow between musicians' musical sound outputs, although it has been used to analyze influences of acoustic properties on perceptual responses (Dean and Bailes, 2010; Bailes and Dean, 2012).

One goal of the present study was to examine whether musicians anticipate what a partner will play solely based on the immediate past of the sounds produced by that partner, by applying GC to the time series of the musicians' audio outputs. At least one study suggests indirectly that this may be the case. Examining GC between the body sway movements of the musicians in a string quartet, Chang et al. (2017) found that even when the musicians could not see each other, the body sway of one musician influenced the body sway of the others (and information flow from the body sway of leaders to followers was greater than vice versa). Given that they could not see each other, body sway could not have been the direct communicative cue. Rather, body sway likely reflects musicians' planning processes related to the sounds they are producing, similarly to how hand gestures reflect planning of speech (Graham and Heywood, 1975; Morsella and Krauss, 2004), and the musicians' sounds themselves contained cues for predicting how each other planned to play in the future. If so, these cues must be present in audio recordings of musical performances. We based our analyses on the audio *amplitude envelope*, a time series consisting of a smooth curve that tracks variations in amplitude (intensity or loudness) over time. We focused on the amplitude envelope because it encodes time-variant acoustic properties of the sound signal.

A second goal of the present study was to examine how auditory-based prediction processes change as a musician becomes familiar with (i.e., learns) to mimic another musician. In this regard, a prominent framework of social interaction involves the idea that co-actors form (learn) *internal models* that simulate the link between motor commands and their sensory consequences across the co-actors (Wolpert et al., 2003). In this framework, when musicians share a common forward (causal) internal model, this allows them to predict each other's actions and their sensory consequences (sounds), enabling them to play synchronously (Heggli et al., 2019). When they accomplish this, the sounds they produce coordinate, and they can arrive at a joint musical expression. According to this framework, we expected that in learning to play a piece together, musicians would initially rely on predictive cues from the movements and/or sounds of the other musicians, but that with practice, the musicians would come to a common musical interpretation, thus forming common internal models. They would then rely less on direct predictive cues through seeing or hearing each others' movements or sounds. Indeed, there is evidence that average GC based on body sway decreases as musicians learn to play a piece together (Wood et al., 2022), and that rehearsal improves movement coordination among piano and clarinet duos (Bishop et al., 2019b). In the present study, we measured Granger causality when sound was the only communicative cue present.

To control the auditory cues present during learning, in the present study, we examined how violinists learn to play with prerecorded pieces containing large amounts of expressive liberty by having them play with each prerecorded violin piece eight times in succession. In this scenario, the only information available for the creation of an internal model of the expression is the sound recording. Our main hypothesis was that the violinists would initially rely mainly on predictive processes based on what they were hearing in the recording—for example, predicting the dynamics and expressive timing of the prerecorded violinist based on their immediate past dynamics and expressive timing as the piece unfolded in time. Over successive playing with the recording, if violinists formed improved internal models of the expressive interpretation of the music on the recording, we would expect them to rely more and more on predictions based on their internal models and less and less on predictions based on the sound itself. We therefore expected that an analysis of Granger causality would show a decrease in information flow from the recording audio to the violinists' audio across repetitions as the violinists learned how the musician on the recording interpreted the piece.

In addition to information flow, we measured the similarity of amplitude envelopes of the violinists' performances and the recordings across pieces and repetitions using cross correlation (CC). CC measures the correlation between two time series across time-delayed ("lagged") copies of one another within a range of positive and negative lags. The CC measure is taken to be the largest CC value across the range of lags. To some degree, CC and GC are complementary measures because information can only flow between time series that are sufficiently dissimilar from one another; Granger causality between two identical time series will necessarily be zero because the second time series cannot add additional information that is not already represented in the first time series. However, both GC and CC are directional measures to an extent. For example, information flow would be expected to be higher from the recording to the violinist than vice versa as the violinist should not be able to influence the recording. Similarly, the sign of the lag at which the largest CC value occurs suggests the temporal precedence between the two time series. While the calculation of CC does not rely on statistical prediction like GC, if one process (e.g., the recording) influences another (e.g., the violinist's performance), we would expect a high CC value to occur when the performance lags behind the recording, and not vice versa. It should be noted that CC does not measure how synchronous the time series are but rather how similar they are. One measure of synchrony is to measure CC with a zero lag (when the two time series are positioned together in time).

In sum, first, we expected GC values to indicate higher information flow from the recording to the performances than vice versa across all trials. Second, because the recording was initially unfamiliar, we expected information flow from the recording to the performances to decrease over successive trials as the violinists became familiar with what they were attempting to match; the more information about the piece they could rely on obtaining from memory (an internal model), the less information they should need from hearing the recording while playing. Third, we expected CC similarity to be highest at lags for which the recording preceded the performances and, fourth, for both similarity and synchrony measures between the recording and the performances to increase across trials as they memorized the expression of the recording and learned to match it more effectively.

