

Interpersonal synchrony and network dynamics in social interaction, volume II

Edited by

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Interpersonal synchrony and network dynamics in social interaction, volume II

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Editorial: Interpersonal synchrony and network dynamics in social interaction, volume II

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Editorial on the Research Topic

**Interpersonal synchrony and network dynamics in social interaction,
volume II**

Human beings are capable of remarkable feats of collaboration—ranging from performing complex symphonic music to constructing pyramids. Yet, the precise mechanisms that enable such finely tuned coordination, particularly the neural processes that support it, remain largely elusive. This Research Topic (Volume II) was launched with the aim of further highlighting and exploring the mechanisms and functions of interpersonal interaction, and of deepening our understanding of these highly interesting and complex phenomena and their downstream effects on real-life social interaction. The Research Topic of contributions includes four Perspective and four Original Research articles written by leading researchers in the field. They showcase the breadth of research studies, going from inter-brain synchronization, desynchronization, and causality, hyper-brain network topology, the representation of self and others in emotional contagion and joint action, effects of individual practice, dynamic embodiment, and sync with oneself to pleasantness in joint musical synchronization. This range exemplifies the promise of this field in being able to span multiple facets of life and social dynamic interaction. The research united under the present Topic also illustrates how theoretical insights go hand in hand with advances in methodological tools, enabling increasingly refined empirical investigations.

Notably, several theoretical advances have been proposed as part of this Research Topic. A recent perspective in social and cognitive neuroscience suggests that interpersonal action coordination and communicative behavior depend on inter-brain synchronization and specific hyper-brain network activity, as studied through hyperscanning methods. A Perspective Article by [Froese et al.](#) explores the role of *inter-brain desynchronization* (IBD) in social interaction, proposing that it complements the established concept of inter-brain synchrony (IBS) in human neuroscience. Hyperscanning approaches, which study neural dynamics during social interactions, have largely focused on IBS, the synchronization of brain activity between interacting individuals. However, the results have been inconsistent,

prompting a re-evaluation of the field's theoretical underpinnings. The authors introduce *irruption theory* (Froese, 2023), which suggests that subjective involvement in social interactions increases neural entropy, leading to IBS, or decreased phase synchrony between brains. This desynchronization may act as a counterbalance to IBS, explaining the observed variability in IBS findings. While IBS has been considered the main marker of social engagement, irruption theory posits that IBD may play a positive role by enabling cognitive flexibility and adaptation in dynamic social contexts, such as turn-taking or complementary behaviors. Potential biases are highlighted within the field that have prioritized IBS over IBD, suggesting that the lack of evidence for IBD may be due to this narrow focus. The authors advocate for broader consideration of IBD, which they argue could provide a more nuanced understanding of social coordination. Moreover, they suggest that the interplay between IBS and IBD, rather than the dominance of one, may be crucial for healthy social interactions and mental wellbeing. Future research should systematically examine the variability of IBS and explore how IBS and IBD together contribute to the dynamic nature of human social behavior.

Emotional contagion is the process by which an emotional state is transferred from one individual to another, describing the spread and mutual influence of emotions among individuals. In contrast, social buffering occurs when an individual's stress response is diminished due to the presence of one or more others. While each process has been extensively studied independently, the relationship between them remains unclear (Reimert and Bolhuis, 2024). A Perspective article by Wang et al. explores the complex interaction between social context, self-representation, and emotional contagion, challenging the notion that emotional contagion occurs automatically and unconsciously. Instead, the authors propose that self-representation—how individuals perceive themselves within a social context—plays a crucial role in shaping emotional contagion. The study highlights how social settings activate specific self-representations, such as one's identity or role, which influence how individuals emotionally respond to others. For instance, when people are aware of their social roles or relationships in a group, their self-representation becomes contextualized, affecting their susceptibility to emotional contagion. The authors introduce a dynamic model that describes a causal loop: social contexts activate self-representation, which then influences emotional contagion, and, in turn, emotional contagion strengthens interdependent self-representation, fostering social connection. This model emphasizes the bidirectional relationship between emotional contagion and social dynamics. The authors also highlight the need to study emotional contagion in group settings and organizational contexts, as well as the role of cultural factors in influencing the relationship between self-representation, social context, and emotional contagion, providing a broader perspective on its impact across different environments.

Throughout various epochs and cultures, humans have come together to make music collectively—a universal behavior that remains both intriguing and only partially understood. As interest in joint music-making continues to grow, recent advancements in this emerging field, integrating insights from behavioral, neural, and computational research, are exciting (Keller, 2023; Abalde et al.,

2024). An Original Research article by Plitchenko et al. investigates how individual practice impacts joint synchronization during musical performances, focusing on sensorimotor synchronization in solo and ensemble settings. Musically trained participants practiced producing a melody by tapping on a keypad, receiving either normal or delayed auditory feedback. The study examined how these solo practices influenced their synchronization when performing as duets. Results showed that synchronization accuracy was higher during joint performances than in solo practices, even though solo tasks involved more temporally regular cues. Interestingly, participants' ability to synchronize improved over time, indicating a learning effect. Delayed auditory feedback in solo conditions increased asynchrony, but when participants practiced with normal feedback, they performed better during subsequent joint tasks. The study also applied a delay-coupling oscillator model, revealing that coupling strength between partners was stronger after normal feedback practice compared to delayed feedback. The findings suggest that individual practice, particularly with accurate feedback, enhances synchronization in duet performances. This supports the effectiveness of solo practice methods commonly used by musicians to prepare for ensemble performances. The study also highlights that joint synchronization benefits from the inherent variability of a partner's timing, which musicians can adapt to more easily than a computer-generated rhythm.

Humans interact through actions mediated by sensory and motor processes, with intra- and inter-brain synchrony oscillations supporting social adjustment. However, it remains unclear whether IBS can be attributed to similar bottom-up processes during synchronous play, or if it instead reflects cognitive top-down control required for periods of higher coordination demands (Müller et al., 2021; Gugnowska et al., 2022; Lender et al., 2023). Varlet and Grootswagers examine the limitations of current hyperscanning research, particularly regarding IBS as a measure of social interaction. Hyperscanning allows for simultaneous brain activity recording from multiple individuals and has been used to explore how brain waves align during social interaction. However, the authors argue that IBS, often used as a proxy for synchronized cognitive and sensory processes, is not sensitive enough to capture interpersonal information alignment, echoing theoretical proposals such as irruption theory (Froese, 2023). Through EEG hyperscanning simulations, they show that IBS remains largely unchanged even when two individuals are exposed to different visual stimuli simultaneously. This suggests that IBS reflects timing alignment rather than the content of sensory and cognitive processes. The study challenges the notion that IBS directly causes synchronized minds and behaviors. Instead, it supports the view that synchronized brain activity is a byproduct of coordinated behavior and cognition, not the driving force behind it. The authors also highlight discrepancies in past hyperscanning studies, where IBS was not consistently observed, even when participants were engaged in social interaction. To address these issues, the article proposes using representational analyses as a more effective method for capturing interpersonal information alignment. Unlike IBS, representational analyses allow for the comparison of information content across individuals, making them a promising alternative for future research. The authors

call for further development of these methods, especially for more naturalistic and complex social tasks, to enhance our understanding of the neuropsychological processes underlying real-time social interactions.

Neural cell assemblies emerging within interacting brains require continuous adjustment and close coordination to support interpersonal dynamics and interactive activities that often operate on millisecond time scales. A *hyper-brain cell assembly* was hypothesized to integrate oscillatory activity both within and between brains, as well as across different oscillation frequencies, forming a unified structure responsible for social and interactive behavior (Müller, 2022). An article by Müller and Lindenberg explores the neural dynamics of ensemble music performance by examining how different brain oscillations (neural frequencies) interact within and between the brains of musicians in a guitar quartet. Using EEG data, the study focuses on cross- and within-frequency coupling (WFC and CFC, respectively) to construct hyper-brain hyper-frequency networks (HB-HFNs), a multilayer network organization, providing insights into how neural coordination supports synchronized musical performance. The findings suggest that low-frequency oscillations (such as delta, theta, and alpha waves) play an integrative role in coordinating actions between musicians, with each guitarist contributing uniquely to the network dynamics. Notably, coupling strength decreases with higher oscillation frequencies. Additionally, the study shows that WFC is generally stronger within individual brains, while CFC is more prominent between brains. The topology of HB-HFNs appears influenced by musical acoustic properties, such as amplitude and frequency. The complex multilayer network structures are also found to be robust against the loss of connections, particularly when the strongest connections are maintained. The authors conclude that HB-HFNs effectively capture the neural processes involved in coordinating interpersonal actions during ensemble performance. The findings highlight how multilayer brain networks dynamically integrate sensory and motor information to support synchronized group behavior. This study extends previous research on neural markers of interpersonal action coordination, particularly in complex, real-time social activities like music performance, and offers a versatile framework for studying neural interactions in various forms of social behavior.

Music-making is a universal process of creating aesthetically pleasing sound patterns through interpersonal synchronization, involving the coordination of actions, emotions, thoughts, and physiological rhythms, yet its impact on the sensorimotor interactions between participants remains unclear. An article by Lazzari et al. investigates how the aesthetic quality of jointly produced sounds influences interpersonal motor coordination. Using a dyadic synchronization-continuation task (dSCT), non-musician pairs tapped in synchrony to a metronome before continuing at the same tempo without it. Each tap generated a note, creating either consonant (pleasurable) or dissonant (less pleasurable) chords. Results showed that dyads synchronized more closely when producing consonant chords and rated these interactions as more enjoyable. Interestingly, consonance affected synchronization only in the joint continuation phase, not in individual metronome-paced tapping. Furthermore, the synchronization effect of consonant sounds was more

pronounced in pairs who initially felt less socially close, suggesting that consonance enhances both coordination and social connection. The findings highlight the role of aesthetic harmony in shaping social and motor synchrony. Beyond academic interest, the results hold potential clinical applications. For example, consonant musical intervals could improve motor synchronization in therapeutic settings, particularly for individuals with sensory-motor deficits, such as those in Parkinson's disease or schizophrenia. Synchronizing to consonant sounds might foster movement coordination, enhance social connection, and improve therapeutic outcomes. This research emphasizes that the aesthetic outcomes of joint activities can have tangible benefits for both movement precision and interpersonal rapport.

Inter-brain coupling is investigated as a predictor of behavioral change, but despite advances in hyperscanning that illuminate its role in social interactions, establishing causal links between brain activity and behavior remains a significant challenge. A Perspective article by Markus and Shamay-Tsoory delves into Research Topic, offering potential methodologies and valuable insights into how inter-brain coupling underpins essential processes in social interactions. While current research has correlated inter-brain coupling with changes in social interaction, proving causation remains difficult due to differing timescales of neural and behavioral responses and a lack of causal-focused methods. To address this, the authors propose two approaches: dyadic neurofeedback, which reinforces inter-brain synchrony to observe whether such coupling affects mutual synchronization attempts, and statistical techniques like Granger causality and Structural Equation Modeling (SEM). Granger causality allows for predicting how neural interactions might drive behavior, while SEM provides a detailed framework for modeling direct and indirect influences of neural synchrony on behavior. The article highlights the need for more robust causal methods within a network model of social interaction, suggesting that Granger causality and SEM could allow researchers to discern directional influences between brain coupling and behavior. The authors propose an expanded model—multilevel SEM (mSEM)—that could integrate multiple behavioral and neural components, enabling a comprehensive view of social interaction dynamics. By testing causality with these methods, future studies could clarify how neural synchrony contributes to social behaviors, moving beyond mere correlation to identify specific causal pathways in social cognition and interaction.

Understanding how groups of people coordinate movement in rhythmic settings remains a central challenge in research on social interaction and collective behavior. Toiviainen et al. tackle this by presenting an innovative modeling approach that captures the dynamics of dance floor behavior. Extending traditional swarmalator models, the authors introduce “directional swarmalators,” integrating gaze direction alongside spatial movement and rhythmic synchronization. This addition allows their model to better simulate how dancers dynamically self-organize based on both musical and visual cues. Validated against motion capture data from silent disco experiments, the model captures emergent patterns such as circular group formations and highlights the importance of visual attention in collective coordination. Despite some instructive limitations—such as overly smooth agent movements and the need for broader datasets—the

model offers a powerful tool for studying large-group social dynamics, with potential applications beyond dance. The authors suggest that future developments could include simulating more naturalistic erratic movement, expanding to other collective behaviors, and integrating anticipatory processes crucial for human synchronization. Overall, this work offers a compelling framework for linking visual perception, rhythmic behavior, and emergent group structures in dynamic environments.

Understanding how individuals coordinate actions in real time is central to studying social interaction, particularly in complex activities like ensemble music performance. Kohler et al. address this by examining the neural representations underlying self- and other-produced actions in duetting pianists. Using multivariate pattern analysis (MVPA) of fMRI data, the study demonstrates that expert pianists maintain parallel, distinct, and content-specific neural representations for their own and their partner's musical parts while playing duets. Remarkably, primary motor cortex (M1) primarily encoded self-produced actions, while premotor cortex (PMC) encoded the partner's actions, with an unexpected lateralization pattern: left M1 for self and right PMC for other. These findings challenge existing notions about hemispheric specialization and provide empirical support for theories positing separate yet integrated internal forward models facilitating interpersonal coordination. Interestingly, the precision of motor representations was not strongly dependent on prior motor familiarity with the partner's part, suggesting that auditory-motor expertise alone may support flexible coordination with novel musical material. By combining univariate and multivariate neuroimaging approaches, the study opens new avenues for understanding the neural architecture of *social action prediction* and *self-other integration* in music and beyond, highlighting how sophisticated internal models guide joint performance even without explicit motor rehearsal.

The coordination of simultaneous actions within a single individual—spontaneous intrapersonal coordination—is an emerging topic that bridges motor control, cognitive load, and rhythm research. Jagadeesan and Grahn investigate how different types of periodic behaviors, such as finger tapping, walking, and vocalizing, coordinate within individuals under varying cognitive demands. Across two experiments, the authors show that simultaneous periodic actions exhibit higher coordination than when performed separately, but this coordination is sensitive to the nature of the task and the presence of additional cognitive load. Coordination between tapping and vocalizing was more stable than between tapping and walking, suggesting that walking imposes greater cognitive demands, likely due to its complexity. Moreover, adding a concurrent cognitive task—such as backward counting or visual pattern matching—reduced coordination stability, particularly for tapping and walking combinations. These findings position spontaneous intrapersonal coordination as a promising avenue for understanding how attentional and cognitive resources modulate motor behavior. They also suggest that coordination stability could serve as a sensitive marker of cognitive load. Overall,

the study highlights the intricate interplay between cognition and action and opens new pathways for examining how the brain manages multiple rhythmic activities simultaneously.

The studies presented in this Research Topic showcase a remarkable breadth of themes and research questions, underscoring the significance of interpersonal action coordination and social interaction across a range of contexts. Collectively, they reinforce the view that neuronal dynamics underlying social interaction are not confined to isolated brain regions but emerge from system-wide processes involving synchronized activity across brains and sensorimotor systems. This inter-brain and inter-system synchrony, which emerges across varying contexts and situations, reflects the inherently complex and distributed nature of human interaction. Importantly, the findings open promising avenues for both fundamental research and clinical applications—particularly in domains such as neurorehabilitation, social cognition, and communication disorders. Furthermore, these contributions demonstrate the growing relevance of hyperscanning methodologies in advancing social neuroscience, offering a powerful framework for understanding how shared neural processes support real-time coordination between individuals.

Author contributions

VM: Conceptualization, Writing – original draft, Writing – review & editing. MF: Writing – review & editing. FV: Writing – review & editing. PK: Writing – review & editing.

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Inter-brain desynchronization in social interaction: a consequence of subjective involvement?

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Hyperscanning approaches to human neuroscience aim to uncover the neural mechanisms of social interaction. They have been largely guided by the expectation that increased levels of engagement between two persons will be supported by higher levels of inter-brain synchrony (IBS). A common approach to measuring IBS is phase synchrony in the context of EEG hyperscanning. Yet the growing number of experimental findings does not yield a straightforward interpretation, which has prompted critical reflections about the field's theoretical and methodological principles. In this perspective piece, we make a conceptual contribution to this debate by considering the role of a possibly overlooked effect of inter-brain desynchronization (IBD), as for example measured by decreased phase synchrony. A principled reason to expect this role comes from the recent proposal of irruption theory, which operationalizes the efficacy of a person's subjective involvement in behavior generation in terms of increased neural entropy. Accordingly, IBD is predicted to increase with one or more participant's socially motivated subjective involvement in interaction, because of the associated increase in their neural entropy. Additionally, the relative prominence of IBD compared to IBS is expected to vary in time, as well as across frequency bands, depending on the extent that subjective involvement is elicited by the task and/or desired by the person. If irruption theory is on the right track, it could thereby help to explain the notable variability of IBS in social interaction in terms of a countertendency from another factor: IBD due to subjective involvement.

KEYWORDS

EEG, hyperscanning, joint action, neural synchrony, social interaction, neural entropy

1 Introduction

Humans have a remarkable capacity for forming social collectives. The behavior of the smallest unit of collectives—dyadic interaction of a pair—has been variously studied in the cognitive sciences, for example as joint action, collective intentionality, we-mode, mutual incorporation, and embodied intersubjectivity. A novel theoretical framework that is emerging from these lines of research is that how we interact with others is irreducibly other-involving (Dumas et al., 2014), especially when there is emotional engagement (Schilbach et al., 2013). This kind of second-person framework fits naturally with the fact that some of the most meaningful experiences in our lives are moments that we share with others. The possibility that two or more people are subjectively involved in one shared experience has been referred to as “genuine intersubjectivity” to distinguish it from the traditional premise of a strict methodological individualism about social experience (Froese, 2018).

The neural mechanisms supporting social interaction are an active topic of research, especially by means of the application of inter-brain synchrony (IBS) and functional network measures to various hyperscanning approaches in the field of human neuroscience (Czieszumski et al., 2020). For the case of investigating the neural basis of naturalistic social interaction at fine-grained temporal resolution, EEG hyperscanning is the established method. Drawing inspiration from the hypothesized role of neural synchrony as a mechanism for large-scale integration of *intra*-brain activity (Varela et al., 2001), a guiding hypothesis of current efforts is to elucidate the role of IBS for large-scale integration of *inter*-brain activity (Müller, 2022). Various frequency ranges are expected to play a role in IBS, with faster ranges, especially gamma, suspected to be especially important for the integration of the neural basis of conscious experience across individuals (Valencia and Froese, 2020).

From a theoretical perspective, despite early recognition of a diversity of conceptualizations of social interaction (Pfeiffer et al., 2013), the field of second-person neuroscience has been predominantly driven by a search for increased IBS. Continued investigation of IBS is justified, as there is growing evidence of the causal role played by IBS in social interaction (e.g., Szymanski et al., 2017; Pan et al., 2021), yet the results of an expanding list of tasks do not always lend themselves to be interpreted in unidirectional increased in IBS (Hamilton, 2021; Holroyd, 2022). Moreover, the field does not yet have an explicit hypothesis to revise and broaden its experimental expectations, which hampers its capacity to see in which direction the rapidly accumulating data is pointing. If there are other factors at play other than IBS, then what are they and what is their role?

Accordingly, there is an opportunity, perhaps even a necessity, to complement the current largely data- and method-driven efforts in the field with a more explicit articulation of a theoretical framework of social interaction that can guide the process of scientific discovery. Steps in this direction had already been taken a decade ago by drawing on insights from embodied and enactive theory (e.g., Di Paolo and De Jaegher, 2012; Schilbach et al., 2013). But since then it has admittedly remained challenging to cross the gap from theory to experiment in the form of novel interpretations and testable predictions (Lehmann et al., 2023).

In this short perspective piece, we sketch the beginnings of a more differentiated theoretical framework for second-person neuroscience. Our proposal is based on the recent proposal of irruption theory (Froese, 2023), which takes inspiration from the neurophenomenology of embodied action (for a recent review, see Froese and Sykes, 2023). In a nutshell, our perspective amounts to the following novel claim: *a person's subjective involvement in social interaction impacts their brain in the form of increased neural entropy, which will lead to inter-brain desynchronization (IBD)*. Accordingly, even if social interaction is generally associated with a tendency for increased IBS, presumably as a basis for interpersonal integration, any concomitant increase in subjective involvement is expected to also increase IBD, and hence to reduce the overall effect of IBS.

2 Irruption theory, neural entropy, and inter-brain synchrony

Irruption theory starts by taking seriously the insights derived by both our *first-person perspective* of lived experience, namely that

we are agents who act in accordance with our motivations, and the *third-person perspective* of scientific observation, namely that we are complex physical systems that operate spontaneously in accordance with material constraints (Froese, 2023). The apparent tension between these two perspectives is resolved by highlighting that neither phenomenology, nor the physical sciences, can provide a complete description of human behavior on its own; they are limited in scope by the opaqueness of the lived body and the uncertainty of the living body, respectively. These foundational assumptions of irruption theory are captured by a set of three axioms:

1. Motivational efficacy: An agent's motivations, *as such*, make a difference to the material basis of the agent's behavior.
2. Incomplete materiality: It is impossible to measure how motivations, *as such*, make a difference to the material basis of behavior.
3. Underdetermined materiality: An agent's behavior is underdetermined by its material basis.

Each of these axioms has been defended by different traditions in the literature, and taken together they come close to an embodied interpretation of the libertarian philosophical tradition on free will (Fuchs, 2021). The novel contribution of irruption theory is to go one step further, and to derive a novel working hypothesis from the integration of axioms 1 and 2: *The more an agent's embodied activity is motivated, the less that activity is determined by its material basis*. In other words, this theory provides a meaningful interpretation of unexplainable variability in neural dynamics: a specific portion of that variability—what is referred to as an *irruption*—is a logical consequence of accepting both (1) that there is irreducible motivational efficacy, and (2) that any such motivational efficacy is unintelligible *as such*, that is, as motivational in nature, within the domain of material constraints.

A key challenge for this theory is to explain how an irruption could make an effective difference to the agent's behavior, given that its immediate impact on the body amounts to a disordering rather than organizing factor. For this purpose, three theses are proposed:

1. Irruption Thesis: The living body is organized as an *incomplete system* such that it is open to involvement of motivations via increased material underdetermination.
2. Scalability Thesis: The living body is organized as a *poised system* such that it amplifies microscopic irruptions to macroscopic fluctuations that can impact behavior.
3. Attunement Thesis: The living body is organized as an *attuned system* such that it responds to scaled up irruptions in a context-sensitive and adaptive manner.

In this regard, irruption theory is consistent with a host of proposals that highlight how our bodies are organized as self-producing, thermodynamically open systems, situated dynamically at the edge of chaos, with a meta-stable grip on the world (for more detailed comparisons, see, e.g., Froese and Karelín, 2023; Froese et al., 2023). Its specific contribution is an alternative conceptualization of how to cash out the role of subjectively guided mental activity non-reductively: not in terms of the popular appeal to top-down constraints (e.g., Kelso, 1995; Freeman, 1999; Juarrero, 1999; Deacon, 2012), but rather as the destabilization of such

spontaneously emergent constraints by irruptions. This is not the place to review the neuroscientific evidence in favor irruption theory, but it is consistent with a growing body of evidence that neural entropy tracks cognition and consciousness (e.g., Carhart-Harris et al., 2014; Lynn et al., 2021; Deco et al., 2022). More specifically, increased neural fluctuations have independently been proposed as the marker for volitional action in the context of the neuroscience of free will (Schurger et al., 2021), and the concept of irruption enables us to make sense of why volition manifests in precisely this way.

In the case of solitary situations, all cognitive tasks involve increased neural entropy production when compared to the resting state (Lynn et al., 2021), and the increase is particularly notable for tasks involving motor coordination, reward and decision making, and higher-order relational perceptual processing. Solitary tasks involving stimuli that represent social situations, e.g., auditory sentence and animation presentations, are associated with medium levels of entropy production. Even leaving aside the interpretative framework of irruption theory, it is reasonable to assume that the neural dynamics associated with real-time embodied social interaction would involve a combination of these task elements, and hence would exhibit elevated neural entropy. What does this kind of entropic disordering of brain dynamics mean for interbrain synchrony (IBS)?

As a first step, let us consider the origins of a popular method for calculating IBS, namely in terms of phase synchrony measured by phase-locking value (PLV). This measure was developed in Varela's group (Varela et al., 2001) and first published by Lachaux et al. (1999). It was applied by Rodriguez et al. (1999) to the neural basis of the perceptual experience, where they found that a meaningful visual stimulus is associated with higher PLV and power in the gamma frequency spectrum.

However, Rodriguez et al. (1999) also observed desynchronization alternating with moments of increased synchrony. Although their focus was on synchrony as a candidate mechanism for perceptual binding or "neuronal glue," the extent of desynchronization seems longer and larger: averaging over the trial would have presumably showed decreased PLV values for meaningful compared to non-meaningful stimuli. Prefiguring irruption theory, they interpreted this prominent desynchronization as a "process of active uncoupling of the underlying neural ensembles that is necessary to proceed from one cognitive state to another." Indeed, to the extent that the formation of the next cognitive state is a self-organizing process based on the emergence of a cell assembly, this *neural synchronization* is, from the perspective of the person, a *passive* happening that is organizing behavior outside of their awareness and control. Hence, Varela's (1995) intuition was that it is rather the moment of *neural desynchronization* that is indicative of the person's *active* doing, that is, of their subjective involvement. Again, irruption theory enables us to explain why the efficacy of their subjective involvement would manifest in precisely this way.

There are important lessons for EEG hyperscanning that can be derived from irruption theory and the original analysis by Varela's group of PLV during meaningful perception. We propose two novel hypotheses for future experimental testing:

- a. Across time, inter-brain synchrony (IBS) is expected to vary in accordance with the level of subjective involvement in the social interaction, and

- b. Averaged over time, increased subjective involvement in social interaction, due to more self- and/or other-related motivations, is expected to result in comparatively lower IBS.

We will now briefly explore these hypotheses in more detail.

3 Degrees of social engagement

The EEG hyperscanning literature has largely ignored the role of individual brain variability when considering IBS in the context of different degrees of social engagement. The general expectation is of a positive association between the extent of inter-personal integration and the extent of IBS, for example based on the self-organization of hyper-brain cell assemblies (Müller, 2022). Consider the following three typical hyperscanning scenarios, as illustrated in Figure 1:

- A. An EEG recording of two independent people in resting state at the same time, as sometimes performed to establish a baseline condition;
- B. An EEG recording when the pair independently perform complex behaviors with respect to a shared task space, as typically studied in the context of joint action;
- C. An EEG recording when the pair engage in an interdependent reciprocally regulated interaction, as typically studied in the context of collective improvisation.

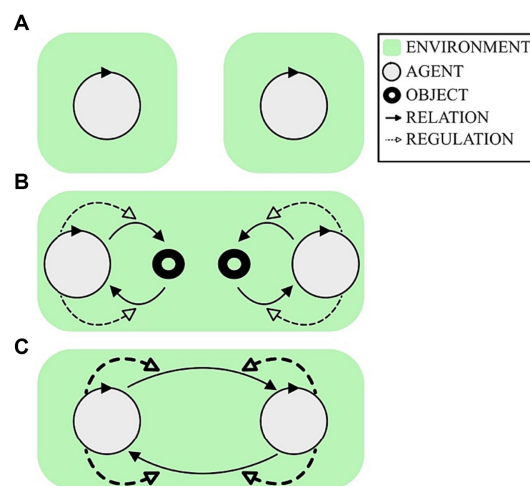


FIGURE 1

Three typical hyperscanning situations. Green represents the environment for each participant. A circular arrow represents a participant as an autonomous agent, following the autopoietic enactive tradition (Di Paolo et al., 2017). The outgoing and incoming black arrows represent the sensorimotor loop of how the agent is affecting and being affected by the environment, respectively. The dashed arrows indicate the agent's active regulation of that sensorimotor loop to engage with the environment.

(A) Simultaneous recording of resting state condition. (B) Two agents can engage in a task involving others, but in such a way that independent behavior regulation is largely sufficient to succeed, such as in many joint action tasks. (C) For some tasks, agents co-regulate how they affect each other in an interdependent manner, such as in practices of joint improvisation. How should we expect inter-brain synchrony (IBS) to vary across these conditions?

As an illustrative example of scenario B, consider the performance of pre-trained, pre-scripted behavioral sequences by duetting musicians (e.g., [Gugnowska et al., 2022](#)). A minimal version of scenario C could then involve the introduction of an unexpected perturbation to which the musicians have to interactively adapt ([Lender et al., 2023](#)). Most researchers engaged in hyperscanning would presumably expect that average IBS would come out as follows: $(C) > (B) > (A)$. But is it so?

Regarding the resting state condition, we may still expect some degree of IBS simply because there is a nonzero probability that neural activity will exhibit similarity ([Moreau et al., 2022](#)). Moreover, if the resting state of the pair of participants was recorded synchronously, then the neural activity of both individuals is implicitly temporally aligned, which could elevate IBS. For example, they have been culturally integrated into the same universal clock system, and they began the resting state condition at the same instant. It is standard practice to consider such externally induced IBS as spurious and to remove it from further analysis ([Holroyd, 2022](#)). However, research employing multi-brain stimulation suggests that such externally induced IBS may still be efficacious for facilitating social coordination ([Novembre and Iannetti, 2021](#)), in which case there actually may be no such thing as spurious IBS. Future work may need to reconsider what counts as baseline, truly inefficacious IBS.

In the case of two participants independently working on a shared task, we may expect average IBS to be increased by the fact that neural activity of both participants is now externally synchronized not only by background temporal alignment, but also by other spatial and environmental factors favoring situational integration, such as shared stimuli ([Hamilton, 2021](#)). In addition, there is an expectation that working toward a shared goal will bring about, and in turn be further facilitated by, increased IBS ([Szymanski et al., 2017](#)), as also confirmed in the duetting musicians ([Gugnowska et al., 2022](#)).

However, compared to the resting state, each of the person's perspective on the shared environment is unique and distinctive, and they will need to regulate their specific actions accordingly. Moreover, even if the task were to involve synchronized identical gestures, such as during action imitation, there is an added element of subjective involvement if imitation occurs spontaneously ([Dumas et al., 2012](#)). From the perspective of irruption theory, this individually and socially motivated increase in subjective involvement would manifest as increased neural entropy at the individual brain level, which would presumably show up as lower power at the intra-brain level and lower synchrony at the inter-brain level. For example, consider a musician's brief disassociation from duetting, e.g., by making an unexpected change independently of the other's behavior. This constitutes an individual perturbation to their joint performance followed by coordinated compensatory adjustments. As we would expect, the immediate decrease in socially motivated subjective involvement is characterized by relatively higher IBS, while the subsequent socially motivated re-alignment stands out because of its relatively higher IBD ([Lender et al., 2023](#)).

As a basic proof of concept, we tested these ideas with a highly simplified model of the general EEG hyperscanning situation, following previous modeling work that used Kuramoto oscillators for this purpose (e.g., [Dumas et al., 2012](#); [Heggli et al., 2019](#); [Loh and Froese, 2021](#); [Moreau et al., 2022](#)). Each artificial "brain" consisted of 10 oscillators with intra- and inter-brain coupling strengths set to 1 and 0.5, respectively. Apart from the lower coupling strength of inter-brain coupling, we did not impose any further "behavioral bottleneck"

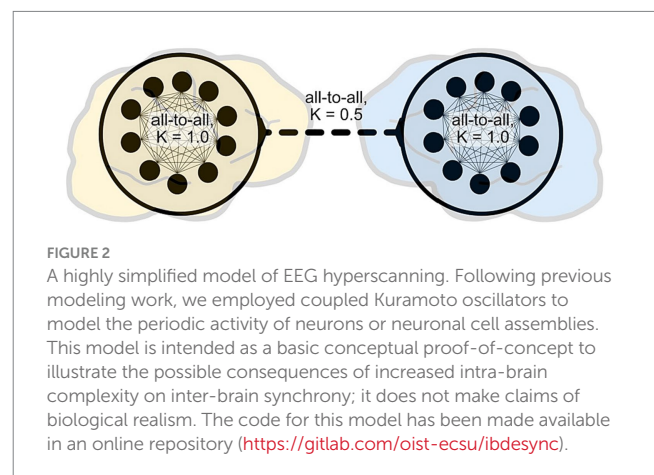
([Kingsbury and Hong, 2020](#)) to avoid biasing the model against IBS ([Figure 2](#)).

The proposed situation of an irruption-based increase in neural entropy, as a manifestation of subjective involvement in social interaction, was modeled in terms of an availability of a broader range of neural frequencies. Note that this increase in neural state space is a conservative choice of modeling irruptions, because their disordering impact may be better captured by an increase in aperiodic neural activity. We compared two conditions C1 and C2: in C1 the natural frequency range of was taken from a uniform distribution of [39, 41], whereas in C2 the range was wider [30, 50]. Each condition was simulated 1,000 times; IBS was calculated using the circular correlation coefficient (CCorr), as advocated by [Burgess \(2013\)](#), and all correlation coefficients were averaged per condition. We found that in C2, compared to C1, the average intra-brain CCorr decreased by more than half, and as expected the inter-brain CCorr also decreased, namely by nearly an order of magnitude (C1: 0.32. C2: 0.045). To be fair, this is only the most minimal proof of concept. Future work could test our predictions more systematically by implementing models with biological realism, and with targeted analysis of experimental data.

4 Discussion

Social neuroscience approaches have been predicting that increased social engagement and interpersonal integration, such as shared goals in joint action ([Zamm et al., 2023](#)), is generally associated with increased IBS across brains and bodies. We have complemented this standard prediction with the working hypothesis of irruption theory, namely that increased subjective involvement will manifest as increased neural entropy ([Froese, 2023](#)), and hence will act as a countertendency of desynchronization in the intra- and inter-brain levels of analysis.

If our theoretical perspective is on the right track, we may wonder why there is not yet significant evidence for the importance of IBD in social interaction, especially when compared to well-known findings of IBS. On the one hand, it is possible that the effect of IBD is equivalent to IBS, thereby leading to null results after averaging, or perhaps the effect of IBD is comparatively smaller when compared to IBS. However, given the field's strong bias toward finding IBS as the main marker of social interaction, concerns have already been raised



that this narrow focus may fail to capture other relevant features (Hamilton, 2021), and that there may have been a factor of IBS “confirmation bias” (Holroyd, 2022). Possibly, null results or contrary findings of significantly increased IBD that did not fit theoretical expectations perhaps did not reach publication stage. It is our hope that this perspective piece helps to broaden the range of hyperscanning findings that can be predicted and interpreted.

Could IBD have a positive role to play in itself? We suggest that IBD is accentuated when the normative conditions guiding behavior are not limited to one person, but are distributed over two or more individuals. Prime examples are turn-taking and giving-taking kinds of social interaction, in which success of one’s behavior is dependent on the other’s complementary behavior (De Jaegher and Di Paolo, 2008). In these situations, irruption theory predicts that the increased subjective involvement in social interaction will have the paradoxical effect of impeding the neural basis of social integration. This injection of IBD in the context of increased IBS may seem counterproductive at first, but it could facilitate the kinds of flexible cognitive-behavioral transitions that characterize normal social coordination (Di Paolo and De Jaegher, 2012). And, conversely, a neural mechanism for the prevention of excessive social integration could be essential for the maintenance of mental health, and may be impaired in some conditions (Galbusera et al., 2019; Froese and Krueger, 2021).

Variability of IBS over time has been known about for some time (Dumas et al., 2010), but it has only recently received renewed attention in the hyperscanning literature (e.g., Li et al., 2021; Haresign et al., 2022; Wikström et al., 2022). Future work could aim to systematically quantify IBS variability as the expected multi-brain signature of a healthy, spontaneously motivated social interaction. We suggest that IBS variability should be understood as the natural expression of the flexible balancing required to coordinate two competing dynamical tendencies, namely IBS and IBD, which are associated with interpersonal integration and subjective involvement, respectively.

Data availability statement

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

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Conflict of interest

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The role of self-representation in emotional contagion

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Although prior research has implied that emotional contagion occurs automatically and unconsciously, convincing evidence suggests that it is significantly influenced by individuals' perceptions of their relationships with others or with collectives within specific social contexts. This implies a role for self-representation in the process. The present study aimed to offer a novel explanation of the interplay between social contexts and emotional contagion, focusing on the contextualized nature of self-representation and exploring the social factors that shape emotional contagion. It further posits a causal loop among social contexts, self-representation, and emotional contagion. Drawing from the lens of self-representation, this study concludes with a discussion on potential research directions in this field, commencing with an exploration of the antecedents and consequences of emotional contagion and self-representation.

KEYWORDS

emotional contagion, self-representation, social context, self-concept, interpersonal relationship

Introduction

Emotional contagion, a phenomenon where our emotions are unconsciously influenced by those of our social surroundings (Hatfield et al., 1993), particularly those closest to us, serves as a vital catalyst for social cohesion. This natural process facilitates the rapid transmission of social signals and is innate, evident even in infancy, as infants often respond by crying to the sounds of other crying babies (Herrando and Constantinides, 2021; Salvadori et al., 2021). Emotional contagion is characterized by affective synchrony, manifesting in various levels of synchrony in emotional experience, expression (such as facial and postural expression), and neural and physiological processes (Hatfield et al., 2009). When two individuals' emotions are dynamically aligned in both form and timing, we refer to this state as affective synchrony, a good indicator of emotional connection and understanding (Wood et al., 2021).

Emotional contagion and empathy share a core feature: a shared emotional experience. However, empathy is a more comprehensive concept that extends beyond emotional contagion. Despite their similarity in shared emotional experiences, they differ in their underlying mechanisms. Empathy comprises two distinct systems: affective empathy and cognitive empathy. Like emotional contagion, the former refers to the automatic emotional response evoked by observing another person's emotional state (Heyes, 2018). The latter, on the other hand, involves a more intricate process of cognitive control (Isern-Mas and Gomila, 2019). Hatfield et al. (2009) emphasized one aspect of empathy as the ability of people to "feel themselves into" another's emotions via emotional contagion. According to Hatfield et al. (2009), the primary distinction between empathy and emotional contagion lies in the element of self-other distinction. Empathy involves a clear distinction between

oneself and others, whereas emotional contagion operates at a subconscious level, without such discrimination. Instead, it relies on a form of “total identification” where the feelings of the self and others overlap, reflecting an innate ability to resonate with the emotions of others (Decety and Moriguchi, 2007; Håkansson Eklund and Summer Meranius, 2021).

The mirror neuron system (MNS) serves as a potential neural foundation for emotional contagion, bridging the gap between perception and action (Likowski et al., 2012; Paz et al., 2022). Although emotional contagion appears to occur automatically, it is not a purely bottom-up process or reflexive imitation. Several studies suggest that the process of emotional contagion is modulated by various social contextual factors such as relationship intimacy (Kimura et al., 2008; Wróbel, 2018; Lin et al., 2024), social similarity (Stockert, 1994; Paukert et al., 2008), and group identity (Joby and Umemuro, 2022). These results demonstrate that the social connection between interacting partners is a prerequisite for emotional contagion. That is, emotional contagion is more likely to occur in an affiliative social context but is attenuated or absent for those reluctant to interact (Hatfield et al., 2014; Hess, 2021). Thus, emotional contagion is a special emotional reaction of the “self” to the emotions of others (Isern-Mas and Gomila, 2019), a process involving the integration of self-representation and other representation in the social context.

According to embodied simulation theory, individuals simulate others’ emotions through the activation of shared neural and physiological representations between themselves and others, which mirror the others’ emotions, leading to vicarious emotional experience (Gallese, 2006). In essence, the effect of social context on emotional contagion is based on how individuals perceive their relationships with others. This perception is closely linked to their self-representation (Cross et al., 2011). Self-representation involves an individual’s self-perception and how they present themselves to the external world (Thagard and Wood, 2015). How people define themselves in relation to others significantly influences their thoughts, emotions, and behaviors, ultimately modulating perception and understanding of others’ emotions in social interactions (Markus and Wurf, 1987; Fischer et al., 2004; Wang et al., 2015).

Therefore, this study emphasizes the pivotal role of self-representation in emotional contagion. It serves not only as a cognitive framework for perceiving and interpreting the emotions of others but also as a modulator of emotional contagion based on the perceived social relationships within a given context. This review integrates this line of research, exploring how self-representation shapes emotional contagion and how it evolves in diverse social settings. Importantly, previous research has primarily focused on self-other relationships as prerequisites for emotional contagion, overlooking the potential for emotional contagion to, in turn, reshape these relationships. We aim to bridge this gap by synthesizing relevant studies and discussing the dynamic interplay between social context, self-representation, and emotional contagion. This interplay not only affects how we perceive and respond to the emotions of others but also how our relationships evolve over time. Future research directions are also outlined, emphasizing the need to further investigate the complex interplay between social context, self-representation, and emotional contagion. By doing so, we can gain a deeper understanding of the psychological mechanisms underlying social interactions and the role of emotional contagion in shaping our social world.

How are people contagious to others’ emotions?