2. Materials and methods

2.1. Participants

We recruited nine professional violinists (five female) from around the Hamilton, ON area and one from Arizona, USA, willing to participate in a remote study and record themselves at home. All participants reported that they performed in a professional capacity in orchestras or chamber music groups, and they all had obtained professional music-related academic degrees (e.g., Bachelor of Music Performance, Master's Degree in Music). Most participants also reported playing in solo performances, and some had their own teaching practices or recording studios. They had an average of 36 years of musical experience (*SD* = 9.6) on their primary instrument (violin for all except one whose primary instrument was viola) and practiced for an average of 18 h per week (*SD* = 13.9) at the time of data collection.

2.2. Stimuli

We sourced recordings of the popular folk tunes *Danny Boy* (Piece 1) and *In The Garden* (Piece 2) from the website www.violinsolos.com, played on solo violin, with accompanying sheet music. We looked for expressive performances so that there was some unpredictability; the performer loosely followed the sheet music, while incorporating tempo shifts, dynamic changes, caesuras, and fermatas. *Danny Boy* was chosen for the familiarity of its melody (all the participants had heard the song before), and relative simplicity. This rendition was played at ∼55 beats per minute in 4/4 time (with one beat equal to one quarter note) in the key of F-major. We chose the second piece to be less familiar (no participants reported having heard the song before) and played at a faster tempo but in a similar expressive way. *In The Garden* was performed at ∼130 beats per minute in 6/8 time (with one beat equal to one eighth note) in the key of B-flat major. This piece was slightly more complex in including double-stops. For both pieces, we removed all markings from the sheet music, including dynamics and bowing, so that it contained only the clef, key signature, time signature, barlines, and notes (see Supplementary materials for the sheet music).

The stimulus recordings were created using *Studio One 3* (Presonus Audio Electronics, 2020). The first ∼90 s of each song was extracted. For each song, eight consecutive identical trials were presented, each consisting of the 90-s excerpt. Voice instructions between each trial indicated that there would be a 15-s period of silence before the pickup clicks for the next trial began. *Danny Boy* included five clicks (one full measure plus the first beat of the measure in which they started playing) preceding the initial three pickup quarter notes of the piece, and *In The Garden* included eight clicks (six eighth note clicks to represent one full measure plus two clicks each representing dotted quarter notes in the measure in which they started playing) preceding the initial pickup eighth note of the piece. The pickup clicks indicated only the starting tempo of the pieces. The entire data collection process for each piece lasted ∼15 min. Full stimulus tracks for both pieces (mixed down as monophonic 16-bit WAV files at 44.1 kHz sampling rate) and accompanying sheet music were sent to violinists in advance, with instructions not to listen to them or play them prior to conducting the experiment. In addition, we created a "practice version" of the stimulus using a different solo violin recording, *Amazing Grace*, performed by the same musician and presented during practice trials in the same way as the other pieces were presented in the experimental trials. We used the practice trials to test participants' recording setups and to familiarize them with the procedure. All the violinists played *Danny Boy* before playing *In The Garden*. See Figure 1 for a depiction of the experimental setup.

2.3. Data collection

Seven of the nine total violinists recorded themselves playing both pieces, one additional violinist played only *Danny Boy* (Piece 1), and another additional violinist played only *In The Garden* so that each piece was played by eight violinists in total. Data were collected at violinists' homes with their own recording hardware and software. Most recorded their sound using a desktop microphone connected to a USB audio interface while simultaneously listening to the stimulus violin track. Because Granger Causality requires the time series of the stimulus track and the participants' recording to be temporally aligned, it was crucial to synchronize the recording of each violinist's performance with the presented audio. The violinists imported the stimulus WAV files we sent them into their recording software (Audacity, Logic Pro, GarageBand, Studio