The Neurocognitive Model of Emotional Contagion underscores the significance of dynamic synchronization activities between two interacting brains in the emergence of emotional contagion. This synchronization arises from the shared neural activities between individuals (Prochazkova and Kret, 2017). Infants, for instance, demonstrate this ability to share emotions through shared representations of their own and others’ behaviors (Herrando and Constantinides, 2021; Salvadori et al., 2021). By mimicking facial expressions, they not only perceive but also empathize with the emotions of those around them (Decety and Sommerville, 2003). In essence, emotional contagion reflects a match between the perceptions of others’ emotions and their feelings, representing a form of shared representation (Preston and Waal, 2002; Teufel et al., 2010).

Self-other shared representation refers to the phenomenon in which individuals share similar representations or models in cognition, emotion, or behavior with others (Decety and Sommerville, 2003). Individuals create shared cognitive frameworks by mapping emotions onto others, leading to shared emotional experiences (Gallese, 2006). Neuroimaging studies have provided compelling evidence for this shared neural representation. For instance, when an individual experiences disgust or pain, the same brain regions are activated as when observing others experiencing these emotions (Wicker et al., 2003; Singer et al., 2004). The shared neural representation, supported by the MNS, bridges the gap between self and others. This enables individuals to comprehend the intentions of others and share their emotional experiences in a manner that goes beyond the self, allowing the “other” to become another “self” (Ferrari and Gallese, 2007).

However, emotional contagion in real life is not a perfect replication of other’s emotional experiences, as each individual’s mental imagery is inevitably colored by their unique life experiences, making it impossible to grasp the exact emotional state of another person entirely. This limitation is a testament to the silent yet significant effect of self-representation on emotional contagion (Arizmendi, 2011). Indeed, the role of self-representation in emotional processing becomes even more evident when considering studies on mental disorders. For instance, individuals with autism spectrum disorders often exhibit abnormalities in brain function activation when recognizing their own faces or attempting to comprehend the emotions of others (Dapretto et al., 2006; Kita et al., 2011). These findings underscore the crucial role of a well-functioning self-representation system in establishing and maintaining emotional connections with others. Moreover, the interdependence between self-representation and emotional contagion becomes apparent.

Overlapping neural substrates of emotional contagion and self-representation

Humans have the ability to understand and perceive the emotions of others by invoking neural activity or internal simulation associated with their own emotional experiences (Preston and Waal, 2002). This suggests that there may be overlapping neural mechanisms involved in both self-related processing and the processing of others’ emotions. Although self-related processing is multifaceted and encompasses

aspects ranging from conceptual to bodily, core brain regions emerge as the nexus of this multifaceted self-concept. [Hu et al. \(2016\)](#) performed activation likelihood estimation (ALE) meta-analyses to investigate this shared neural representation, focusing on the physical and psychological self. They found that the dorsal anterior cingulate gyrus (dACC), left inferior frontal gyrus (IFG), and insula are key regions involved in self-representation.

These regions are also crucially involved in emotional contagion. For instance, some neuroimaging studies revealed that the insula and dACC were activated when individuals observed others' emotions ([Singer et al., 2004](#); [Cheng et al., 2010](#)). Furthermore, compared to strangers, the intensity of activation in these brain regions is greater when perceiving the emotions of a close one, which may imply that self-related stimuli can easily be mapped to one's representation system. The IFG has been demonstrated to play a crucial role in self-representation ([Sugiura et al., 2000](#); [Uddin et al., 2005](#)), and there is also consistent evidence for the involvement of the IFG in emotional contagion ([Shamay-Tsoory, 2011](#)). [Jabbi et al. \(2007\)](#) found that observing positive and negative facial expressions activated parts of the IFG, and another study showed that cortical lesions involving the IFG are associated with impaired emotional contagion and deficits in emotion recognition ([Shamay-Tsoory et al., 2009](#)).

Another overlapping network for emotional contagion and self-representation is the MNS, including the IFG, inferior parietal lobule (IPL), insula, and supplementary motor area (SMA). [Molnar-Szakacs and Uddin \(2013\)](#) argue that understanding self and others belongs to the same system. By prioritizing access to our own physical and mental states, we can then better understand the physical and mental states of others through embodiment and mentalizing, and the MNS and default network both support these cognitive processes ([Wu et al., 2015](#)). MNS provides a simulating mechanism for emotional contagion, whereby we understand others' behavior and emotions by "embodying" them ourselves ([Gallese and Sinigaglia, 2011](#)). The observer's MNS uses a mechanism that resembles an imitation mechanism to process others' emotions. In this process, other's emotional states are mapped to the observer's motor repertoire. If the other person is more similar and familiar to the observer, the mapping mechanism produces a better fit, resulting in increased neural

resonance. [Figure 1](#) shows the overlapped brain regions between self-representation and emotional contagion.

Emotional contagion and self-representation in a social context

Effect of social context on emotional contagion

Emotional contagion is not merely a replication of feelings; rather, it is a complex phenomenon influenced by a person's cognition, past experiences, and various social contexts and cues ([Hatfield et al., 2014](#)). Interpersonal relationships play a pivotal role in shaping emotional contagion, and the effectiveness of emotional information transmission during social interactions hinges on individuals' perception of their relationship with others. People are more prone to experiencing emotional resonance with those who share affiliations with them, such as members of their ingroup, partners, or individuals with collaborative intentions. A study conducted by [Wróbel \(2018\)](#) manipulated the closeness of relationships to investigate its impact on emotional contagion. The findings revealed that "second-hand" happiness, where senders watched emotional videotapes and subsequently transmitted their perceived emotions to receivers, occurred exclusively among friends and not among strangers. More recently, [Lin et al. \(2024\)](#) investigated the influence of interpersonal closeness on the intensity of emotional contagion and physiological synchrony between interacting partners. In this study, pairs of friends and strangers participated, with the sender watching a film clip while the observer passively observed the sender's facial expressions. The results demonstrated that under conditions of positive emotion, more significant emotional contagion and physiological synchrony (in terms of heart rate and heart rate variability) were more likely to occur among friend dyads compared to stranger dyads. Furthermore, relationships can also modulate neural synchronization during emotional interactions. Romantic partners, for instance, exhibit greater behavioral synchronization and brain-to-brain neural synchrony during emotional communication compared to strangers ([Kinreich et al., 2017](#)). This underscores the intricate interplay

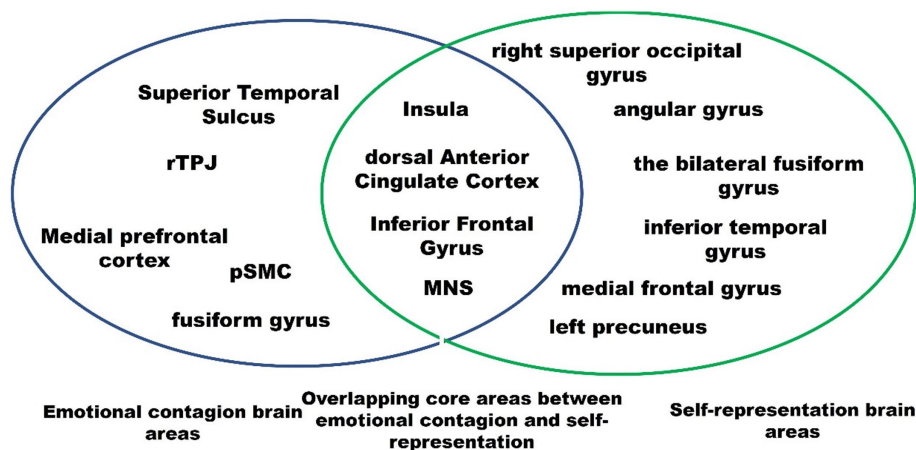


FIGURE 1
Overlapping core brain regions of emotional contagion and self-representation.

between interpersonal relationships and the dynamics of emotional contagion.

Other factors, such as social power within interpersonal relationships, have also been shown to influence the dynamics of emotional contagion (Kimura et al., 2008). Beyond interpersonal bonds, the impact of social identity, especially in the context of group membership, has been identified as a significant factor in emotional contagion. This was evident by Joby and Umemuro (2022) which reveals that emotional contagion and favorable social attitudes, including trust, empathy, liking, bonding, and prosocial orientation, are notably more prevalent within ingroup interactions compared to out-group interactions. This suggests that the nature and strength of our social bonds and our perception of group membership play a crucial role in shaping our emotional responses and the transmission of emotions within social groups.

Social context and the self: contextualized self-representation

Self-concept, as described by James (2018), is a multifaceted construct that can be represented in various forms. Sedikides and Brewer (2001) identified three fundamental types of self-representation: the individual self, the relational self, and the collective self. The individual self encapsulates those aspects that distinguish a person from others, highlighting their unique characteristics and identity. In contrast, the relational self emphasizes the similarities between one's representation of self and others. It incorporates attributes shared with close individuals and defines the roles within dyadic relationships. The collective self, on the other hand, encapsulates an individual's intergroup aspect. It comprises attributes that are shared with members of the ingroup and differentiated from outgroups, reflecting one's membership in a particular social group (Brewer and Gardner, 1996; Sedikides et al., 2011). The relational self and the collective self can be collectively referred to as the social self. This aspect of self-representation captures the overlap between one's representation of self and others (Ellemers et al., 2002). Importantly, these three types of selves coexist, and individuals can switch between perceiving themselves as distinct individuals, relational partners, or interchangeable group members. Therefore, self-representation serves not only for self-awareness but also to represent the self-other relationship and interpersonal interactions (Tsakiris, 2017).

However, the dominance of a particular self-representation depends on an individual's motivational state or contextual factors (Andersen and Chen, 2002). For instance, when an individual's group identity is emphasized, the collective self becomes prominent (Turner et al., 1987). Similarly, when we are in the presence of a significant other, memories related to the self and that significant other, both in abstract and experiential forms, are activated, manifesting as the relational self (Hinkley and Andersen, 1996).

Interaction between social context and emotional contagion: the role of self-representation

Humans are constantly engaged in the construction and reconstruction of their social selves throughout their lifetimes. This

process is deeply influenced by social interactions, life experiences, and feedback from others. The self-concept is a dynamic and ever-evolving representation that adapts and changes in response to these diverse inputs (Mead, 1913; Oyserman et al., 2012).

Social contextual cues and individual motivational states play a crucial role in shaping self-representation. For instance, when individuals are immersed in close relationships, the relational self, characterized by a strong preference for interpersonal connection, becomes particularly prominent (Aron et al., 2013). A key aspect of the relational self is the overlap between self and others, which occurs through a process of self-expansion. In this process, individuals integrate resources, and perspectives of other individuals into their self-concept, emphasizing the representational similarities between the self and others (Aron et al., 1991; Zi and He, 2019).

Driven by the motivation for self-expansion, the boundaries between self and others are often redefined, leading to updates in self-representation that reflect the relationship between the self and others. This expansion of the self-concept results in a shared cognitive construction of the self and others, where it becomes difficult to distinguish memories and traits that are relevant to the self from those that are relevant to close others (Mashek et al., 2003).

Furthermore, this expansion facilitates the brain's ability to represent the perceived emotions of others as if they were the emotions of the self. For instance, in close relationships, people tend to internalize their partner's positive emotions as their own (Meixner and Herbert, 2018). fMRI studies have provided further evidence that when individuals perceive the emotions of significant others, brain regions associated with self-representation functions are more strongly activated, and the activation pattern is similar to when they experience the emotions themselves (Singer et al., 2004; Cheng et al., 2010). In contrast, non-affiliative relationships (e.g., hostile or competitive relationships) tend to activate the individual or independent self-representation (Cristina-Corina, 2012), resulting in less emotional resonance or even opposite emotional responses (Lanzetta and Englis, 1989; Wróbel and Imbir, 2019).

The influence of self-representation on emotional contagion extends beyond individual interactions to encompass group dynamics. Gardner et al. (2002) found that the activation of the collective self leads individuals to perceive the success of group members as a positive event, while the activation of the individual self may evoke unpleasant feelings in response to such success. Individuals with a strong sense of belonging to a group tend to merge their personal identity with that of the group, resulting in a blurred boundary between the individual self and the collective self (Swann et al., 2012). This process reflects a shift from an emphasis on the individual self to an emphasis on group identity within the self-concept. According to social identity theory (Hogg, 2016), people derive a sense of self-esteem and identity from their membership in social groups, and a highly integrated self is characterized by a strong identification with the group and prioritization of group identity over personal identity (Liu et al., 2022). Therefore, when the collective self dominates, people are more likely to understand and view the world based on group members' perspectives, accept the group's views and emotions, and value the connection with the group (Hareli and Rafaeli, 2008; Blocker and McIntosh, 2017; Han, 2018).

Emotional contagion is not only a natural outcome of social interactions but also an antecedent that can profoundly shape

interpersonal relationships and social behavior. It occurs when individuals unconsciously catch and reflect the emotions of those around them, often leading to a shared emotional experience. This process not only strengthens social bonds but also alters one's perception of self and others. Indeed, emotional mimicry, a common behavior associated with emotional contagion, involves unconsciously mirroring the facial expressions and gestures of others. Studies have demonstrated that this mimicry enhances feelings of affiliation and closeness between interaction partners (Cheung et al., 2015; Hess et al., 2016). Those who engage in emotional mimicry tend to develop a self-concept that is more interdependent, emphasizing the importance of interpersonal relationships and the prioritization of others' emotions and needs (Chartrand and Bargh, 1999). Even mere action imitation can alter interactants' self-concept, with the mimicked individual's self-concept becoming more interdependent and the imitator experiencing enhanced feelings of interdependency (Ashton-James et al., 2007; Hamilton, 2017). Furthermore, emotional contagion goes beyond mere mimicry. It involves a deeper level of self-involvement, where individuals share feelings with others, even for brief moments, strengthening their emotional connection (Mariadhas, 2019; Mayo et al., 2023). This shared emotional experience can have great effects on individuals' sense of self and their relationships with others.

Another notable aspect of emotional contagion is its ability to induce synchrony in attention, emotion, and behavior. When people are emotionally synchronized, they are more likely to perceive themselves as part of a larger group or collective, blurring the boundaries of independence (Good et al., 2017). This affective synchrony enhances not only emotional integration but also perceptual coherence, bridging the psychological distance between individuals and fostering a sense of "we" rather than "you" and "I."

Overall, emotional contagion is a process that is complicated and linked to self-experience. The way individuals respond to the emotions of others is significantly influenced by their perception of their relationships, which involves alterations in their

self-representation. Social contexts play a pivotal role in regulating emotional contagion by shaping an individual's self-representation. Specifically, self-representation is dynamically constructed and activated during interpersonal interactions, contingent on the prevailing social contexts. This, in turn, affects their emotional perception, cognitive functions, and information processing, ultimately either enhancing or weakening their capacity to perceive and comprehend the emotions of others and exhibiting adaptive emotional responses. Conversely, emotional synchrony facilitates connection and mutual understanding between individuals, shaping how they view themselves and others. This shift strengthens emotional bonds among individuals, thereby influencing their social behavior (see Figure 2).

Conclusion and future directions

This study integrates theories and empirical research from self-concept and emotional contagion to propose a mechanism that explains the interaction between social context and emotional contagion, emphasizing the crucial role of self-representation. Drawing inspiration from embodied simulation theory, we posit that the capacity to share in others' emotions is also rooted, at least in part, in self-representation. When an individual perceives the emotions and actions of others, internal self-representations associated with these experiences are activated, as if the observer were experiencing them directly (Gallese, 2006). Moreover, a significant and novel aspect of our proposal lies in its articulation of the dynamic interplay between emotional contagion and social context. The social context shapes individuals' emotional responses to the emotions of others by activating specific self-representations. In short, when individuals are situated within a particular social context, they may become aware of their identity, roles, or relationships within that setting, and contextualized self-representation is activated. Consequently, their emotional responses and behaviors are influenced by these activated

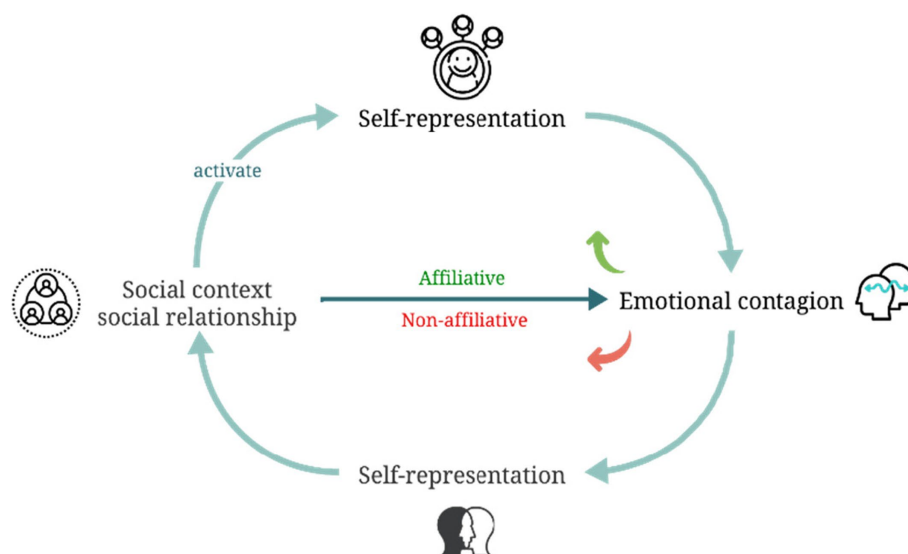


FIGURE 2

Schematic representation of the interplay between social context, self-representation, and emotional contagion.

self-representations. Additionally, the downstream effects of emotional contagion manifest in the enhancement of interdependent self-representation, which in turn fosters social connection. This underscores the intricate link between emotional contagion, self-representation, and social context, highlighting the dynamic and interactive nature of these processes.

Based on the dynamic interplay between social contexts, self-representation, and emotional contagion, several future research directions are proposed. First, while we have established the relationship between these constructs through empirical research and theory, there is still a need for direct evidence validating this model. Future studies can explore how self-representation shapes emotional contagion in social interactions. For instance, it would be interesting to investigate whether specific social contexts trigger different forms of self-representation, such as a relational or individual self, and how these forms predict an individual's susceptibility to emotional contagion from others.

Second, longitudinal studies could be conducted to assess the evolution of self-expansion and its impact on emotional contagion across various stages of interpersonal relationships. Such studies would provide valuable insights into the dynamic and interactive nature of these processes, allowing us to better understand how changes in self-representation affect emotional contagion over time.

Third, although previous research has demonstrated the top-down modulating effects of social relationships on emotional contagion (Kimura et al., 2008; Wróbel, 2018; Franklin, 2019), there is a need to further explore the reverse relationship. Few studies have examined how emotional contagion influences social relationships and other prosocial behaviors. Future research should aim to investigate the bidirectional nature of this relationship and explore whether contextualized self-representation plays a role in mediating these effects.

Fourth, while much of the existing research has focused on interpersonal emotional contagion, it is important to recognize that emotional contagion can have significant effects on intergroup and ingroup behaviors in organizations. Future research should explore the extent to which emotional contagion influences intergroup dynamics, such as group cohesion, cooperation, and conflict resolution. This line of study has the potential to yield important insights into how emotional contagion can shape organizational behavior and performance.

Finally, it would be interesting to explore the role of cultural factors in shaping the relationship between social context, self-representation, and emotional contagion. Different cultures may have distinct norms and values that influence how individuals perceive themselves and others, which could, in turn, impact the extent of emotional contagion within those cultures.

In summary, these future research directions offer opportunities to further understand the complicated relationships between social contexts, self-representation, and emotional contagion. By addressing these gaps, we can gain deeper insights into the mechanisms underlying emotional contagion and its impact on social interactions and relationships.

Data availability statement

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

Author contributions

DW: Conceptualization, Writing – original draft, Writing – review & editing. CL: Writing – review & editing. WC: Writing – review & editing, Conceptualization, Funding acquisition, Supervision.

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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.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

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Effects of individual practice on joint musical synchronization

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Successful music-making requires precise sensorimotor synchronization, both in individual (solo) and joint (ensemble) social settings. We investigated how individual practice synchronizing with a temporally regular melody (Solo conditions) influences subsequent synchronization between two partners (Joint conditions). Musically trained adults practiced producing a melody by tapping on a keypad; each tap generated the next tone in the melody. First, the pairs synchronized their melody productions with their partner in a baseline Joint synchronization task. Then each partner separately synchronized their melody with a computer-generated recording of the partner's melody in a Solo intervention condition that presented either Normal (temporally regular) auditory feedback or delayed feedback (by 30–70 ms) in occasional (25%) randomly placed tone positions. Then the pairs synchronized again with their partner in a Joint condition. Next, they performed the second Solo condition (normal or delayed auditory feedback) followed again by the Joint condition. Joint synchronization performance was modeled with a delay-coupled oscillator model to assess the coupling strength between partners. Absolute asynchronies in the Solo Intervention tasks were greater in the Delayed feedback condition than in the Normal feedback condition. Model estimates yielded larger coupling values between partners in Joint conditions that followed the Solo Normal feedback than the Solo Delayed feedback. Notably, the asynchronies were smaller in the Joint conditions than in the Solo conditions. These findings indicate that coupled interactions in settings of two or more performers can be improved by individual synchronization practice.

KEYWORDS

musical synchrony, social interaction, duet synchronization, practice effects, delaycoupling

1 Introduction

A primary goal of musical ensembles is to create a synchronous performance with fellow musicians. However, the majority of musical practice is accomplished individually, prior to an ensemble performance. How do solitary practice conditions influence subsequent joint performance? Auditory-motor synchronization, the simultaneous production of sound with a perceived auditory stimulus, can play a vital role in the perceived pleasantness of music (Bégel et al., 2022). We focus here on musical synchrony among partners; synchrony among species members is found in many life forms (Moiseff and Copeland, 2010) that display a simultaneous production of action with sound (Strogatz and Stewart, 1993; Large et al., 2015). Social interaction among group members also influences musical synchrony. For example, comparisons of individuals who synchronized with a metronome or with a partner changed the temporal predictability and adaptation of the partner's behavior (Dumas and Fairhurst, 2021). Social interaction in musical groups requires strong coordination and is often

characterized by coupled physiological systems (Delius and Mueller, 2022). Fewer studies have examined how individual practice helps musicians improve their ability to synchronize with others. The current study addresses how individual synchronization practice influences joint performance in dyadic synchronization among musicians.

1.1 Learning effects in music performance

A few studies have examined the impact of types of musical practice on the development of music performance skills. Caramiaux et al. (2018) investigated effects of tempo variability and different learning regimens in non-musician participants' improvement in timing and motor skills during piano performance. Non-musicians were trained with different types of piano practice and then performed novel finger sequences on a piano keyboard. The performers' timing displayed greatest improvement when the tempo during learning matched the tempo during transfer to the novel melodies. Furthermore, the study found a carryover effect of previously acquired skills in transfer to novel melodies, regardless of the movement task complexity. Thus, Caramiaux et al. (2018)'s finding suggest that musical practice can improve subsequent performance regardless of the mechanical difficulty; improvement was found from learning task to subsequent transfer task, whether the consistent tempo was fast or slow.

Stambaugh (2011) examined the impact of different practice conditions on musicians' solo performance. Novice clarinetists learned novel melodies in blocked or random practice conditions. Participants in the random condition completed six trials of each of the 3 melodies in a random order on each day of the practice. Participants in the blocked condition performed a single melody for 18 trials on each day of the practice. Outcomes were judged by the clarinetists' performance accuracy, tempo, temporal evenness and attitude. The assessment of learning effects was done on the last trials of the final day, while retention was evaluated 24 h after the last day. Differences between the blocked and random training were found only in the performance tempo. The group in the random condition showed a higher playing tempo during retention and maintained their accuracy, in contrast to the blocked group. This suggests that the random interleaving of practice can enhance subsequent performance.

Bégel et al. (2024) addressed the causal relationship between practice in dyadic musical synchronization and subsequent solo synchronization. Pairs of musician and non-musician participants took turns synchronizing their melody by tapping with a metronome (each tap generated the next melody tone). In the Joint Intervention conditions, participants attempted to synchronize their melodies simultaneously with their partner either with normal auditory feedback (normal feedback) or with randomly placed delayed feedback on 25% of melodic tones (delayed feedback). After each Intervention, the turn-taking condition of synchronizing with the metronome was repeated. Partners' asynchronies with the metronome were larger following the delayed feedback performances than following the normal feedback performances. Furthermore, partners' social interaction ratings of connectedness, relationship with their partner, and synchronization judgments were reduced after the delayed feedback condition relative to the normal feedback condition. These findings suggest that practice with a partner increases synchrony

that carries over to subsequent individual performance. We ask the reverse question in this study: Does individual practice affect subsequent dyadic performance with a partner?

1.2 Learning and reliance on auditory feedback

A key factor in music performance training is a reduced reliance on auditory feedback to guide future actions. For example, musically trained individuals can perform familiar music accurately in the absence of auditory feedback (Finney, 1997; Repp, 1999), and beginners rely on that feedback during practice more so than advanced musicians (Luciani et al., 2022). Other studies have confirmed that auditory feedback is critical for initial learning of novel musical pieces but is relatively independent at retrieval, once learned (Finney and Palmer, 2003). One explanation for this is that auditory imagery can reduce a performer's reliance on auditory feedback (Highben and Palmer, 2004; Bishop et al., 2014).

Group music-making forces a higher reliance on auditory feedback in order for musicians to perceive one's own performance outcomes relative to those of other musicians. Interaction among musical group members requires them to distinguish sounds produced by oneself from those produced by others (Keller et al., 2016). Studies have addressed distinctions between self-other integration and self-other segregation in trained musicians (Liebermann-Jordanidis et al., 2021). We address here the extent to which individual practice that enables musicians to distinguish their own actions from a recording, via manipulations of auditory feedback, influence the subsequent balance of self-other integration and segregation in joint performance.

1.3 Synchronization models of joint performance

Musically trained individuals tend to show smaller asynchronies of their tone productions with a regular auditory stimulus than do untrained individuals (Repp and Su, 2013), suggesting that long-term practice on a musical instrument improves synchronization. Large et al. (2015) proposed that sensory and motor networks interact to improve musical synchrony and the overall timing as individuals gain performance experience. A sensory (auditory) network and a motor network were modeled with nonlinear oscillators whose coupling strength increased as a function of the periodic signals encountered in musical stimuli. Participants tapped along with the perceived pulse in the melodies presented. Large et al.'s (2015) model predicted the perception of a regular musical beat at specific frequencies, consistent with the empirical findings. The model captured the degree of coupling between auditory and motor neural oscillations that influenced the participants' perception of a regular musical beat and synchronization. Musicians' increased auditory-motor interactions contribute to improved memory for musical sequences as well (Palmer, 2005; Mathias et al., 2015).

Several findings suggest that human synchronization with a regular auditory cue, such as a metronome, tends to be anticipatory, called a negative mean asynchrony (Repp and Su, 2013). Anticipation refers to the tendency for participants' tone onsets to occur earlier

than the tones with which they intend to synchronize. The integration of information at a central level from different sensory modalities was proposed to account for the anticipatory nature of synchrony in single-subject auditory-motor studies (*cf.* Aschersleben and Prinz, 1995; Castro-Meneses and Sowman, 2018). Other explanations of anticipatory behavior have been proposed that distinguish among internal states (Palmer and Demos, 2022): the first, weak anticipation, suggests the creation of an internal model that helps an individual to make predictions of future events and act on those predictions (Clark, 1997). The second explanation is strong anticipation, which assumes a relationship between an external stimulus “driver” oscillation, such as an auditory metronome, and an internal “driven” oscillation, such as a human (Voss, 2000). In this theory, one of the oscillators creates the oscillation while the other oscillation follows that oscillation at a time delay, predicting anticipation via a time-delayed memory of the system’s previous state (Stepp, 2009; Stepp and Turvey, 2010; Demos et al., 2019). These models, called delay-coupled oscillator models, have been applied to musical ensembles (Demos et al., 2019; Palmer and Demos, 2022) and to other physical systems (Machado and Matias, 2020) to explain coupling relationships and their influence on synchronization.

Demos et al. (2019) tested a strong anticipation model fit to the synchronization of dyadic partners’ musical performances. A bidirectional delay-coupling model was applied to the partners’ asynchronies as their auditory feedback was manipulated. Equation 1 shows the delay-coupled model applied to two partners’ relative phase values (measure of tone onset asynchrony). The bidirectional coupling permits interaction and synchrony of two oscillators (partners) that receive and adapt to the auditory feedback from themselves and from their partner (Stepp and Turvey, 2010; Bégel et al., 2022). Three parameters include ω , the oscillator’s intrinsic frequency (represented as period, the inverse of rate); a coupling term k that influences the amount of adaptation of one oscillator to another; and a time delay t (ms) that represents the system’s memory for a past state [for full constraints on the model’s parameters, see Demos et al. (2019) Supplementary materials].

$$\dot{\theta}_1 = \omega_1 + k_1(\theta_2 - \theta_{1,\tau 1}), \dot{\theta}_2 = \omega_2 + k_2(\theta_1 - \theta_{2,\tau 2}) \quad (1)$$

Demos et al. (2019) tested the model in musical duets by removing the auditory feedback matching one partner’s part (for example, the driven partner) from both partners to test the model’s ability to adapt to the leader role (the partner whose auditory feedback was not removed). Unidirectional coupling occurred when the partner whose feedback was removed (the “driven” partner) attempted to maintain their synchrony with the partner who is not able to adjust (the “driver” partner). Importantly, the driven partner showed anticipatory synchrony by performing slightly before the driver partner. The partners’ asynchronies were fit with the delay-coupled model whose findings showed a stronger coupling between partners when full feedback was present; a unidirectional coupling of the partner whose feedback was removed to the partner whose feedback was present; and no coupling when both partners’ feedback were removed. The degree of coupling corresponded to the size and directionality of the asynchronies among the partners across the auditory feedback conditions. Thus, this study illustrated that delay-coupled models of synchrony can address anticipatory behavior in terms of coupling

between partners, without the need for an internal model. We apply the model here to examine how the unidirectional coupling experience offered in solo synchronization with a computer-generated recording can influence bidirectional coupling that typically occurs in joint (dyadic) synchronization.

Alternative models have proposed that synchronization in a musical ensemble relies on a process of mutual correction and adjustment among the performers that can be defined via linear error correction factors (Wing et al., 2014; Jacoby et al., 2015). An error correction model was applied to the synchronization measures from members of two string quartets (Wing et al., 2014). The linear phase correction model showed that the other performers exhibited stronger correction of their tone onsets’ relative phase values to follow the leading part (the first violin). Estimates of the correction gain were slightly below the 0.25 chance value for 4 performers, considered an optimal value for minimizing the asynchrony variability.

Some synchronization models are built on the assumption of internal models that generate predictions for a partner’s actions. Keller et al. (2007) measured pianists as they synchronized with a recording of their own performance or a partner’s performance recording; asynchronies were reduced in the condition in which they synchronized with their own performance relative to other performances. These findings were interpreted as support for an internal model for one’s own performance, compared with a less precise internal model for other pianists’ performances. Van der Steen and Keller (2013) proposed the adaptation and anticipation model (ADAM), that posits both adaptive and anticipatory behaviors of sensorimotor synchronization. The ADAM model has been extended to duet performance, but it has not tested effects of learning on subsequent performance or comparisons between solo and joint performance. Thus, there remains a gap in understanding how individual synchronization practice influences synchronization in joint music performance.

1.4 Current study

The focus of the present study was to investigate the impact of learning interventions in which musically trained individuals synchronized their melodies with a computer-generated auditory recording of a partner’s melody, on subsequent joint performance. Adult participants with musical training participated in Solo practice conditions in which they synchronized with a computer-generated recording, followed by Joint Performance conditions in which they synchronized with a partner. In one Solo Intervention condition, normal auditory feedback was presented, and in the second Solo Intervention condition, auditory feedback was occasionally delayed on 25% of randomly placed tones; the order of the Solo Intervention conditions was counterbalanced across pairs. All participants performed both Solo interventions and in subsequent Joint performance conditions. Synchronization performance was measured during all Solo and Joint conditions. First, we predicted that synchronization in the Solo conditions would be worse for the occasional delayed auditory feedback than for the normal feedback. Second, we predicted that synchronization measures in the Joint performance conditions should improve more following the Solo intervention with normal feedback than delayed feedback. Third, we predicted greater coupling between partners in Joint

synchronization conditions that followed normal auditory feedback than delayed feedback, based on a delay-coupled bidirectional model (Demos et al., 2019) applied to the partners' asynchronies.

2 Methods

2.1 Participants

The participants were recruited from the Montreal community through Facebook and through the McGill community participant pool. All 50 participants (age range = 18–33 years, $M = 22.3$, $SD = 3.4$; 37 were female), referred to here as Musicians (years of training on a musical instrument = 6–16 years, $M = 10.2$, $SD = 2.4$) had at least 5 years of private instrumental musical training on their primary instrument in a classical Western style that includes the goal of synchronous tone onsets in joint performance. Participants were excluded if they exhibited hearing loss in a screening test or did not meet the study requirements to synchronize their taps with a regular metronome. Two additional participants were excluded due to data loss resulting from experimental error. An audiometry screening confirmed that participants had normal hearing in the frequency range of stimuli used in the experiment (<30 dB HL for single tones in the 125–750 Hz range). The study was approved by the McGill University Research Ethics Board for the duration of the research project.

2.2 Equipment and stimuli

Participants tapped an eight-note melody on a force-sensitive pad controlled with Arduino and connected to a Linux computer (Dell T3600 running Fedora 16) via MIDI. Participants heard the melodies through the headphones (AKG K240 Studio) in a marimba timbre (GM2, patch #13, channel #1;2; fixed velocity: 100) produced with a Roland Studio Canvas SD-50 tone generator and MOTU soundcard. Metronome beats were presented in a high-pitched woodblock timbre (GM2, patch #116, channel #4; fixed velocity: 127). Timing of the presented metronome sounds was controlled by the FTAP program (Finney, 2001). Delay between the tap onset on the force-sensitive pad to the tap being recorded, was less than 3 ms, which includes the signal passing through Arduino to M-Audio Uno MIDI device then into Linux internal delay and FTAP (Tranchant et al., 2022). The time delay from a finger tap on the Arduino pad to the start of the sound was less than 1.0 ms (Scheurich et al., 2018, Supplemental materials).

An ascending/descending melody in G major, composed of G4 – A4 – B4 – C5 – D5 – C5 – B4 – A4, was used for partner A's higher-pitched feedback in all experimental conditions. The same melody in G major, one octave lower (G3 – A3 – B3 – C4 – D4 – C4 – B3 – A3) was used for partner B's lower-pitched feedback in all experimental conditions. The G major melody was chosen for its familiarity and the pitch difference between the two melodies was created to ensure that each partner's melody could be differentiated by the participants.

Stimuli in both the Joint and Solo synchronization conditions were based on synchronization-continuation trials. Each trial began with 8 beats of a metronome sounded every 450 ms (C6) with a woodblock timbre, to set the initial tempo. Participants started tapping on the 9th beat and the metronome stopped after another 8 beats

while the participants continued to synchronize with their partners for 9.5 melody repetitions (76 taps) until the sound delivered to headphones ended, indicating the trial end. The data from each trial in all Solo and Joint performance conditions included the first 72 taps (9 repetitions) after the metronome ceased; the final 4 taps were excluded from analysis.

Additionally, stimuli in the Solo intervention conditions presented a computer-generated recording of one partner's melody with either Normal auditory feedback (temporally regular tone onsets) or Delayed auditory feedback. The Delayed Auditory feedback occurred in 25% of the tones (distributed evenly among the two melodies) and ranged from 30 to 70 ms with a mean delay of 50 ms. The delay was pseudo-randomly positioned in the melodies to avoid the initial and final tones in each trial.

2.3 Design

Each pair of participants performed all tasks in this within-subject design. The experiment consisted of two different synchronization tasks: A Joint performance task and a Solo intervention task. The Joint performance task occurred three times and alternated with the Solo intervention task which occurred twice. The order of tasks is shown in Figure 1. The three Joint performance conditions are referred to Baseline Joint (initial condition), Post-Delay Joint (following the Delayed Auditory Feedback) and Post-Normal Joint (following the Normal Auditory Feedback). As shown in Figure 1, the conditions alternated in order to measure the impact of the interventions on the subsequent Joint performance.

The order in which the partners received the two Solo intervention conditions was counterbalanced across pairs. Additionally, the order in which the two partners assigned to upper or lower melody (A or B) performed the Solo intervention conditions was counterbalanced across pairs. Each of the Solo intervention and Joint performance conditions contained one practice trial and 3 experimental trials.

2.4 Procedure

Two randomly paired participants were scheduled to take part in the experiment at the same time. Upon arrival, participants completed a consent form and the audiometric screening in which pitches in the range of 250–750 Hz were presented; participants' auditory thresholds were <30 dB SPL. The two participants were then invited to join their partner in the same testing room where they faced each other at two separate tables, each with its own force-sensitive pad setup. A screen was placed between them so that they could only see their partner's head and shoulders, to avoid visual influence of the partners' finger movements. Partners tapped on a force-sensitive pad using the index finger on their dominant hand. They were told that each tap would produce the next tone in the melody. Each participant was explicitly instructed to synchronize their taps with the tones they heard from their partner over headphones. The partner who produced the low-pitched melody was labeled as partner A while the one with the high-pitched melody was labeled as partner B. All participants first practiced tapping their melody (24 taps or 3 melody repetitions) before the start of the trials. Then the two partners took turns synchronizing their melody with the metronome beats.

Baseline → Solo Interv1 → Joint1 → Solo Interv2 → Joint2

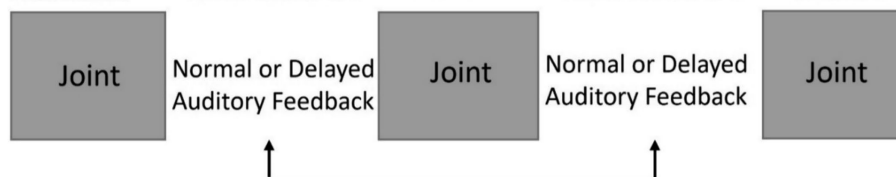
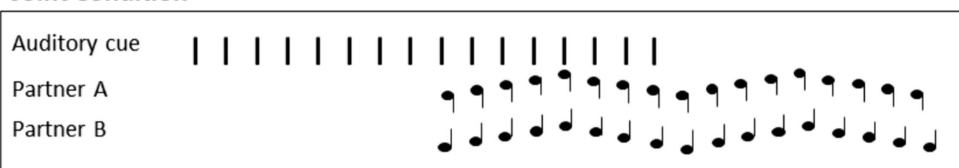


FIGURE 1

Order of the Solo Intervention conditions and the Joint synchrony conditions. Half of the partner dyads performed the Interventions in the two different orders.

Joint Condition



Solo Condition, Delayed feedback

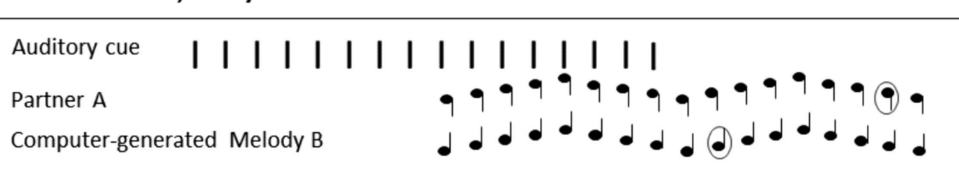


FIGURE 2

Example trials in the Joint performance and Solo-Delayed feedback conditions.

Next, the partners performed together in the Joint Performance Task (Figure 2) in which they were asked to tap together in synchrony with the metronome and to continue tapping together after the metronome ended until the sound heard over headphones ceased. After at least one practice trial and three experimental trials, the Joint performance condition was completed and participants advanced to the first Solo Intervention condition (Normal or Delayed feedback).

Each partner completed the Solo intervention condition while their partner completed musical background and Edinburgh Handedness questionnaires. Partner A was instructed to begin synchronizing their taps with a computer-generated recording of partner B's melody after 8 beats of the metronome, and to continue synchronizing until the sound heard over headphones ceased while partner B had their headphones turned off and completed questionnaires. Then, partner B completed the same Solo intervention condition while partner A filled out their questionnaires. Neither partner could hear the other partner's auditory feedback, which was delivered separately through headphones, during all Intervention trials.

Then participants completed the next Joint performance condition, in which they synchronized with their partner after the metronome clicks started and continued until the sound ceased, indicating the end of the trial. Then the partners completed the second Solo Intervention condition (either Normal or Delayed Intervention) and then completed the third Joint performance condition (Post-Normal or Post-Delay Joint condition). The entire experiment lasted

approximately 60 min, and the participants received a small fee or course credit for their participation.

2.5 Data analysis

An *a priori* power analysis was conducted using G*Power 3.1.9.7 (Faul et al., 2007) to establish the minimum sample size required to test the primary hypothesis that the order of intervention conditions would influence the pairs' joint synchronization performance (Bégl et al., 2024). Results indicated the required sample size to achieve 80% power, at a significance criterion of $\alpha = 0.05$, was $N = 25$ for a two-tailed *t*-test. Thus, the obtained sample size of $N = 25$ pairs was adequate to test the study hypothesis.