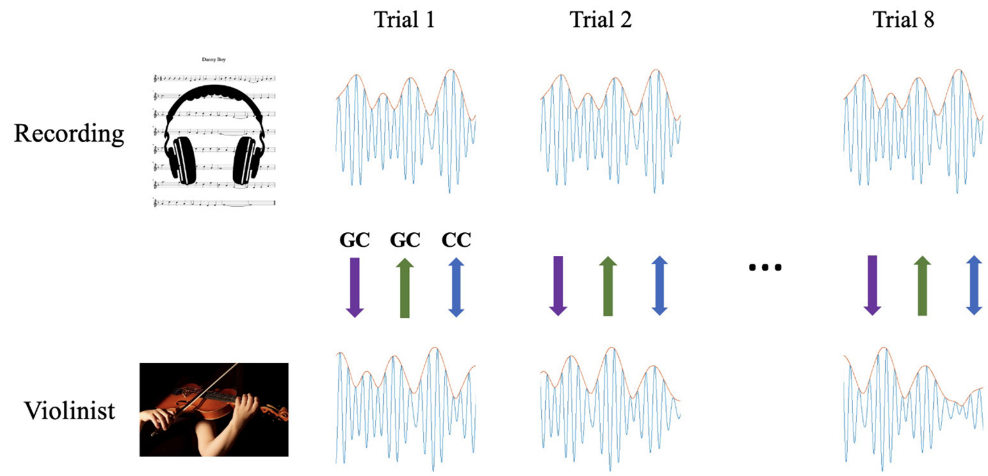

FIGURE 1
Experimental design and procedure. The violinists listened to the recordings through headphones while looking at the sheet music **(top)** and recorded themselves playing along with them **(bottom)** across eight successive trials. We then calculated Granger causality in both directions (from the recordings to the performances, shown in purple, and from the performances to the recordings, shown in green) and cross-correlation (for similarity and for synchrony, shown in blue) for each trial separately.

One, Reaper, or Avid ProTools) as one track and made a second track to record themselves. They then recorded themselves playing into the second track (at 44.1 kHz sampling rate) while listening to the first track through headphones. In most cases, participants used wired, non-noise-canceling headphones (open-back headphones or in-ear buds) so they could also hear the sound of their own instrument over the recording. They recorded all eight trials in succession in one take (see Figure 1). They then mixed down both tracks as separate 16-bit WAV files and sent them back to us. Using the same set of time markers for each piece, we cut each participant's performance and recording files into separate tracks for each trial (the recording for each trial began at the beginning of the participants' playing and excluded the pickup clicks). Theoretically, each stimulus track should be exactly the same, but we analyzed versions exported directly from the violinists' own recording software to account for differences in track levels and other software-specific settings. This resulted in 16 WAV files for each of eight participants for each of two pieces.

2.4. Data analysis

2.4.1. Amplitude envelopes

Waveforms were extracted from the WAV files as time series using the SciPy package for Python. They were rectified (absolute value taken) and filtered twice, once forward and once backward, using a 3rd order Butterworth IIR filter with a critical (cutoff) frequency of 11.025 kHz (half the Nyquist frequency, with the 44.1 kHz sampling rate), resulting in arrays that represented the amplitude envelope time series with the same length as the waveforms. The arrays were saved as text files and then downsampled to ∼8 Hz (5,513 points) by averaging the time points within consecutive, non-overlapping 125-ms windows.

2.4.2. Granger causality

We calculated the magnitude of Granger causality (GC) from the amplitude envelope time series of the recordings to the amplitude envelope time series of the performances—and vice versa—for each participant and each trial following the procedure implemented in the Multivariate Granger Causality (MVGC) Toolbox for MATLAB (Barnett and Seth, 2014). All time series met the assumption of stationarity required for GC. An optimal model order (the number of past points in the time series included in the model) was chosen for each trial for each participant using the Akaike information criterion. Then, for each participant for each piece, the maximum model order out of their eight trials was used to calculate GC values for all eight trials. In other words, model orders were specific to each participant and piece, but within a participant, the same model order was used for all trials of the same piece. The average model order for participants when playing *Danny Boy* was 6.63 (*SD* = 0.52), which corresponded to 0.829 s. The average model order for participants when playing *In The Garden* was 8.63 (*SD* = 1.41), which corresponded to 1.079 s.

2.4.3. Cross-correlation

To measure the similarity between the sounds of the violinists' performances and the recording they followed, we calculated cross-correlations (CC) between the amplitude envelope time series of the recordings and the performances for each trial for each participant. CC coefficients were calculated across the entire waveforms for each trial for lags between -10 and 10 points (10 points amounts to 1.25 s; approximately the duration of three eighth notes in each piece, corresponding to about 1.5 beats for *Danny Boy* and three beats for *In The Garden*). The maximum of the coefficients across all time lags was taken as the CC value for each trial, resulting in one cross-correlation coefficient for each trial for each participant. Because this CC measure evaluates similarity but not necessarily synchrony between the recording and performer (maximum correlations could have occurred at any lag within our range), we repeated the CC analysis while confining the time lag to zero and used this as a measure of phase alignment or synchrony between the two amplitude envelopes.

The lag at which the maximum correlation occurred (optimal lag) in each trial indicates the time delay between the two time series that produced the highest degree of similarity. A positive optimal lag indicates that the time series were most similar when the recording preceded the performance, and vice versa for a negative optimal lag. An optimal lag of zero indicates no temporal precedence between the time series (i.e., synchrony).

3. Results

3.1. Information flow direction

We compared the GC values in the two directions (performance to recording; recording to performance) within-subjects for each piece separately (see Figure 2). GC values from the recording to the performance were larger than from the performance to the recording across all trials for Piece 1 (*Danny Boy*), $t(63) = 7.038$, $p < 0.001$, and for Piece 2 (*In The Garden*), $t(63) = 9.659$, $p < 0.001$. These results are as expected; because the recording was fixed, information was expected to flow from the recording to the performance rather than the reverse. This establishes that information flow between the musical output of two violinists can be meaningfully measured.