Behavioral analyses were run in R Statistical Software (afex package; Singmann et al. 2023 v4.2.0–0). Tests of the synchronization measures included ANOVAs that addressed the Solo and Joint tasks separately. Measures of synchronization in the Solo tasks included signed asynchronies (stimulus onset minus participant onset), their variability (standard deviation), and their absolute value. Synchronization in the Joint tasks were measured by the standard deviation of the signed asynchronies (partner A's onset minus partner B's onset) and by their absolute value. Synchronization in the Solo tasks was analyzed in terms of the independent variables of Intervention condition (Delay, Normal) and Intervention Order

(Delay first; Normal first), with the participant as random variable. Synchronization between partners in the Joint performance conditions were analyzed in terms of the independent variables of Post-Intervention condition (Post-Delay, Post-Normal) and Intervention Order (Delay first; Normal first), with the pair as random variable. Similar analyses were conducted on the model parameters (k , ω). Linear contrasts were run with the emmeans package (n 1.8.7; Lenth, 2023) and p -values were corrected using a Bonferroni correction.

2.6 Model analysis

Model analyses were conducted on the Joint performance asynchronies by taking the mean of the eight melody repetitions within each trial ($N=224$ trials total). The delay-coupled model was fit to these asynchronies in two separate iterations, similar to previous delay-coupling applications to joint performance (Demos et al., 2019; Bégel et al., 2022). In the first stage, a global parameter search was conducted using a genetic algorithm. Parameters were allowed to vary within the following bounds: The difference between the partners' intrinsic frequencies ($\omega_1 - \omega_2$) was allowed to vary within a range of -300 ms to $+300$ ms, based on previously observed ranges for partners' intrinsic frequencies (Zamm et al., 2016; Scheurich et al., 2018). The coupling strength parameters k were allowed to vary from 0 (no coupling) to 50. The τ parameters were allowed to vary with a range of 0 (no time delay) to 50 ms. The model was fit 10 times to each trial. In the second stage, the optimized parameter values obtained with the genetic algorithm were passed to a local search algorithm (constrained nonlinear multivariate function). Root Mean Square Error (RMSE) values for each model fit per trial were computed between the observed asynchronies and the model's estimates of asynchronies. The best-fitting (smallest) RMSE of the 10 fits was chosen. The τ value associated with this best fit for each trial was then analyzed to yield the median value computed across participants and trials ($\tau = 19.7$ ms), a value similar to the median τ obtained in other joint music performance studies (Demos et al., 2019; Bégel et al., 2022).

In a second stage, the fitting procedure was repeated with τ set to the median value (19.7 ms). Coupling and intrinsic frequency parameters were allowed to vary within identical boundaries to those used in the first model fits. The second run also consisted of 10 model fits to each trial. Fits that yielded parameter boundary cases ($k \geq 49$ ms; $\omega_1 - \omega_2 \geq 299$ ms or ≤ -299 ms) were excluded from considerations of the best-fitting model, which was then chosen for each trial (based on the smallest RMSE value). The parameter values associated with the final model fits were analyzed similarly to the behavioral asynchrony measures.

3 Results

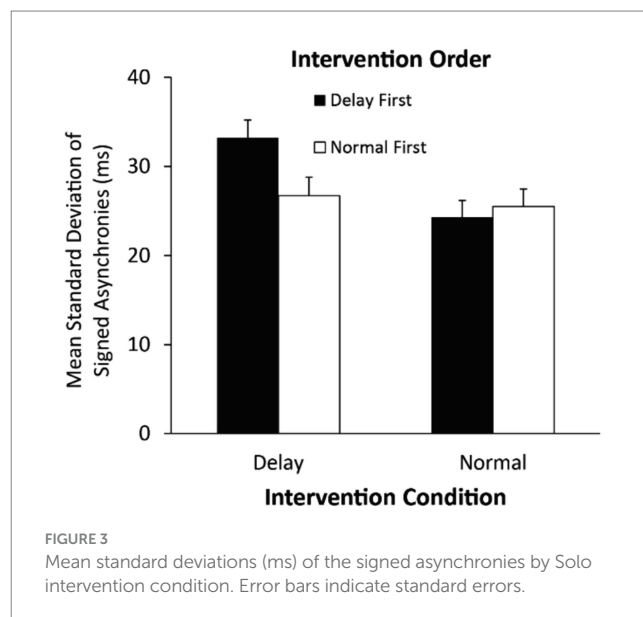
3.1 Solo intervention conditions

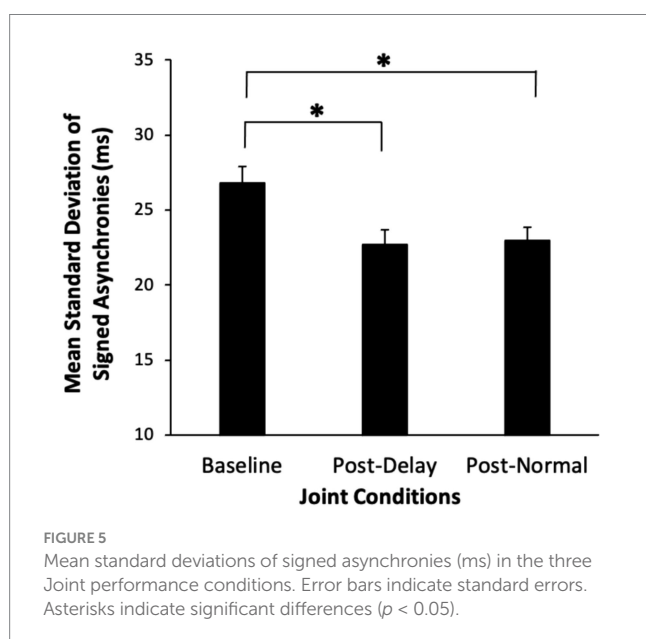
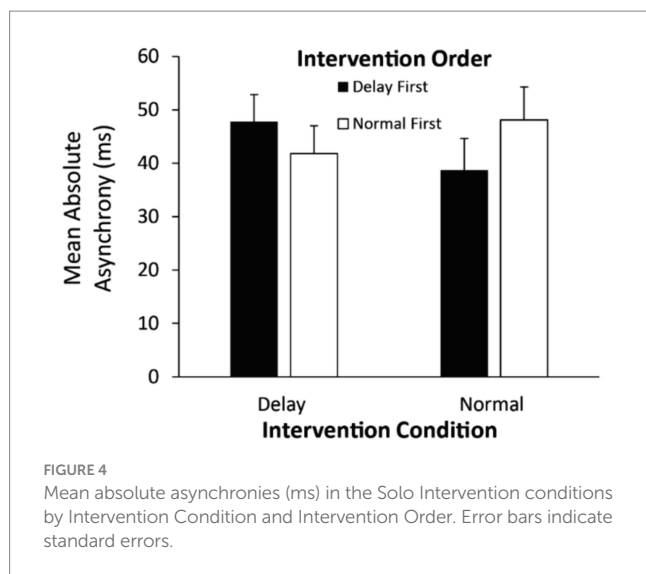
We conducted a two-way ANOVA on the mean intertap intervals by Solo Intervention Condition and Intervention Order, to determine whether individuals were able to maintain the cued tempo (450 ms). The analysis revealed no significant effects, indicating a stable tempo across Solo Intervention conditions with a mean intertap interval of 449.2 ms ($SE = 0.179$).

We next tested the standard deviations of the signed asynchronies in Solo interventions to determine differences due to the auditory feedback interventions. A two-way ANOVA on the standard deviations of asynchronies by Intervention condition (Delay/Normal feedback) and Intervention Order (Normal feedback first/Delayed feedback first) indicated a main effect of Intervention condition, $F(1, 48) = 12.66$, $\eta^2_G = 0.064$, $p = 0.0008$, and a significant interaction of Intervention condition with Intervention Order, $F(1, 48) = 7.42$, $\eta^2_G = 0.038$, $p = 0.009$. The Delayed Intervention/Delay-first order differed significantly from the Delayed Intervention/Normal-first order [linear contrasts, $t(48) = 2.67$, $p = 0.028$], the Normal Intervention condition/Delay-first order [$t(48) = 4.53$, $p < 0.01$], and the Normal Intervention/Normal-first order [$t(48) = 2.76$, $p < 0.01$]. As shown in Figure 3, greatest variability occurred during the Delayed Intervention condition when it was learned first.

We also tested the absolute asynchronies between individuals' taps and the computer-generated melody in the Solo Intervention conditions. A two-way ANOVA on the mean absolute asynchronies by Intervention Condition (Delay/Normal feedback) and Intervention Order (Normal feedback first/Delayed feedback first) revealed a significant interaction [$F(1, 48) = 6.88$, $\eta^2_G = 0.019$, $p = 0.011$]. As shown in Figure 4, the absolute asynchronies were greater in the intervention that was conducted first, suggesting some improvement over the course of the experiment. There were no significant main effects.

Finally, we computed the signed asynchronies in the Solo intervention conditions in order to determine whether individuals anticipated the computer-generated recording. Overall, the asynchronies were negative in each condition, indicating that the participants anticipated the metronome cue (mean = -39.1 ms). The same ANOVA on the signed asynchronies by Intervention condition and Intervention Order showed no main effects but a statistically significant interaction [$F(1, 48) = 5.09$; $\eta^2_G = 0.014$, $p = 0.03$]. Performance during the Solo intervention conditions was more anticipatory during the Normal feedback intervention than during the Delayed feedback intervention, when the participants received the Normal feedback intervention first (Bonferroni-corrected contrasts, $t = 2.86$, $p < 0.04$). Asynchronies were equivalent in Delayed and Normal feedback conditions when the Delayed feedback condition was first.





3.2 Joint synchronization conditions

We first compared the Baseline Joint performance condition (before Solo Interventions) with the synchrony observed in the other Joint performance conditions. An ANOVA on the standard deviations of the asynchronies by Joint condition (Baseline, Post-Delay intervention, Post-Normal intervention) and Intervention Order (Delay first/Normal first) indicated a significant main effect of Joint condition [$F(2, 46) = 26.8$, $\eta^2_G = 0.136$, $p < 0.00001$]. As shown in **Figure 5**, the standard deviations were larger in the Baseline condition (mean SD = 26.8 ms) than in the Post-Delay condition [mean SD = 22.7 ms, Bonferroni-corrected $t(23) = 5.48$] and the Post-Normal condition [mean SD = 23.0; Bonferroni-corrected $t(23) = 6.24$]. Thus, participants showed improvement in synchronization from Baseline to later Joint performances, and the pairs that were assigned to the different Solo Intervention orders did not differ at Baseline.

Next, we examined the mean absolute asynchronies by Joint Condition (Baseline, Post-Delay, Post-Normal) and Intervention order (Delay first/Normal first). This ANOVA yielded a non-significant effect of Post-Intervention condition [$F(2, 46) = 2.74$, $p = 0.075$] with similar patterns to the standard deviations; absolute asynchronies tended to be higher in the Baseline condition (mean SD = 25.4 ms) than in the Post-Delay (mean SD = 23.0 ms) or Post-Normal conditions (mean SD = 22.9 ms). No other tests approached significance.

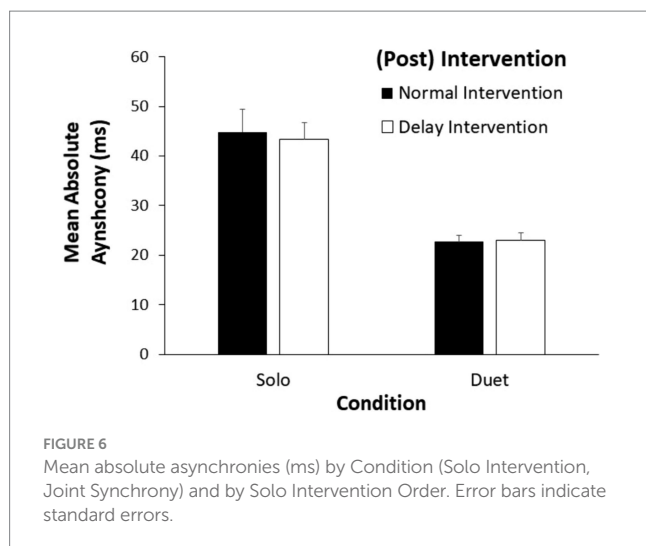
Finally, we compared the absolute asynchronies across the Solo intervention conditions and the Joint performance conditions, to test whether performing with a computer-generated performance (that permitted only unidirectional coupling from human to computer) or with a slightly irregular partner (that permitted bidirectional coupling from human to human) would generate better synchrony. A two-way ANOVA on each pair's absolute asynchronies by Task (Solo/Joint) and Intervention type (Delay/Post-Delay or Normal/Post-Normal) showed a significant main effect of Task [$F(1, 24) = 61.70$, $\eta^2_G = 0.340$, $p < 0.00001$] and no other significant main effects or interactions. As shown in **Figure 6**, participants were more synchronous when performing with a partner than when performing with a temporally regular recording – whether or not that recording contained occasional delayed auditory feedback.

3.3 Model fits

We examined the model fits to the partners' mean signed asynchronies in the Joint performance conditions. An example of the model's predicted asynchrony values with the observed asynchrony values from one pair's performance is shown in **Figure 7** for the Joint performance condition that followed the Solo Normal-feedback Intervention.

Statistical analyses were performed on the coupling parameter k for each partner, to compare the effects of Intervention conditions on the pairs' Joint performance. A Wilcoxon signed-ranks test on the median coupling parameter values in each condition indicated that the coupling values were significantly higher in the Post-Normal Joint performance condition (Mdn = 16.44) than in the Post-Delay Joint performance condition (Mdn = 12.96, $z = 1.97$, $p = 0.024$). As shown in **Figure 8**, the model's coupling values were increased in the joint synchronization experienced after the Normal feedback intervention relative to the Delayed feedback intervention. Decreased coupling during synchronization with a partner that followed the Delayed feedback Intervention suggests that the Delayed feedback disrupted participants' subsequent ability to synchronize their productions.

Next, we tested the delay-coupled model fits to the intrinsic frequency (ω) parameters. Intrinsic frequency differences between partners are related to tempo or rate of performance; a larger difference between partners, computed in absolute ms, is expected to yield larger mean absolute asynchronies. A Wilcoxon signed-ranks test on the absolute value of each pair's ω differences by Joint performance condition (Post-normal, Post-delay) indicated no significant differences ($z = 0.38$, $p = 0.35$). Therefore, it is unlikely that the intrinsic frequency parameter accounted for the Solo Intervention effects on the coupling parameters in subsequent Joint synchronization.

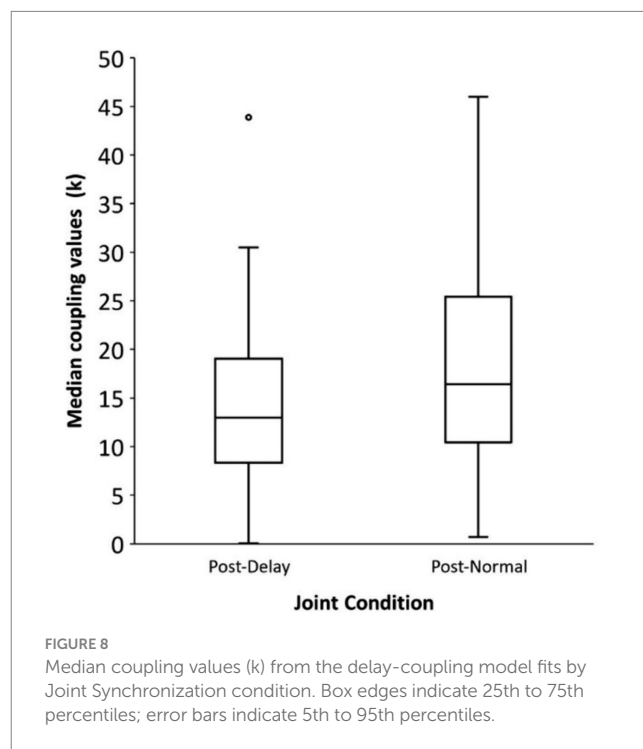
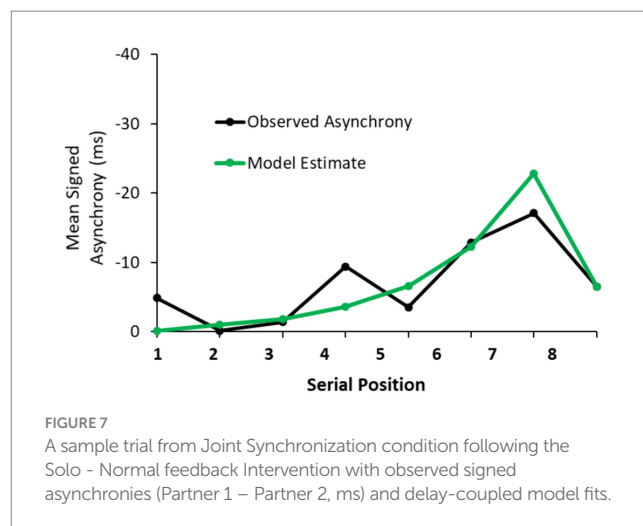


Finally, we compared the delay-coupling model with a simpler model that removed the coupling parameter, to ensure its necessity in accounting for Joint synchronization performance. The bidirectional delay-coupling model was compared with a linear model that contained only the intrinsic frequency (ω) parameter while k , the coupling term, was set to 0 (thus cancelling the time delay parameter as well; see Equation 1). Root mean squared error values (RMSE) were generated for the two models fitted to the partners' asynchronies in the Joint performance conditions. A one-way ANOVA was then conducted on the RMSE values by model (delay-coupling model and intrinsic frequency model). The RMSE values indicated a statistically significant difference among the models [$F(1,24)=49.157$, $\eta^2_G=0.131$, $p<0.001$]. The model fits with the coupling value set to 0 produced higher average RMSE values ($M=7.348$), indicating a worse fit, than the model fits with the coupling term allowed to vary ($M=6.359$). Thus, the coupling parameter was necessary to capture the partners' Joint performance synchronization.

4 Discussion

The impact of individual synchronization practice on joint synchronization was examined with musically trained partners in a within-pair design that presented different individual (solo) practice conditions. Effects of Solo synchronization practice with normal or delayed auditory feedback were evaluated on subsequent Joint duet performance as participants synchronized the production of simple melodies with an auditory cue (Solo conditions) or with a partner (Joint conditions). The within-pair design allowed us to compare Intervention order effects on the partners' subsequent joint synchronization. The application of a delay-coupling model to the partners' joint synchronization measures allowed us to compare the amount of coupling between partners as a function of the individual practice conditions.

The auditory feedback manipulations in the Solo intervention conditions resulted in higher variability in asynchronies during the Delayed Feedback condition than the Normal feedback condition. These results are consistent with previous findings that indicate that delayed auditory feedback hinders participants' attempts to synchronize (Repp et al., 2011; Bégel et al., 2022). In addition, absolute asynchronies in the Solo intervention conditions indicated that the auditory feedback type interacted with the order of Intervention conditions; participants were worse at synchronization in the first Solo



intervention they experienced, and better at synchronization by the last Solo intervention, suggesting that learning occurred despite the type of auditory feedback.

The dyads' Joint synchronization performance indicated that the asynchrony variability improved from the initial Joint performance to later Joint performance, also supporting a learning effect as participants progressed through the tasks. Fortunately, there were no initial differences in Joint synchrony across the groups of participants who completed different two orders of the Solo interventions, suggesting that pairwise differences in synchronization did not account for the Solo intervention effects. Although the Solo intervention conditions did not directly influence the immediately following Joint performance asynchronies, the model's coupling parameter fits suggested that the auditory feedback manipulations in the Solo practice influenced bidirectional synchronization in the subsequent Joint performances.

Fits of the delay-coupling model to the Joint synchronization performances indicated increased coupling values between partners when the Joint performances followed the normal auditory feedback (Solo) practice, relative to the delayed feedback practice. Furthermore, the remaining model parameter that was allowed to vary, the intrinsic frequency parameter, did not differ across the Joint synchronization conditions. We also tested whether the coupling parameter was necessary by comparing the delay-coupling model fits to those of a reduced model that contained only the intrinsic frequency parameters (with coupling set to 0). The reduced model provided a substantially poorer fit, suggesting that the coupling parameter was necessary to account for the partners' asynchronies in joint performance. Future work may compare the delay-coupled model presented here with other numerical solutions (cf. Roman et al., 2019; Shahal et al., 2020; Calabrese et al., 2022), as well as with analytical solutions such as linear delay differential equations (cf. Yi and Ulsoy, 2006) and networks of delay-coupled oscillators (Pérez et al., 2011).