3.2. Changes in information flow across trials

The violinists became more familiar with the recordings after each successive trial. To test the effect of trial on information flow, we modeled GC (only from the recording to the performance) as an outcome variable in a linear mixed effects model using the "lme4" package in R version 4.2.1 for each piece separately, as the pieces differed in tempo, note density and other structural features. The maximum likelihood approach uses ANOVA to compare full and reduced mixed models. Our full model included trial (eight trials) as a fixed effect, and participant (eight participants) as a random effect. The reduced model was identical except that it excluded the fixed effect of trial. The coefficient estimates of trial for Piece 1 were $\beta = -0.005$ with semi-partial $R^2 = 0.225$ and, for Piece 2, $\beta = -0.003$ with semi-partial $R^2 = 0.199$. Both were statistically significant ($p < 0.001$). This indicates that GC decreased significantly across trials from the recording to the performance (see Figure 3).

To examine the nature of the decrease in GC values across trials, we ran a set of linear contrasts (comparisons) including all eight levels of trial (as a quantitative ordered factor). This revealed a significant decreasing linear trend of GC for Piece 1, $F(1, 56) = 9.819$, $p = 0.003$, and for Piece 2, $F(1, 56) = 4.141$, $p = 0.047$, indicating a linear decrease over trials in both cases as hypothesized.

3.3. Changes in similarity and synchrony across trials

We modeled the CC coefficients as fixed effects of trial and random effects of participant, using the same full and reduced models as for GC, except with the maximum CC coefficient for each trial as the outcome variable. Coefficient estimates of trial were significant for Piece 1 ($\beta = 0.005$, semi-partial $R^2 = 0.069$, $p = 0.046$), and trending significant for Piece 2 ($\beta = 0.005$, semi-partial $R^2 = 0.062$, $p = 0.057$). Linear contrasts identical to those for GC were also run on the CC values, but neither piece produced a significant linear trend [for Piece 1, $F(1, 56) = 0.357$, $p = 0.553$, and for Piece 2, $F(1, 56) = 0.887$, $p = 0.350$; see Figure 4A].

Our measure of maximum CC coefficient for similarity, above, (using a lag window of ±1.25 s) does not necessarily capture phase alignment or synchrony between the two times series as the maximum CC value may occur when the two time series are lagged with respect to each other. To examine synchrony, we restricted the lag to 0 and re-ran the same CC analysis. The linear mixed model estimate of trial was significant for the Piece 1 ($\beta = 0.006$, semi-partial $R^2 = 0.087$, $p = 0.024$) and for Piece 2 ($\beta = 0.007$, semi-partial $R^2 = 0.146$, $p = 0.003$). As for the similarity analysis, neither piece exhibited a significant linear trend with 0 lag [for Piece 1, $F(1, 56) = 0.519$, $p = 0.474$ and for Piece 2, $F(1, 56) = 2.135$, $p = 0.150$; see Figure 4B].

There were no significant differences across trials for what lags produced the maximum cross-correlations (optimal lags). Importantly, average optimal lags were almost all positive or zero (98.5%) for both pieces for all trials, indicating that

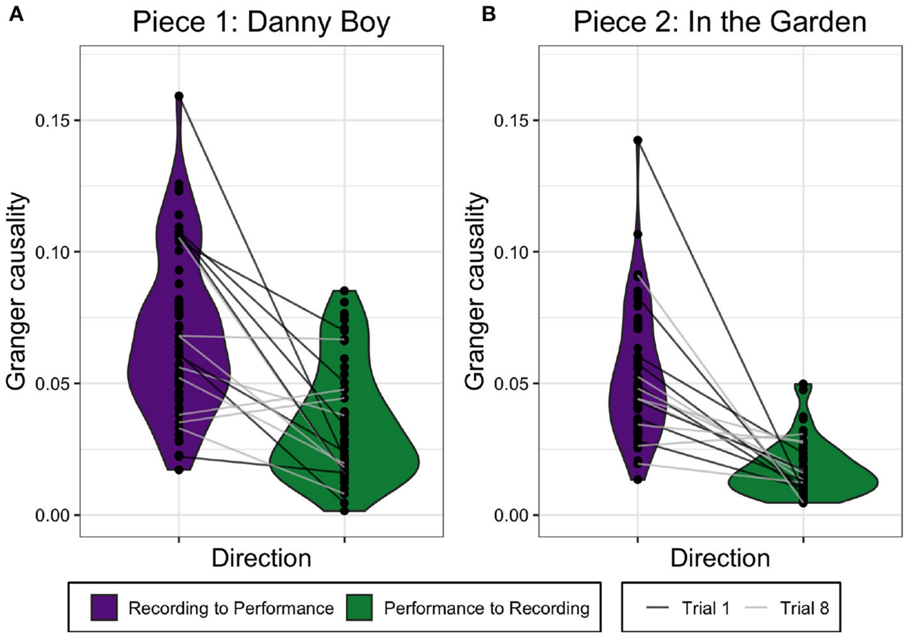

FIGURE 2
Granger causality values for both directions, recording to performance and performance to recording, for *Danny Boy* **(A)** and *In The Garden* **(B)**. The lines show how each participant's GC values changed between the two directions for Trial 1 and Trial 8.

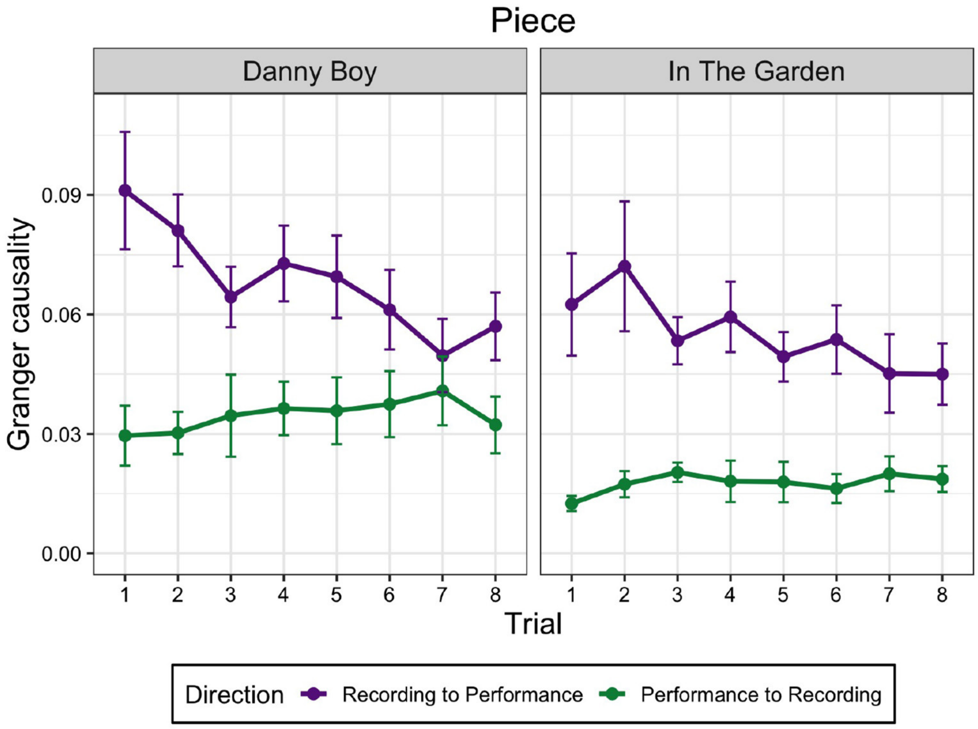

FIGURE 3
Granger causality (GC) values in both directions for each piece separately across the eight trials. Error bars represent standard error.