Finally, musicians' synchronization was compared across Solo performances and Joint (dyadic) performance. The absolute asynchronies were greater in the Solo performances with a computer-generated performance than in the Joint performances with a partner. This finding may seem surprising, as the Solo interventions contained temporally regular inter-tone intervals (with the exception of 25% of delayed tone onsets in one condition), whereas all of the Joint synchronizations contained partners' normal temporal variability. These findings can be reconciled if partners' Joint synchronization reflects *predictable* temporal variability that allows each performer to adapt to their partner; previous studies have also documented reduced asynchronies for duet partners compared with the same partner's synchronization with a temporally regular recording (Demos et al., 2017). The greater predictability of duet synchronization is also consistent with findings that showed better fit of nonlinear oscillators to the normal temporal variability in piano performances than to metronomically regular performances (Large and Palmer, 2002). Future studies may address how bidirectional coupling between partners develops as they learn to synchronize with more complex music than the simple melodies used here.

The current study addressed musical synchronization in the context of Western classical music forms. Some studies have identified different performance timing in other genres. Butterfield (2010) examined asynchronous timing between bass and drums players in swing groove music, in which a sense of constant time was negotiated between performers. Johansson's (2010) analysis of Scandinavian folk music for fiddle similarly argued that rhythmic tolerance calls for tone onset ambiguities among performers. Danielsen (2018) identified extended beats in a musical genre of neo-soul groove, where an expectation for active anticipation among partners can yield aesthetic choices that result in asynchronies. Thus, performance norms in groove, jazz, and neo-soul musical forms may differ from classical music performance norms typical of the current study, which included an emphasis on temporal precision and synchronous tones.

In conclusion, the findings document short-term learning effects of solo performance on joint synchronization by musically trained partners. The Joint synchronization conditions indicated that synchronization with a partner becomes more accurate over the course of the experiment; the Solo Intervention conditions demonstrated that the quality of auditory feedback influences coupling between duet partners in future joint performances. This finding reinforces the

validity of musicians' common solo practice methods, which can enhance subsequent performance in ensemble situations. Future directions may address distinctions between unidirectional coupling of individual practice with a recording (common in musicians' play-along practice albums) and bidirectional coupling that arises in joint performance. Physiological changes that occur during ensemble performance conditions, such as joint influences on respiration or heart rate, may also impact partners' coupling (Wright et al., 2022; Høffding et al., 2023). Finally, further investigations may compare influences of solo practice on joint synchronization in terms of frequency of practice (such as performers who practice music daily and those who do not).

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/t72ze/?view_only=87d29c4afcb64e6b889177802554f2a2.

Ethics statement

The studies involving humans were approved by McGill University Research Ethics Board. The studies were conducted in accordance with the local legislation and institutional requirements. The participants provided their written informed consent to participate in this study.

Author contributions

PP: Data curation, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. VB: Conceptualization, Formal analysis, Writing – original draft, Writing – review & editing. CP: Conceptualization, Formal analysis, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing.

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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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Hyper-brain hyper-frequency network topology dynamics when playing guitar in quartet

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Ensemble music performance is a highly coordinated form of social behavior requiring not only precise motor actions but also synchronization of different neural processes both within and between the brains of ensemble players. In previous analyses, which were restricted to within-frequency coupling (WFC), we showed that different frequencies participate in intra- and inter-brain coordination, exhibiting distinct network topology dynamics that underlie coordinated actions and interactions. However, many of the couplings both within and between brains are likely to operate across frequencies. Hence, to obtain a more complete picture of hyper-brain interaction when musicians play the guitar in a quartet, cross-frequency coupling (CFC) has to be considered as well. Furthermore, WFC and CFC can be used to construct hyper-brain hyper-frequency networks (HB-HFNs) integrating all the information flows between different oscillation frequencies, providing important details about ensemble interaction in terms of network topology dynamics (NTD). Here, we reanalyzed EEG (electroencephalogram) data obtained from four guitarists playing together in quartet to explore changes in HB-HFN topology dynamics and their relation to acoustic signals of the music. Our findings demonstrate that low-frequency oscillations (e.g., delta, theta, and alpha) play an integrative or pacemaker role in such complex networks and that HFN topology dynamics are specifically related to the guitar quartet playing dynamics assessed by sound properties. Simulations by link removal showed that the HB-HFN is relatively robust against loss of connections, especially when the strongest connections are preserved and when the loss of connections only affects the brain of one guitarist. We conclude that HB-HFNs capture neural mechanisms that support interpersonally coordinated action and behavioral synchrony.

KEYWORDS

within-and cross-frequency coupling, graph-theoretical approach, EEG hyperscanning, phase synchronization, hyper-brain hyper-frequency networks, social interaction

Introduction

Music possesses an extraordinary ability to transcend boundaries, uniting people and creating harmonious connections. In the realm of music, quartet playing represents a sublime fusion of individual creativity and collective synergy. The magic unfolds when four skilled musicians, specifically guitarists, blend their unique styles and emotions, crafting melodies or sounds that resonate deeply with the human soul. Recent research indicates that synchronized

brain activity, especially inter- or hyper-brain synchronization, accompanies coordinated behavior and plays a crucial role in social or musical interaction (Lindenberger et al., 2009; Sängner et al., 2012, 2013; Müller et al., 2013, 2018b; Keller et al., 2014; Müller and Lindenberger, 2019, 2022, 2023; Gugnowska et al., 2022). This synchrony can occur at the same or at different frequencies and can be indicated by within- and cross-frequency coupling (WFC and CFC, respectively). Such coupling or synchronization (i.e., within and between brains and within and between frequencies), reflecting the common integrated state of interactors and supporting hyper-brain hyper-frequency network (HB-HFN) activity, is of paramount importance. Moreover, these different types of oscillatory and network interactions reveal a superior degree of complexity that is essential for superorganismic organization and functioning (cf. Delius and Müller, 2023). The dynamics of the HB-HFN topology have a profound impact on the way we interact and respond to each other. However, the neural mechanisms responsible for facilitating coordinated actions between individuals and promoting social interaction remain elusive, especially when such interactions involve groups of more than two individuals, such as a guitar quartet or similar (Thompson and Varela, 2001; Frith and Frith, 2007; Hari and Kujala, 2009; Müller et al., 2018b, 2021; Müller, 2022).

The performance of even a simple piece of music demands precise control of timing to adhere to a hierarchical rhythmic structure. Additionally, musicians must skilfully control pitch to produce specific musical intervals based on frequency ratios. Music thus imposes unique demands on the nervous system, and an understanding of these demands can, in turn, provide insights into certain aspects of neural function (Zatorre et al., 2007). Furthermore, the expectations associated with rhythm and beat are an important component of temporal predictions in music. The ability to tune to an external auditory stimulus or a complex rhythm allows multiple individuals to synchronize their behavior in time by integrating the flow of information across different sensory modalities (Keller, 2008; Repp and Keller, 2008; Merker et al., 2009; Battich et al., 2020). All this necessitates an interaction of different frequencies and their integration in the entire network.

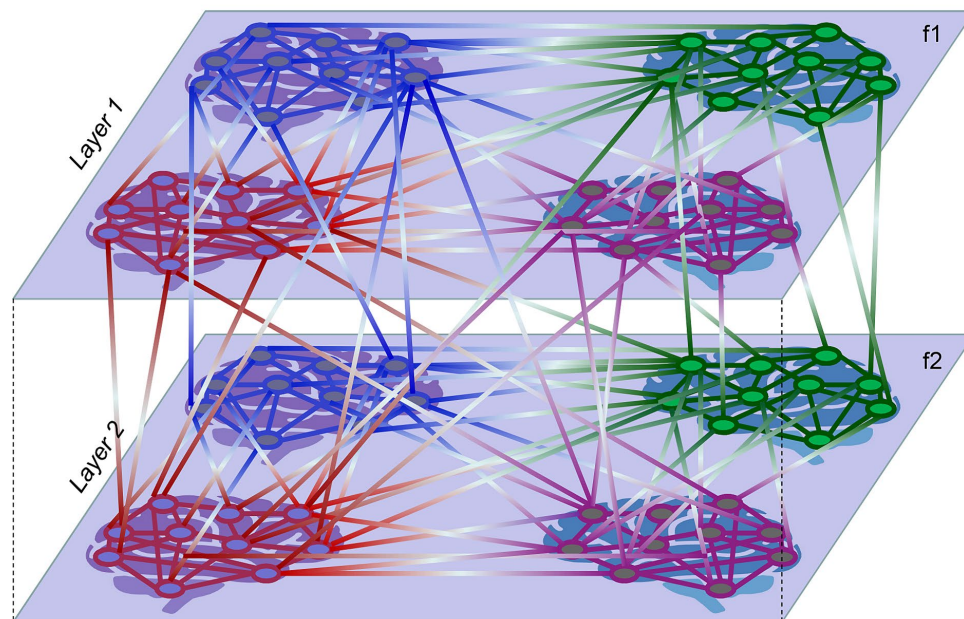
From our daily experiences, it is evident that social endeavors like music-making require learning and practice to become proficient and seamless. Through the process of learning, achieved by engaging in these social activities repeatedly, extraneous elements in interpersonal interactions are gradually refined, leading to enhanced fluidity in movement and improved motor skills. As highlighted by Müller (2022), there is an intrinsic relation between oscillatory activity, neural cell assemblies, and behavioral or cognitive entities. In the context of this relation, a hyper-brain cell assembly hypothesis has been suggested that states that cell assemblies can be formed not only within but also between brains, following roughly the same 'Hebbian' rules as within brains. Such hyper-brain cell assemblies, connecting two or more brains and triggering the simultaneous activation (firing) of neural components within these brains or the shared hyper-brain cell assembly, represent superordinate systems that encompass and integrate oscillatory activity within and between brains. This collective hyper-brain unit, which can also have a multidimensional or multilayer dynamic organization based on WFC and CFC within and between brains, serves as the foundation for social and interactive behaviors (Müller, 2022). Comparable concepts have also been discussed previously (Shamay-Tsoory, 2022). In this work, the author

introduces the notion of *interbrain plasticity* or learning through interaction, where "interbrain plasticity" serves as a metaphor symbolizing the ability of inter-brain networks (which also rely on intra-brain connections) to reconfigure their functional organization in response to learning facilitated by interaction. Interbrain plasticity refers to the ability of multiple brains to adapt to experiences, resulting in both short- and long-term changes in inter-brain connectivity. These connectivity or coupling changes can then influence the behavioral repertoire of the individuals involved in the interaction (see also May and Shamay-Tsoory, 2024). For example, think about a sports team or ensemble practicing together. As they train and play together over time, their brains become more synchronized in coordinating movements and strategies. This enhanced inter-brain connectivity reflects the plasticity of their collective neural networks, enabling them to perform better as a team or ensemble.

Complex networks (e.g., HFNs or HB-HFNs) can be regarded 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; Kivela et al., 2014; De Domenico, 2017; Pilosof et al., 2017; de Arruda et al., 2018). In this context, WFC represents communication within layers and CFC depicts communication between different 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; Müller, 2022). Figure 1A exemplarily shows a complex two-layer four-brain network or HB-HFN of a guitar quartet. In a number of studies, it has been shown that multilayer networks can be represented as a supra-adjacency matrix, allowing conventional graph-theoretical approach (GTA) tools to be used to investigate their properties (Kivela et al., 2014; Müller and Lindenberger, 2014; Brookes et al., 2016; De Domenico et al., 2016; Müller et al., 2016, 2019b; De Domenico, 2017; Müller, 2022). Figure 1B schematically illustrates two GTA measures, the clustering coefficient (CC) and characteristic path length (CPL), which we used in this work for network topology representation. In a concert study involving a quartet of guitarists and four audience members, the network topology dynamics (NTD) of the entire HB-HFN (quartet and audience) and the dynamical structure of guitar sounds showed specific guitar-guitar, brain-brain, and guitar-brain directional associations, indicating multilevel dynamics with upward and downward causation (Müller and Lindenberger, 2023).

The next important issue of interacting networks is their robustness, signifying the ability to maintain integrity and functionality of the network even after the removal of nodes or edges. This ability of the network is a prominent feature of most biological systems and social groups (Barabási and Pósfai, 2016; Liu et al., 2020; Bellingeri et al., 2020a), and may be useful for understanding interpersonal action coordination and the underlying hyper-brain networks. It has been reported that removing nodes according to weighted rank and also removing links in accordance with their weights produce the highest damage in real-world complex networks (Bellingeri and Cassi, 2018; Bellingeri et al., 2019, 2020a). Moreover, it has also been found that the robustness of the real-world complex networks against link removal is negatively correlated with link-weight heterogeneity (i.e., when the weights were randomly assigned to the links) and that the removal of a small fraction of strong links can rapidly decrease the efficiency and total flow in these networks (Bellingeri et al., 2019). It has also been reported that the removal of a single node or link has only limited impact on a network's integrity,

A Hyper-brain hyper-frequency multilayer network of a guitarist's quartet



B

Graph-Theoretical Approach (GTA)

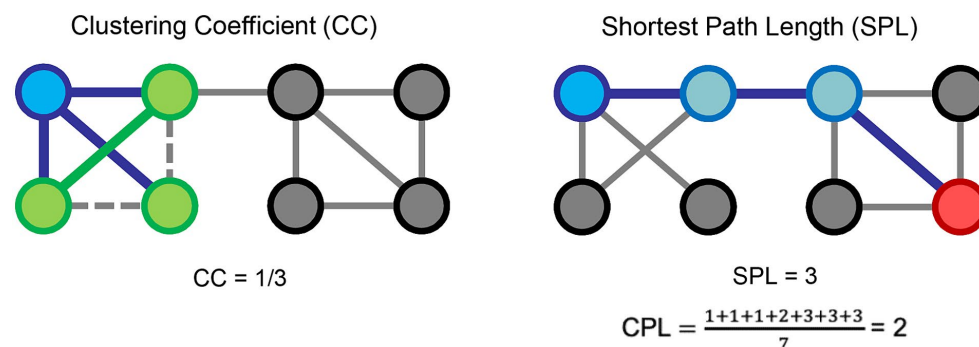


FIGURE 1

Schematic representation of HB-HFN and GTA. (A) Exemplary representation of a hyper-brain hyper-frequency multilayer network of a guitarist quartet. Four brains of the guitarist quartet within two layers with within- and between-layer connections are presented. The layers represent two different oscillation frequencies (f1 and f2), and connections within the layers indicate WFC, while connections between the layers indicate CFC. (B) Exemplary representation of two GTA measures: CC and CPL. On the left, CC for a target node (blue) is calculated as the ratio of one closed triangle to the three possible triangles, equaling 0.333. The three neighbors of the target node are presented in green. On the right, a shortest path length (SPL) is presented between the target node (blue) and another node (red) in the network, equaling 3. CPL is then calculated as the average of SPLs from the target node to all other nodes in the network, equaling 2. Note that for simplicity, a binary unweighted network was used in this representation. In the case of a directed weighted network, such as HB-HFN in our study, the direction and weights of links will play a role.

while the removal of several nodes or links can break a network into several isolated components or destroy the components of the network so that the network communication between remote nodes can no longer take place (Newman, 2003; Barabási and Pósfai, 2016). Most networks are robust against random vertex removal but considerably less robust to targeted removal of the highest-degree vertices (Newman, 2003).

In our previous analyses of data from a guitar quartet, which was restricted to WFC, we showed that different frequencies participate in intra- and interbrain coordination and exhibit different network topology dynamics that underlie coordinated actions and interactions (Müller et al., 2018b). However, many of the couplings both within

and between brains are likely to operate across frequencies (Müller and Lindenberger, 2014; Müller et al., 2021; Müller, 2022). Hence, to obtain a more complete picture of hyper-brain interaction when guitarists play as a quartet, we considered both WFC and CFC that are used to construct a multilayer HB-HFNs integrating all the information flows within and between different frequencies oscillating at distinct cortical regions/brains and providing important details about ensemble interaction in terms of network topology dynamics (cf. Müller, 2022). Our hypothesis was that hyperbrain coupling strengths among the four guitarist brains would decrease with higher oscillation frequencies, thereby eliciting corresponding effects on the NTD. Furthermore, it has been shown that there is a specific coupling

between musicians' brains and musical instruments (Müller and Lindenberger, 2019, 2022, 2023). In this context, it is to be expected that guitar sounds not only correlate with, or predict each other, but that this correlation or prediction also concerns guitar–brain relations. To substantiate these relations (i.e., guitar–guitar, guitar–brain, and brain–brain), we calculated Pearson's product correlation and multivariate Granger causality (GC) for amplitude and frequency modulations of guitar sounds and corresponding HB-HFN topology changes within the two performed music pieces: *Libertango* and *Comme un tango*. In addition, we investigated the behavior or robustness of the HB-HFN and the role of different types of network connections upon simulated gradual elimination of these connections in 15 %-steps, both within the whole HB-HFN and within individual guitarists' brains. We examined how this loss of connections or link removal changes network topology within the whole HB-HFN and the individual guitarists' brains. Our expectation was that the behavior of the HB-HFN and the underlying NTD would remain relatively robust in response to the loss of connections, particularly if the loss only affected the brain of one guitarist.

Methods

Participants

A quartet of professional guitarists (Cuarteto Apasionado, Berlin) participated in the study (cf. Müller et al., 2018b). Participants' mean age was 46.5 years (SD = 1.7). All participants (females) were right-handed and had been playing the guitar professionally for more than 35 years (mean = 37.8 years, SD = 1.3). The Ethics Committee of Max Planck Institute for Human Development approved the study, and it was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. All participants volunteered for this experiment and gave their written informed consent prior to their inclusion in the study.

EEG data acquisition and preprocessing

EEG measurement took place while the quartet played two music pieces: *Libertango* (Astor Piazzolla) and *Comme un tango* (Patrick Roux). These musical pieces were chosen with regard to different aspects of interpersonal action coordination such as different phases of musical performance, consonant playing, changes of tempo, phases with different musical complexity, etc. The guitarists were positioned in an arc formation (refer to [Supplementary Video S1](#) for visualization). EEG was simultaneously recorded using four electrode caps with 28 Ag/AgCl EEG active electrodes each, placed according to the international 10–10 system, with the reference electrode at the right mastoid and the ground electrode at the AFz position. Vertical and horizontal electrooculogram (EOG) was recorded to control for eye blinks and eye movements. The sampling rate was 5,000 Hz. Recorded frequency bands ranged from 0.01 to 1,000 Hz. All amplifiers (BrainAmps MR and BrainAmps ExG from Brain Products, Gilching, Germany) were connected to the same computer through PCI interfaces and synchronized by using BrainVision recorder software. Through one microphone each, the sounds of the guitars were recorded on four ExG channels, simultaneously with the EEG

recordings. In addition, video and sound were recorded using a video camera connected to EEG computer through FireWire socket and Video Recorder as a component of BrainVision software (Brain Products, Gilching, Germany), synchronized in this way with EEG data acquisition. Data were re-referenced offline to an average of the left and right mastoid separately for each participant. Eye movement correction was accomplished by independent component analysis (Vigário, 1997). Thereafter, artifacts from head and body movements were rejected by visual inspection. Spontaneous EEG activity was resampled at 1000 Hz and divided into 5-s epochs. Event markers were set by a professional musician and correspond to different musical situations. The list of the events and their short description for both music pieces is presented in [Supplementary Table S1](#). There were 10 and 14 segments in *Libertango* and *Comme un tango*, respectively, that were free of artifacts for all four guitarists. Further, to calculate the phase coupling, we used a moving time window approach with a window width of 500 ms and a time delay of 50 ms. A total of 91 time windows were captured using this moving time window approach.

Phase synchronization (coupling) measures

Our analyses were conducted in a data-driven, directed, and frequency-resolved manner. To investigate phase synchronization within and between the frequencies, we applied an analytic complex-valued Morlet wavelet transform to compute the instantaneous phase in the frequency range from 2.5 to 60 Hz for nine different frequencies of interest (FOI): 2.5, 5, 10, 15, 20, 25, 30, 40, and 60 Hz. It is worth noting that both the choice of FOI and the parameter for the moving time window approach were selected to enable comparison with previous analyses. Furthermore, the FOI are in specific integer ratios to each other (e.g., 1:2, 1:3, 2:3, 1:4, 2:5, etc.) to ensure consistent analysis of CFC. The complex mother Morlet wavelet, also called Gabor wavelet, has a Gaussian shape around its central frequency f :

$$w(t, f) = \left(\sigma^2 \pi\right)^{-1/4} e^{\left((-t^2/2\sigma^2) + 3/2\pi jft\right)}, j = \sqrt{-1} \quad (1)$$

in which σ is the standard deviation of the Gaussian envelope of the mother wavelet. The wavelet coefficients were calculated with a time step of 5 leading to a time resolution of 5 ms and frequency resolution of 0.5 Hz. To identify the phase relations between any two channels within and between the frequencies, a generalized phase difference ($\Delta\Phi$) was used to calculation of within- and cross-frequency coupling:

$$\Delta\Phi(t) = n \cdot \phi_m(t) - m \cdot \phi_n(t) \quad (2)$$

where m and n are integers, and $\phi_{m,n}$ are phases of two oscillators. In the case of WFC with $\phi_m = \phi_n$, the phase difference $\Delta\Phi$ is calculated in the same way by setting $m = n = 1$. WFC and CFC within and between brains were determined using the *adaptive Integrative Coupling Index (aICI)* algorithm described in our previous study (Müller and Lindenberger, 2014), which allowed us to calculate this coupling index depending on the angle of phase differences determined in a given time window. In other words, *aICI* no longer reflect *in-phase* synchronization, where the angle of phase differences

is close to zero, but is suitable for the determination of phase coupling at any chosen or previously determined phase angles. For these purposes, the Phase Synchronization Index (*PSI*) was determined first. It is defined by Müller et al. (2013):

$$PSI_{\Delta\Phi}(f_{m,n}) = \left| e^{j\Delta\Phi^k(f_{m,n})} \right|, j = \sqrt{-1} \quad (3)$$

where $\Delta\Phi^k$ is the phase difference between the instantaneous phases of the two signals at the frequencies f_m and f_n across k data points in the segment. During calculation of the *PSI*, we not only determined the mean direction or the length of the vector but also the angle of this vector ($\theta_{\Delta\Phi}$) in the complex space:

$$\theta_{\Delta\Phi}(f_{m,n}) = \arctan\left(\frac{\langle j \sin \Delta\Phi^k(f_{m,n}) \rangle}{\langle \cos \Delta\Phi^k(f_{m,n}) \rangle}\right), j = \sqrt{-1} \quad (4)$$

Given the estimates of the phase difference between two signals, it is 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 in a defined time window. So, we divided the range between $\theta - \pi/4$ and $\theta + \pi/4$ into two ranges and distinguished between positive and negative deviations from phase angle $\theta_{\Delta\Phi}$. Within a time window of 500 ms, we separately counted the number of phase difference points in the range between $\theta - \pi/4$ and θ (negative deviations) and in the range between θ and $\theta + \pi/4$ (positive deviations). Phase difference values beyond these ranges were considered as non-synchronization. Before counting, successive points in the defined range (between $\theta - \pi/4$ and $\theta + \pi/4$) with a time interval shorter than a period of the corresponding oscillation at the given frequency ($T_i = 1/f_i$) were discarded from the analysis. This cleaning procedure effectively eliminated instances of accidental synchronization. On the basis of this counting, we obtained several synchronization indices: (1) the *Positive Coupling Index*, *PCI*, or the relative number of phase-locked points in the positive range (between θ and $\theta + \pi/4$); (2) the *Negative Coupling Index*, *NCI*, or the relative number of phase-locked points in the negative range (between $\theta - \pi/4$ and θ); (3) the *Absolute Coupling Index*, *ACI*, or the relative number of phase-locked points in the positive and negative ranges (i.e., between $\theta - \pi/4$ and $\theta + \pi/4$); (4) the *adaptive Integrative Coupling Index*, *aICI*, calculated by the formula (Müller and Lindenberg, 2014):

$$aICI = \frac{PCI + ACI}{2 \cdot ACI} \cdot \sqrt{PCI} \quad (5)$$

The *aICI* is an *integrative* coupling index integrating the positive and negative shifts in phase difference of two signals and indicating the dominance of the positive shift in phase difference related to the common or absolute coupling. The *aICI* is equal to 1 when all points are phase-locked and positive; if all phase-locked points are negative or are out of range, the *aICI* will approach 0. Thus, the *aICI* measure ranges between 0 and 1 and is asymmetric ($aICI_{AB} \neq aICI_{BA}$), indicating the relative extent of positive phase synchronization. Moreover, by using the framework of “The Virtual Brain” (TVB, www.thevirtualbrain.org), simulation results in our previous study showed that all three measures (*PSI*, *ACI*, and *ICI*) capture the intended coupling properties (Müller et al., 2013). We restrict the description

of our study results to the *aICI* measure, which is the most informative due to its directionality.

It should be noted that inter-brain synchronization measures (e.g., *aICI*) are robust to the detection of spurious phase synchronization between individuals, i.e., where no volume conduction is possible. Spurious phase synchrony at each individual level can occur because of the volume conduction problem (Tognoli and Kelso, 2009) but using only 28 electrodes per person with larger distances between the electrodes considerably reduces such influences, if any.

Network construction and graph-theoretical approach (GTA)

Using the aforementioned directed coupling index (*aICI*), we constructed a HB-HFN of the guitarist quartet during playing. This network comprises four brains with 28 electrodes each and 9 oscillation frequencies, and correspondingly includes coupling (WFC and CFC) within and between brains. Figure 2A represents this HB-HFN in form of a supra-adjacency matrix, where conventional GTA tools can be used to investigate the network properties. As already mentioned, this supra-adjacency matrix or the HB-HFN can be considered as a multilayer network, where WFC represents connections within each layer and CFC represents connections between the layers (see Figure 2B for details). This network comprises 1,008 nodes in total and more than 1 million edges if it is fully connected. For our analyses, we used thresholded networks with a connectivity threshold of 0.3, which was always higher than the significance level determined by the surrogate data procedure ($p < 0.0001$). At this threshold, the cost level of the networks (the ratio of the number of actual connections divided by the maximum possible number of connections in the network) was approximately 20%, corresponding to high sparsity of the resulting networks and allowing more accurate examination of the network topology. For the HB-HFN analyses, we used three well-known GTA measures capable to describe key network properties, including connectivity strength and the degree of the network segregation and integration.

Degrees and strengths

As *aICI* is a directed measure, we obtained the node in- and out-degrees, in which the in-degree is the sum of all incoming connections of node i , $k_i^{in} = \sum_{j \in N} a_{ji}$, and the out-degree is the sum of all outgoing connections, $k_i^{out} = \sum_{j \in N} a_{ij}$. To calculate strengths,

we then replaced the sum of the links by the sum of the weights, $k_i^w = \sum_{j \in N} w_{ij}$, and calculated in- and out-strength, respectively. Overall

strengths (S) are given by the sum of in- and out-strength. For statistical evaluation, we determined strengths for each node in the whole HB-HFN of the guitarist quartet and then calculated them for WFC and CFC as well as for the within- and between-brain connections separately.

Clustering coefficient and characteristic path length

If the nearest neighbors of a node are also directly connected to each other, they form a cluster. For an individual node, the CC_i is

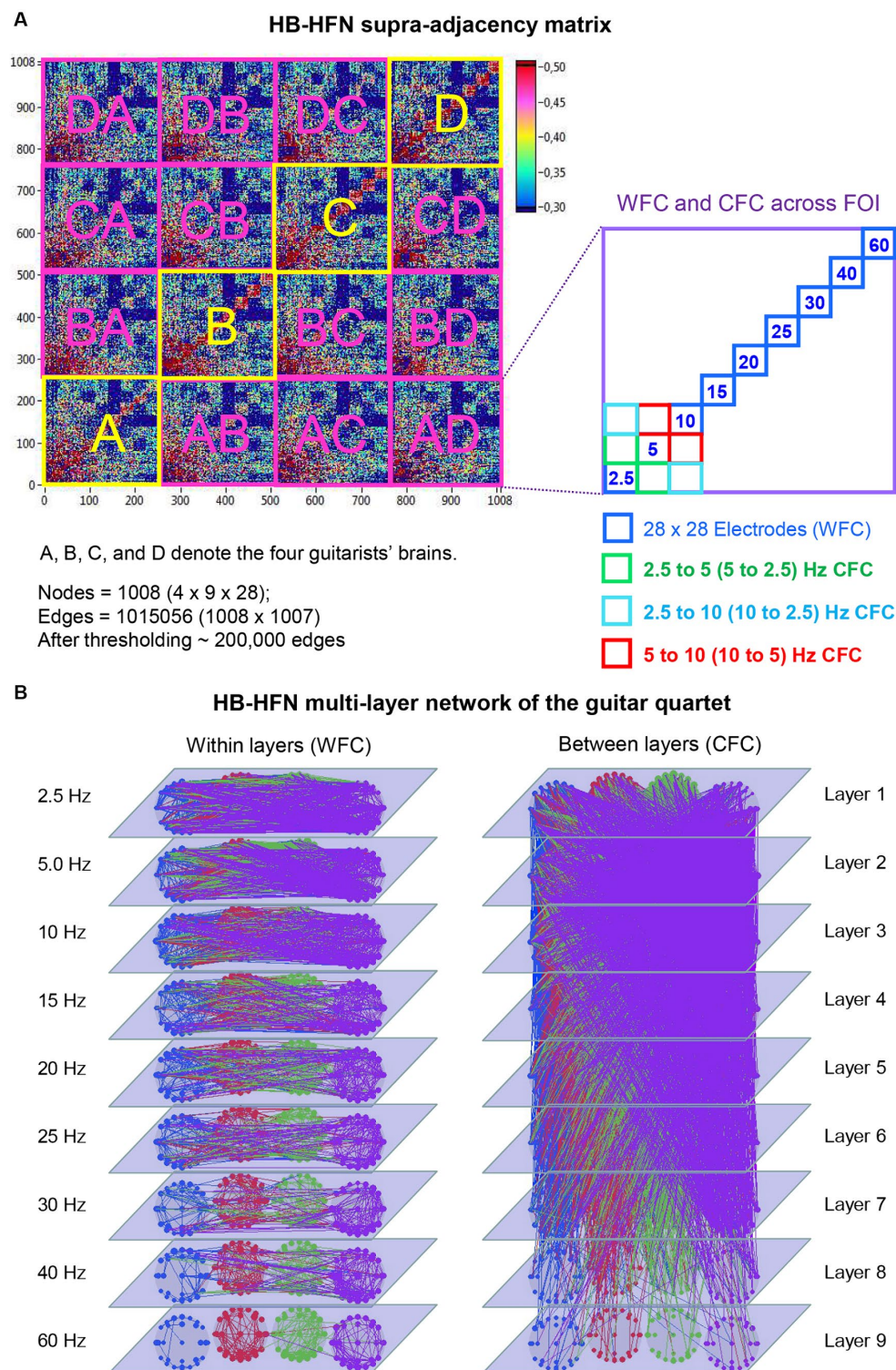


FIGURE 2

Representation of HB-HFN as a supra-adjacency matrix and a multilayer network. **(A)** HB-HFN supra-adjacency matrix. The supra-adjacency matrix (1,008 × 1,008) includes within-brain connectivity of the four guitarists (indicated in yellow) and between-brain connectivity (indicated in pink). The HB-HFN nodes comprise three components: guitarist's brains (4), electrode sites (28), and oscillation frequency (9). As shown on the right, each guitarist's brain (or a pair of brains for between-brain connectivity) consists of links between 28 electrodes within each of 9 frequencies (WFC) and between them (CFC). **(B)** HB-HFN multilayer network of the guitarist quartet. The within-layer communication (WFC on the left) and the between-layer communication (CFC on the right) are presented separately for visualization purposes. The 9 layers correspond to the 9 FOI. The predominance of low-frequency connections within and between the layers is evident here.

defined as the proportion of the number of pairs of i 's neighbors that are connected to the total number of pairs of i 's neighbors (see [Figure 1B](#) for details). In the case of a weighted directed graph the CC_i^{wd} and the mean CC^{wd} are calculated as follows ([Fagiolo, 2007](#)):

$$CC^{wd} = \frac{1}{n} \sum_{i \in N} CC_i^{wd} = \frac{1}{n} \sum_{i \in N} \frac{t_i^{wd}}{(k_i^{out} + k_i^{in})(k_i^{out} + k_i^{in} - 1) - 2 \sum_{j \in N} a_{ij} a_{ji}} \quad (6)$$

$$\text{with } t_i^{wd} = \frac{1}{2} \sum_{j, h \in N} \left[(w_{ij}^{1/3} w_{ih}^{1/3} w_{jh}^{1/3}) + (w_{ji}^{1/3} w_{hi}^{1/3} w_{hj}^{1/3}) \right]^3$$

being the number of weighted directed triangles around a node i . The clustering coefficient is a measure of segregation.

Another important measure is the *CPL*. In the case of an unweighted graph, the shortest path length or distance d_{ij} between two nodes i and j is the minimal number of edges that have to be passed to go from i to j (see [Figure 1B](#) for details). This is also called the geodesic path between the nodes i and j . The *CLP* of a graph is the mean of the path lengths between all possible pairs of vertices ([Watts and Strogatz, 1998](#)):

$$CPL^{wd} = \frac{1}{n} \sum_{i \in N} CPL_i^{wd} = \frac{1}{n} \sum_{i \in N} \frac{\sum_{j \in N, j \neq i} d_{ij}^{wd}}{n-1} \quad (7)$$

where CPL_i^{wd} is the average shortest or characteristic path length from node i to all other nodes. In the case of a weighted and directed graph, the weight and direction of the links will be considered. *CPL* shows the degree of network integration, with a shorter *CPL* indicating higher network integration. Similar to strength, *CC* and *CPL* were calculated individually for each node, representing nodal measures (i.e., CC_i^{wd} and CPL_i^{wd}).

Relationships between the guitar sounds and the network topology measures

Further, we investigated the relationships between the guitar sounds and the HB-HFN topology indices. For these purposes, we first calculated amplitude and frequency modulations of the guitar sounds by Mean Power Frequency (*MPF*) and Envelope (*ENV*) for each of the guitar signals captured by microphones. The *MPF* was calculated by using the short-time Fourier transform (STFT) spectrogram from the biomedical LabVIEW tool and the MATLAB envelope function integrated LabVIEW was used for the *ENV* calculation. *MPF* and *ENV* underwent processing using the moving window approach (averaging within 500-ms time windows shifted by a 50-ms time delay), mirroring the methodology employed for the calculation of connectivity and topology indices in EEG signal analysis. To explore the associations between guitar sounds (i.e., *MPF* and *ENV*) and NTD indicated by temporal changes in different topology measures, we calculated (1) Pearson's product correlation (*R*), reflecting linear relationships between the signals, and (2) multivariate Granger causality (*GC*), indicating causal or directional associations between the signals. For this calculation, the guitar

sound and NTD data across the 91 time windows and 10 (Libertango) or 14 (Comme un tango) music sequences were collapsed together, thus providing a cascade-shaped time series of 910 (91×10) or 1,274 (91×14) data points for Libertango and Comme un Tango, respectively. For this analysis, the NTD indices were consistently averaged for each guitarist separately. In this way, we investigated the guitar–guitar, guitar–brain, and brain–brain relationships between guitarists (or even guitar–brain relationships within a guitarist).

Robustness of HB-HFNs by stepwise elimination of different types of edges

To assess the robustness of HB-HFNs and elucidate the role or significance of network connections, we systematically manipulated the loss of various connection types within the entire HB-HFN and within individual guitarists' brains. Our investigation focused on understanding how the removal of connections impacted the network topology both across the entire HB-HFN and within individual guitarists' brains. This process involved a gradual elimination of connections in 15 5%-steps, utilizing three distinct types of removal: elimination of the weakest, strongest, and random connections. Subsequently, we computed the network topology at each manipulation step. For statistical evaluation, we determined the means and 95% confidence intervals (CIs) of the corresponding network topology indices at each step of the manipulation process. This comprehensive analysis sheds light on the robustness of HB-HFNs and provides insights into the dynamic role played by various types of connections in shaping the overall network topology.

Statistical analysis

The three nodal measures (*S*, *CC*, and *CPL*) were initially determined for each time window and subsequently averaged across them within each music sequence. As mentioned above, the network nodes are a composition of three components: guitarist's brain, electrode site, and oscillation frequency. Individual electrodes were grouped into three electrode sites: F (frontal – Fp1, Fpz, Fp2, AF7, AF8, F7, F3, Fz, F4, F8), C (central – T7, C5, C3, Cz, C4, C6, T8), and P (parietal – P7, P3, Pz, P4, P8, PO7, POz, PO8, O1, Oz, and O2). For the statistical evaluation of HB-HFN properties, nodes were regarded as cases that vary on three between-subject factors: Guitarist (A, B, C, and D), Site (F, C, and P), and Frequency (f1, f2, f3, f4, f5, f6, f7, f8, and f9). The music sequences of Libertango (10 sequences) and Comme un tango (14 sequences) were treated as within-subject factors in mixed ANOVAs. Further, to investigate the within- and between-brain (wB and bB, respectively) WFC and CFC, we summed up the couplings within these four groups of interest and collapsed the music sequences by averaging them for Libertango (MP1) and Comme un tango (MP2), respectively. We then conducted separate mixed ANOVAs for WFC and CFC, incorporating three between-subject factors as before and two within-subject factors: Coupling (wB and bB) and Music Piece (MP1 and MP2). When necessary, Greenhouse–Geisser epsilons were employed in all ANOVAs for nonsphericity correction. The Scheffé test was utilized for post-hoc testing of condition or network property differences. All statistical analyses were carried out using IBM SPSS Statistics 23.0 (SPSS Inc., Chicago, IL).

Results

Figure 3A shows an HB-HFN in the form of a circle, with the nodes arranged clockwise, and illustrates the relationships between different guitarists, electrode sites, and frequencies. It can be seen that the four guitarists mainly communicate with each other using the low frequencies. The network topology metrics determined in HB-HFNs at different time windows were first averaged over the different time windows within the music sequences. **Figure 3B** illustrates the network topology dynamics indicated by *S*, *CC*, and *CPL* across the 1,008 nodes over the 24 music sequences (left) and average values of the four guitarists across the music sequences of Libertango (10 sequences) and Comme un Tango (14 sequences). The **Supplementary Video S2** features a 5-s music sequence from Libertango, providing a real-time display of connectivity changes in the HB-HFN throughout this duration.

Network structure and topology dynamics across music sequences

The nodal network topology indices (*S*, *CC*, and *CPL*) determined in the HB-HFN and averaged over the different time windows were analyzed using mixed ANOVAs with the three between-subject factors Guitarist (A, B, C, and D), Site (F, C, and P) and Frequency (9 frequencies), which capture the HB-HFN structure, and one within-subject factor Sequence (10, respectively 14). To assess the dynamics within the music sequences, we determined not only the mean values over the time windows, but also the standard deviations (SDs) and subjected them to the same mixed ANOVAs. All ANOVAs for both mean values and SDs revealed significant main effects and significant interactions for all network metrics (all $P_s < 0.001$; see **Supplementary material** for details). The main effects for the factors Guitarist, Site, and Frequency are presented in **Figures 4A,B** for Libertango and Comme un Tango, respectively. Significant differences in the topology indices between the four guitarists apparently indicate different roles of the guitarists in the common network. Interestingly, guitarist D showed higher strength and *CC* as well as the shortest *CPL* in both music pieces, indicating her high segregation and integration in the common HB-HFN. Significant differences in the topology indices between the electrode sites mostly indicate the predominance of centro-parietal sites in the HB-HFN. It can also be seen that the strengths of nodes in the common HB-HFN decrease with high frequency, while *CC* and especially *CPL* increase (*CPL* becomes longer). All the changes across the frequencies are highly significant and indicate different contributions of these frequencies to network topology and functioning. As shown in **Figure 3**, the network topology also changes across sequences, indicating that the network topology is nonstationary and contingent on musical situation. These changes also vary across the four guitarists, indicating that the guitarists significantly change their impact on the quartet play. Moreover, significant interactions among all the factors indicate that the observed changes in the network topology are not absolute but are influenced by each other and are in permanent interplay.

The main effect of the SD differences for the factors Guitarist, Site, and Frequency are presented in **Figures 5A,B** for Libertango and Comme un tango, respectively. It can be seen that the variability in the

network topology determined by the SD differs among the four guitarists and also varies with the electrode sites, oscillation frequency, and music sequences in the two pieces of music (see **Supplementary material** for further details). Interestingly, despite the different changes in the network topology shown in **Figure 4**, the SD decreases with higher frequency for all topology metrics (see **Figure 5**).

WFC and CFC as well as intra- and inter-brain strengths

To investigate the coupling within and between layers in the multilayer HB-HFN, we determined WFC and CFC within and between brains separately for each node and averaged these across time windows and music sequences for Libertango and Comme un tango, respectively. WFC and CFC strengths were subjected to two separate mixed ANOVAs with three between-subject factors Guitarist, Site, and Frequency and two within-subject factors Music Piece (MP1 vs. MP2) and Coupling (within-brain vs. between-brain coupling). All main effects and most interactions were highly significant (all $P_s < 0.001$, with some exceptions). Results of these ANOVAs are presented in the **Supplementary materials**. As shown in **Figure 6A**, the WFC or coupling within the layers was much stronger within brains than between brains, while CFC (or coupling between the layers) was significantly higher between brains than within them. **Figure 6B** shows that the coupling within the layers (WFC) increases with higher frequency and the coupling between the layers (CFC) decreases. The increase in WFC is primarily due to the within-brain coupling, WFC between the brains increases only up to 10 Hz and then gradually decreases. As shown in **Figure 6C**, the four guitarists showed different coupling patterns with high WFC in guitarist D and high CFC in guitarist A for both MP1 and MP2, respectively. This indicates that the coupling within and between the layers differs among these guitarists, especially within their brains. The coupling is also different in the two music pieces, with overall higher WFC and also CFC in MP2 than in MP1. Moreover, as shown in **Figure 6D**, the guitarists differ also in WFC and CFC as well as in their within- and between-brain coupling with respect to the topological distribution or brain sites (see **Supplementary materials** for more details).