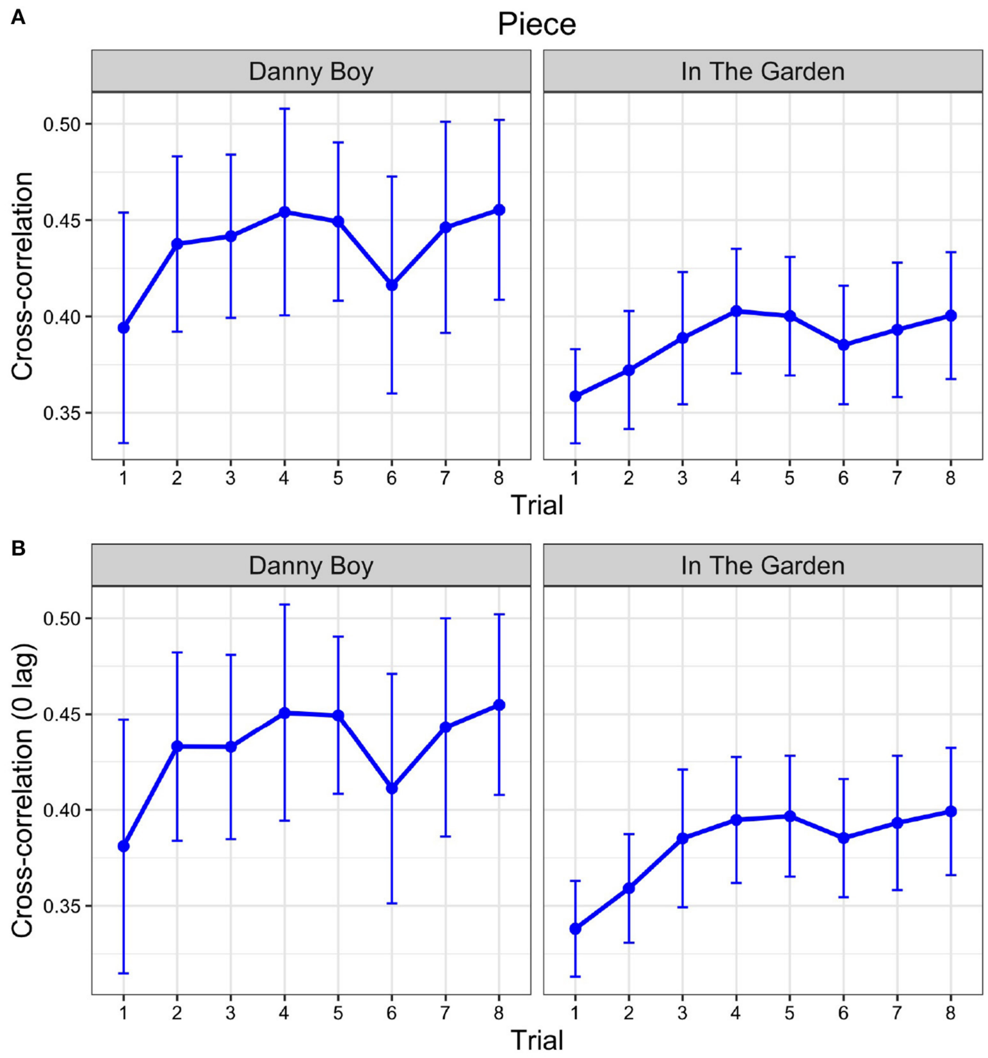

FIGURE 4
Cross-correlation (CC) values for each piece separately across the eight trials. **(A)** Similarity, calculated using the maximum CC value on each trial for lags between −1.25 and +1.25 s. **(B)** Synchrony, calculated using a lag of 0 s.

similarity was greatest at a lag where the recording preceded the performance, or when the two were aligned, and never when the performance preceded the recording.

4. Discussion

A strong theoretical position states that social coordination in general and playing music with others in particular rely on predictive mechanisms because motor movements and communicative messages require time to plan (Knoblich et al., 2011; Keller, 2014; Keller et al., 2014; Dobson and Gaunt, 2015). Thus, reacting to the actions or sound output of others rather than anticipating them will make coordination with others difficult and synchronization inaccurate. While most previous studies in naturalistic musical contexts have focused on actions such as musicians' body sway to examine how musicians anticipate how each other will move in order to adjust the timing of their own movements (Goebl and Palmer, 2009; Glowinski et al., 2012, 2013; Ragert et al., 2013; Chang et al., 2017, 2019; Colley et al., 2018, 2020; Hilt et al., 2019; Wood et al., 2022), here we focused on the musical sound output itself to examine whether a musician can predict how another musician will play next based solely on sound. Previous research examining musicians' sound output in joint performance tasks has focused primarily on measures of synchrony, either between MIDI note onsets or tapping timing (e.g., Repp and Keller, 2008; Goebl and Palmer, 2009; Keller and Appel, 2010; Repp and Su, 2013), but none has directly measured information flow in the continuous sounds of performing musicians. Using the context of a Western musician playing with a recording, we were able to control one musician (the recording) to be identical for all the performing musicians. Our GC analyses clearly showed that information flow was much higher from the recording to the musicians than vice versa, indicating that musicians can learn to predict how another musician will play next on the basis of the sounds they just produced.

A second question of interest concerns two possible sources of predictive information and how musicians learn through practice to create a shared expressive model of how to interpret a piece of music together. Here we examined this in the simplified and controlled situation where one musician was a sound recording that a second musician performed with, playing each piece eight times in succession. We deliberately chose two solo violin pieces that offer room for a large amount of expressive variability so that simply playing the correct notes would not be sufficient; the musicians playing with the recording needed to match the recording musician's interpretation. One source of predictive information is directly in the musical sounds of the recording musician, whereby the performing musician may be able to predict how the recording musician will play next based on how they just played. A second source of predictive information is based on prior knowledge about how the musician on the recording is likely to play the piece. Initially, the performing musicians only have prior knowledge of the recording based on their understanding of the Western musical genre and how they may have heard the piece or similar pieces performed in the past. However, through repeatedly hearing the recording across the eight trials, we would expect the performing musicians to improve their prior knowledge by building up an internal representation (or memory) of precisely how the recording musician played the piece. In turn, this should allow them to anticipate and synchronize more accurately with the recording and come to rely more on this alternative source of predictive information. Consistent with this interpretation, we found, as predicted, that GC values from the recording to the performing musicians decreased across the eight trials, suggesting that as they became more familiar with, that is, learned, the expressive rendition of the recording musician, they relied moment to moment less on predictive cues based on what the recording musician had just played and more on predictions based on their memory or internal model built from having heard this particular performance repeatedly.

Performances typically consist of interacting live musicians, involving non-verbal communication and prediction of how each other will play, and the refinement through experience of an internal model or knowledge of how the other will play. The use of generative models to explain "top-down" influences on perception rests in the predictive processing paradigm (a centuries old philosophical tradition; Swanson, 2016) that also supports the active inference framework (Friston and Kiebel, 2009; Vuust and Witek, 2014; Friston and Frith, 2015; Heggli et al., 2019). In this view, independent interacting agents infer the causes of sensory information, which includes that generated by the other agent, and act to minimize their uncertainty. One caveat of our study is that the recording was fixed, so only the performing musician was able to adapt their internal model. Still, our results are consistent with the active inference perspective in that information flowed from the recording to the musician rather than vice versa, and that the performing musician came to rely less on immediate inferences (i.e., GC decreased) through practice, consistent with the musician building a more accurate internal predictive model through repetition.

As the performing musicians came to rely less on predictive cues in the musical sounds on the recording and more on an internal model based on learning (or memory of) the interpretation of the recording musician, we expected that their performances would become more similar to that of the recording musician. Past studies have used a cross-correlation (CC) measure of the similarity between musicians' movements and note onsets (e.g., Goebl and Palmer, 2009; Wing et al., 2014; Colley et al., 2018, 2020; Bishop et al., 2019b) and tapping timing (e.g., Pecenka and Keller, 2011; Schultz and Palmer, 2019). In the present study examining the musical outputs of musicians, we expected CC to increase across trials as GC decreased. Indeed, a previous study from our lab observed this inverse pattern in the body sway times series of members of a string quartet (Wood et al., 2022), where GC decreased across trials while CC increased. In line with our predictions, we found that CC increased across trials for both pieces (trending significant for Piece 2); however, linear trends for increasing CC across trials were not significant (as they were for decreasing GC values), indicating that CC increased more at some points during learning than at others, perhaps reflecting in part that musicians may have fatigued towards the end of the eight repetitions.

Given that CC measures the maximum absolute correlation within a range of time lags between the recording musician and the performing musician (±1.25 s), this measure does not necessarily inform us about how synchronized or phase aligned the performing musicians were with the recording. To examine this, we ran a CC analysis using only a lag of zero, that is, we examined correlations between the recording and performer sound outputs when aligned in time. In this case, we found that CC increased significantly across trials for both pieces. In sum, we found evidence that the sound outputs of the recording and performing musicians became more synchronized over trials—indicating that the performing musicians' ability to synchronize or phase align with the recordings increased the more times they heard and played the piece.

Our measures of similarity and synchrony displayed an almost-identical pattern of increasing values over trials. This means that restricting the range of time lags over which the cross-correlation coefficients were calculated had little effect because in most cases the maximum absolute coefficient occurred close to a lag of zero. However, these optimal lags were almost always positive or zero (98.5% including both pieces). The positive sign observed in these values indicates that the maximal similarity of the two time series occurred when the recording preceded the performance. Although this does not necessarily reflect any causal interaction, one process that causes another would be expected to occur ahead of it in time.

In interpreting these results, however, it should be kept in mind that we performed our analyses on the amplitude envelope of the sound. While the amplitude envelope captures details of intensity changes over time, it misses many other aspects of musical expression, including pitch changes. For instance, two or more slurred notes can be played in succession with a single bow stroke, producing very little change in the overall intensity of the sound; nor will the amplitude envelope capture expressive micro-pitch changes, such as those associated with vibrato. Thus, while the amplitude envelope reflects many of the small continuous adjustments musicians make, it should be considered an imperfect, albeit useful, proxy for musical expression and some expressive characteristics present in our participants' performances were likely inaccessible to our analysis. It is possible that a frequency-based comparison between the two sound streams, such as spectral coherence, could prove fruitful. Expert ratings of performance synchrony could serve as another useful (although non-objective) measure.

Several of our results differed slightly across the two pieces. In particular, the increase in similarity was only trending significant for Piece 2. Although minor, given that all but one violinist in each group performed both pieces, these differences suggest structural aspects of the two specific pieces played a role in violinists' process of learning to match or synchronize with them. Both pieces were chosen for the high level of expressive freedom taken by the performer but had other important differences, related to both difficulty and familiarity. All performing musicians reported having heard and played *Danny Boy* previously but none had heard *In The Garden* before, which we expected given the general popularity of *Danny Boy* within the context of Western music. Regarding difficulty, *In The Garden* had a faster tempo (130 vs. 55 beats per minute), a higher note density (∼1.70 vs. ∼1.09 notes per second) and included double stops, consistent with some violinists anecdotally reporting finding it more challenging. Both of these factors might be expected to affect learning rates.

In naturalistic contexts, musicians likely use movements, sights and sound to predict how each other plan to play, and the extent of their reliance on different cues likely depends on the situation. For example, changes in body movement dynamics in joint performance have been shown to track changes in task demands. Motion capture data revealed that head movements of violinists become more regular and predictable when playing in a quartet vs. solo (Glowinski et al., 2013) and that gestures become more coordinated and smoother during periods of temporal instability as a group learns unfamiliar music (Bishop et al., 2019b). Research in this vein highlights how sensory signals arriving by auditory and visual modalities interact; when one type of information is unavailable or insufficient, another may become more important. Leaders in piano duos tend to lift their fingers higher and play less synchronously when they get less auditory feedback from partners, suggesting that the lack of information in the auditory domain increased the importance of visual cues (Goebl and Palmer, 2009). Bishop and Goebl (2015) showed that pianists played less synchronously with a video recording of a performance when they could only see but not hear the recording, but that in this condition synchrony increased during periods after long pauses, pointing to the importance of visual cues for synchronizing when a partner's performance is difficult to predict.

The performance task we asked musicians to undertake of matching their performance to a recording was not representative of how they would typically perform. However, this highly controlled experiment clearly establishes that information flow in musical sound output between musicians reflects the dynamics of interaction and learning. It is exciting in opening the door to understanding subtleties of how musicians jointly create complex musical performances at the sound level. It also opens a rich set of questions regarding how movements (such as body sway) and auditory perception interact to achieve joint musical goals. Immediate questions that need to be explored include measuring information flow between the sounds of live pairs of musicians as well as larger groups. We would expect to see mutual predictive influences between the sounds of live musicians playing together, effects of leadership whereby the sounds of leaders affect the sounds of followers more than vice versa, increases in information flow when a piece is played more expressively, and decreases in information flow as a piece is rehearsed and common joint internal models are formed. Extending to more than one live musician presents challenges in measuring each musician's sound output separately and would require either pickups or highly directional microphones that can record each instrument's audio separately with little residual bleeding between the recordings, or signal processing techniques, or some combination of these. While MIDI can get around this issue, examining the rich sound output of non-percussion instruments that create continuous sound, as in the present study, would be very informative. Having musicians perform in separate rooms would solve this issue and introduce the ability to compare seeing and non-seeing conditions.

The present study investigated information flow through sound in the context of Western music performance in which musicians played a pre-composed piece from a score. However, many other styles and genres of music exist both within and beyond Western music. For example, in improvisation, such as occurs in jazz ensembles or jam bands, musicians compose new music in real-time. The increased uncertainty that this engenders may make predictions of what fellow musicians will play on the basis of what they just played even more important than in non-improvised contexts. Across cultures, there are marked differences in scales used, rhythmic complexity, degree of polyphony, and whether precise synchrony is a goal or not. To determine whether information flow and synchrony can reveal coordination dynamics of joint music making universally, they will need to be measured in many contexts and across different cultures. We hope that the results of this study, conducted in a highly controlled setting, will lay the groundwork for future application of Granger Causality to musical sound coordination in more varied and ecologically valid performance contexts. We believe this approach could serve as a useful tool for investigating information flow between the sound outputs of live performing musicians, similar to what has been done for body sway.

Data availability statement

The scripts used to analyze the dataset for this study can be found in the online repository at: https://github.com/trainorlab/violinfollowing. The datasets are available from the corresponding author upon request.

Ethics statement

The studies involving human participants were reviewed and approved by McMaster Research Ethics Board, McMaster University. The patients/participants provided their written informed consent to participate in this study.

Author contributions

DB, LK, LT, and EW contributed to the conception and design of the study. LK created the stimuli, acquired the data, and performed the data analysis with help from EW. LK wrote the first draft of the manuscript, with edits from LT. All authors contributed to the interpretation of the results and revised and approved the manuscript.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fnhum.2022.982177/full#supplementary-material

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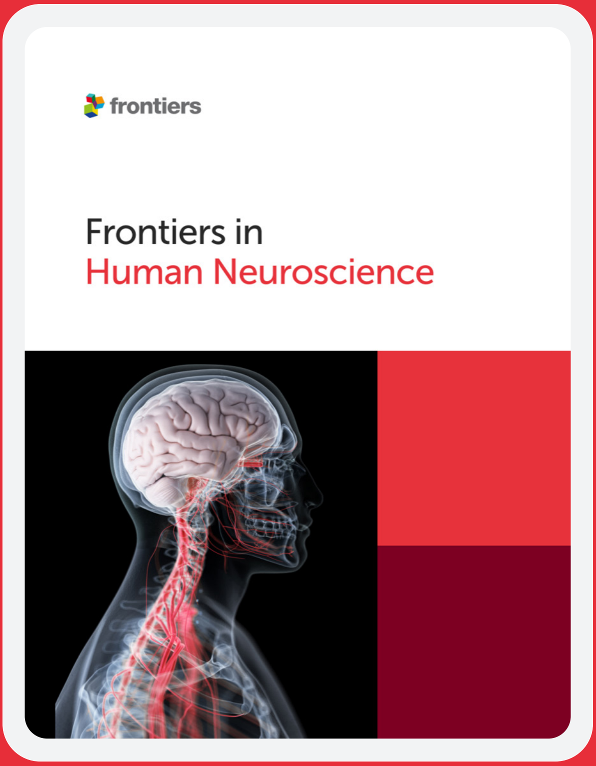
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