Network topology dynamics and its relationship to the guitar sounds

The previous analyses have shown that the network topology metrics exhibit a certain variability. Here we aim to examine whether this variability or underlying dynamics in network topology is related to the amplitude and frequency modulations of guitar sounds. For these purposes, we calculated two different characteristics of guitar sounds of the four guitarists (*MPF* and *ENV*) and related them to the HB-HFN topology metrics averaged for each guitarist's brain. In these analyses, instead of the *CPL*, we used its inverse ($1/CPL$), to obtain the same direction of changes as other topology measures. These dynamics are exemplarily presented in **Figure 7**. To investigate the relationships between all these signals, we calculated for each of the pieces of music: (1) Pearson's product correlation (*R*), reflecting linear relationships between the signals, and (2) multivariate Granger causality (*GC*), indicating causal or directional associations between the signals. **Figure 8** shows the relationships between the guitar sound

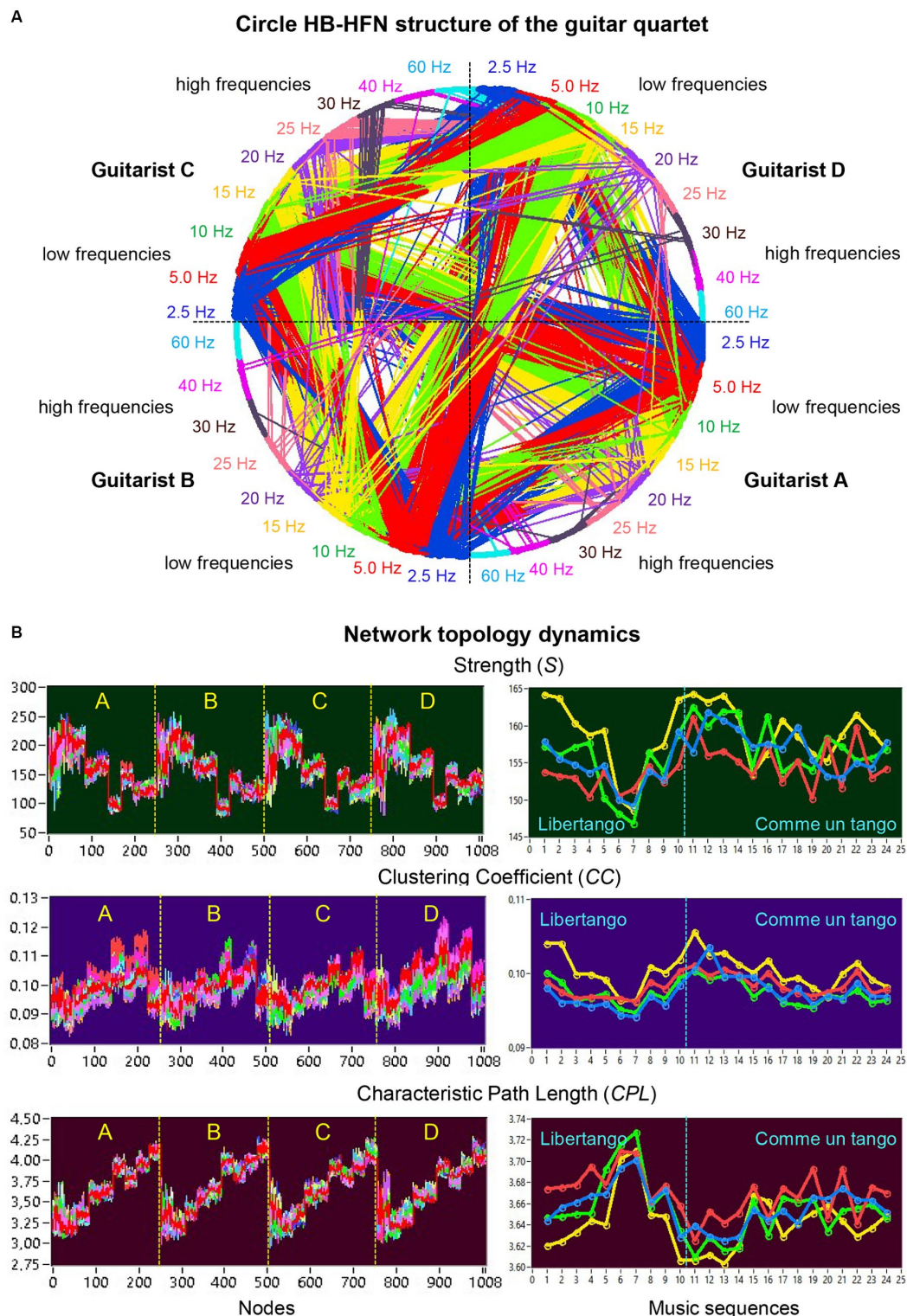


FIGURE 3

Circle HB-HFN structure of the guitar quartet and network topology dynamics. **(A)** Circle HB-HFN structure of the guitar quartet. The network nodes are arranged clockwise, starting from guitarist A (middle-right). Different frequencies (FOI) are represented by color. The predominance of low-frequency connections is also evident here (cf. Figure 2B). **(B)** Network topology dynamics. On the left, S , CC , and CPL are presented across the 1,008 nodes for 24 music sequences, indicated by color. On the right, the same GTA measures, averaged separately for the four guitarists' brains (guitarist A in blue, guitarist B in red, guitarist C in green, and guitarist D in yellow), are depicted across the 24 music sequences: 1–10 for Libertango and 11–24 for Comme un tango.

characteristics (MPF and ENV) and the three HB-HFN measures (S , CC , and inverse CPL). It can be seen that the linear relationship determined by the Pearson's product correlation is relatively strong

between the four musician's guitar sounds and especially between NTD indices. The correlation between the guitar sounds and the NTD is moderate for MPF signals, especially during Libertango. The

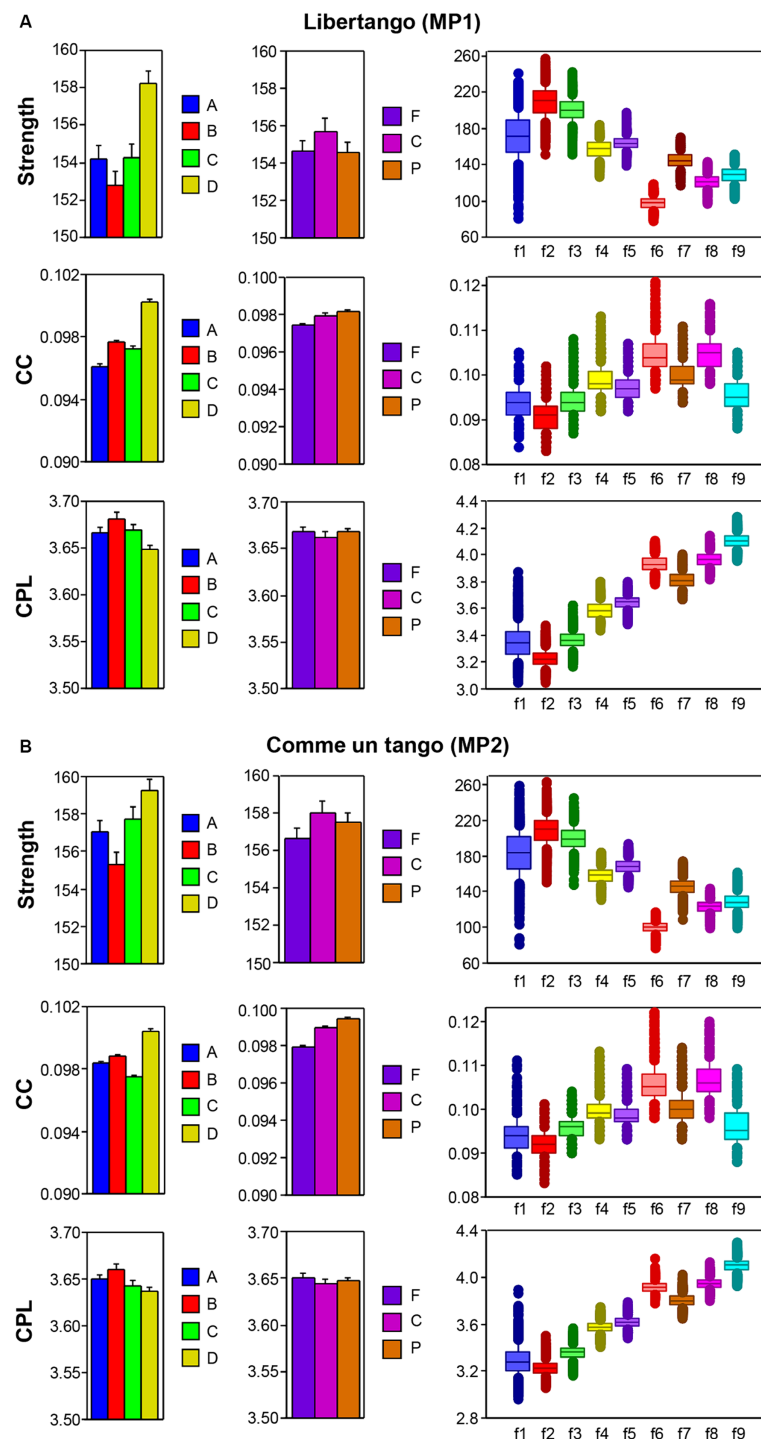


FIGURE 4

ANOVA results for mean values of the three GTA measure (S, CC, and CPL) for Libertango and Comme un tango, respectively. **(A)** ANOVA results for Libertango. Main effects of the factors Guitarist (A, B, C, and D), Site (F, C, and P), and Frequency (f1-f9) are presented here. **(B)** ANOVA results for Comme un tango. The same main effects as in **(A)** are presented here. The main effects of the factor Sequence for both music pieces can be obtained in Figure 3 presented for the four guitarists.

multivariate Granger causality also shows specific relationships between the guitar sounds and between the NTD indices but also between the sounds and NTD, particularly during Libertango. Most interestingly, the last relationships are mostly unidirectional and mostly go from guitar sounds to NTD indices. In other words, guitar sounds affect or influence the hyper-brain communication more strongly than

vice versa. Figure 9 displays the relationships between the guitar sounds and the coupling within (WFC) and between (CFC) the HB-HFN layers. As to be seen, the four guitarists are more similar in terms of inter-layer or CFC communication as compared to the intra-layer or WFC communication. MPF shows stronger relationships with NTD, especially with respect to within-layer coupling or WFC and especially

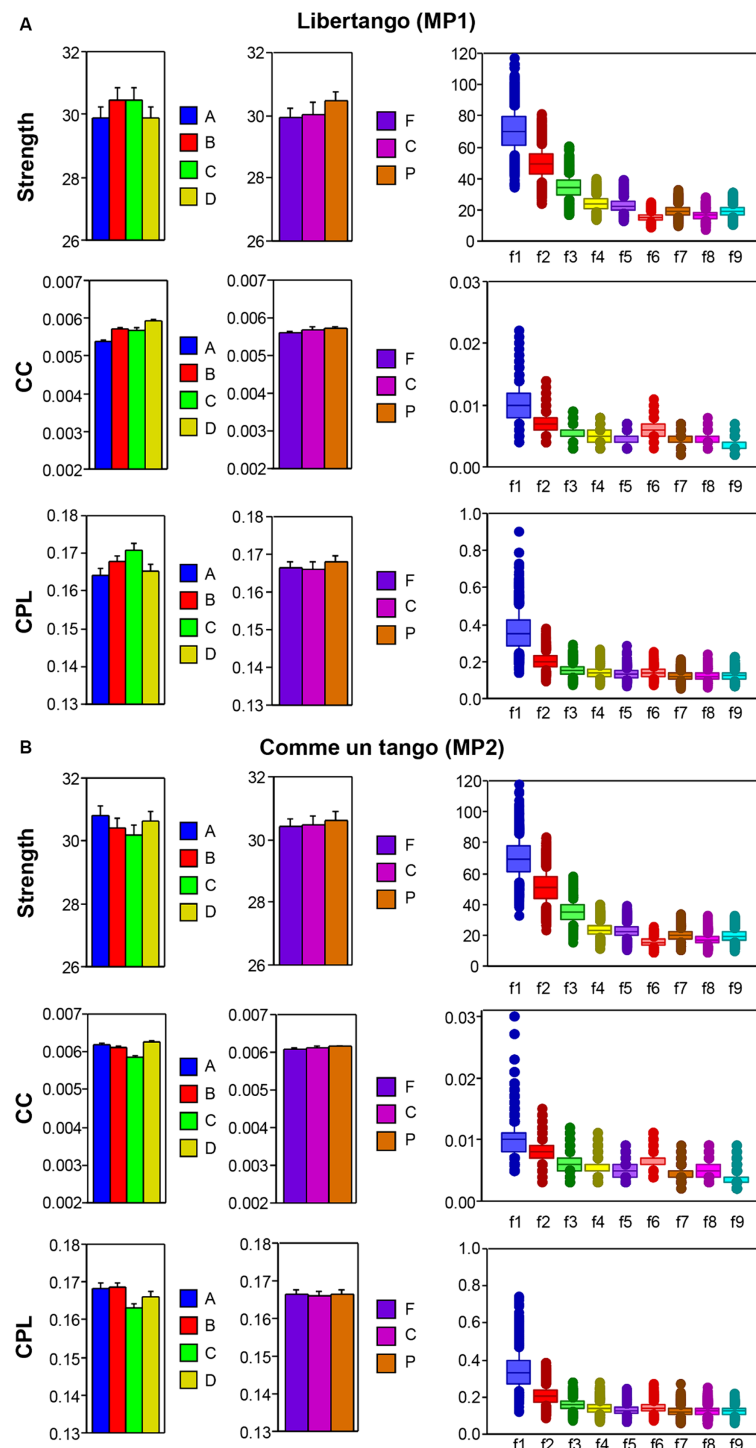


FIGURE 5

ANOVA results for SD values of the three GTA measure (S, CC, and CPL) for Libertango and Comme un Tango, respectively. (A) ANOVA results for Libertango. Main effects of the factors Guitarist (A, B, C, and D), Site (F, C, and P), and Frequency (f1–f9) are presented here. (B) ANOVA results for Comme un tango. The same main effects as in (A) are presented here. The main effects of the factor Sequence for both music pieces can be found in the [Supplementary materials](#).

during Libertango, also mostly directed from sounds to the HB-HFN coupling. [Figure 10](#) illustrates the relationships between guitar sounds and the intra- and inter-brain couplings. As expected, the inter-brain couplings of the four guitarists are strongly related to each other in the case of a linear relationship (correlation) but practically disappear (with

some exceptions) in the case of multivariate GC because of the absence of clear directional connections. Interestingly, there are relatively strong correlations between intra- and inter-brain coupling strength in each of the guitarists. In other words, high intra-brain strengths in a guitarist are strongly related to the connection strengths from this guitarist to

all others. In the case of multivariate GC, this relationship, if present, is mostly unidirectional and goes from inter-brain to intra-brain strength, and may involve not only the same, but also the other guitarists (see [Figure 10](#) for details). There are several connections between guitar sounds and strengths (both intra- and inter-brain) mostly going from guitar to brain, especially during Libertango, but also from brain to guitar, especially during Comme un tango.

Robustness of HB-HFNs by stepwise elimination of different types of edges

To investigate the robustness of the HB-HFN and the role of network connections, we manipulated the loss of the different types of connections within the whole HB-HFN and within individual guitarists' brains and examined how this loss of connections changes the network topology both within the whole HB-HFN and in individual guitarists' brains. To do so, we gradually eliminated connections in 15 5%-steps with three different types of loss, of the weakest, the strongest, and of random connections, and calculated the network topology each time. We compared these changes with the network topology without loss of connections. [Figures 11A–C](#) depict the respective manipulations for a 75% loss across the entire network and specifically for the in- and out-degree of guitarist A. [Figures 11D,E](#) illustrate the dynamics of both lost and retained strengths throughout the 15 elimination steps for the 9 FOI. The removal of the weakest connections involves both high and low-frequency connections or nodes, but the low-frequency connections with high strengths are consistently preserved throughout all 15 elimination steps. The removal of the strongest connections mainly impacts the low-frequency connections, and the preservation of these connections and their strength rapidly decreases across the 15 elimination steps. Interestingly, when the connections are removed randomly, the low-frequency connections are increasingly affected, and the preservation of these connections also decreases at a high rate, but they persist throughout all elimination steps.

All topology measures were averaged across the time windows within a music sequence and mean values ($\pm$ CI) are presented in the diagrams for different types of connection loss compared to no loss. [Figure 12A](#) shows changes of CC (left) and CPL (right) in the whole HB-HFN when the loss of connections was also manipulated in the entire network. As expected, CC decreases and CPL increases or becomes longer as connection loss increases, especially when the strongest or random connections are lost. Importantly, CPL remains relatively robust when the weakest (and partly also random) connections are lost, while CC decreases significantly even when the weakest connections are lost. [Figure 12B](#) shows the changes in network topology in the entire HB-HFN when the loss of connections was simulated only in the brain of one guitarist (here guitarist A) with regard to the in-degree. Since the out-degree manipulation showed similar results in terms of network topology changes across the entire HB-HFN, it is not shown here. It can be seen that NTDs undergo similar changes as before, but the extent of these changes is much smaller. Most importantly, the topology mostly does not change significantly when the strongest connections of a guitarist are retained. Only when the strongest (or even random) connections are lost in one of the guitarists do the changes in the NTD become significant, especially in the CPL, which is apparently less robust than the CC,

although the changes in the CC are also significant. In [Figures 12C–F](#), the robustness within an individual brain (here guitarist A) is displayed when the loss of connections is manipulated in the same guitarist's brain ([Figures 12C,D](#)) or in the other guitarist's brain (here guitarist D; [Figures 12E,F](#)). When the loss of connections is manipulated in the same guitarist's brain, CC does not change at all when the strongest connections remain, and it decreases non-linearly when the strongest or random connections are lost, regardless of whether the in-degree or the out-degree has been manipulated ([Figures 12C,D](#)). The CPL in this case becomes longer, especially when the in-degree is manipulated, and especially when the strongest connections are lost. If the strongest connections are retained, the functionality of the individual subnetwork is largely preserved. When the loss of connections in the brain of the other guitarist (here guitarist D) is manipulated, CC in the brain of guitarist A decreases for all types of manipulations (especially when the strongest connections are lost), regardless of whether the in-degree or the out-degree was manipulated ([Figures 12E,F](#)). The CPL in this case does not change significantly when the in-degree of guitarist D is manipulated, while it increases or becomes longer when the out-degree of guitarist D is manipulated or decreases, especially when the strongest connections are lost. Similar results of network topology changes in relation to guitarist D can be found in the [Supplementary materials](#), which indicate invariance of topology changes with respect to different guitarists.

Discussion

The primary objective of this study was to investigate the multilayer hyper-brain network dynamics and architecture in a quartet of guitarists playing together, where the WFC indicates coupling within the layers and the CFC indicates coupling between them. The main findings are that: (a) the four guitarists significantly differ in their network topology dynamics, apparently indicating their different roles in the common hyper-brain network during play; (b) hyper-brain coupling strengths involving the four guitarist brains decrease with higher oscillation frequency, while CC and especially CPL increase with ascending frequency (CPL becomes longer); (c) the couplings within (WFC) and between (CFC) the layers as well as within and between brains differ with respect to the guitarists, oscillation frequency, brain sites, and the two music pieces, with generally higher WFC within the brains and higher CFC between the brains; (d) the variability of all NTD measures exponentially decreases with higher oscillation frequency, indicating high variability of low-frequency nodes in HB-HFN; (e) different NTD measures show linear and causal relationships with guitar sounds, varying in amplitude (ENV) and frequency (MPF) characteristics, with the guitar sounds having a stronger influence on the brain's NTD than vice versa; (f) the HB-HFN behavior and underlying NTD are relatively robust against the loss of connections, especially when the strongest connections are preserved and especially when connection loss only affects the brain of one guitarist.

As suggested, significant differences in the topology indices among the four guitarists apparently indicates that the guitarists have different roles in the common HB-HFN, with guitarist D characterized by high segregation and high integration of coupling in the common HB-HFN. Furthermore, the differences between guitarists vary depending on the oscillation frequency and brain

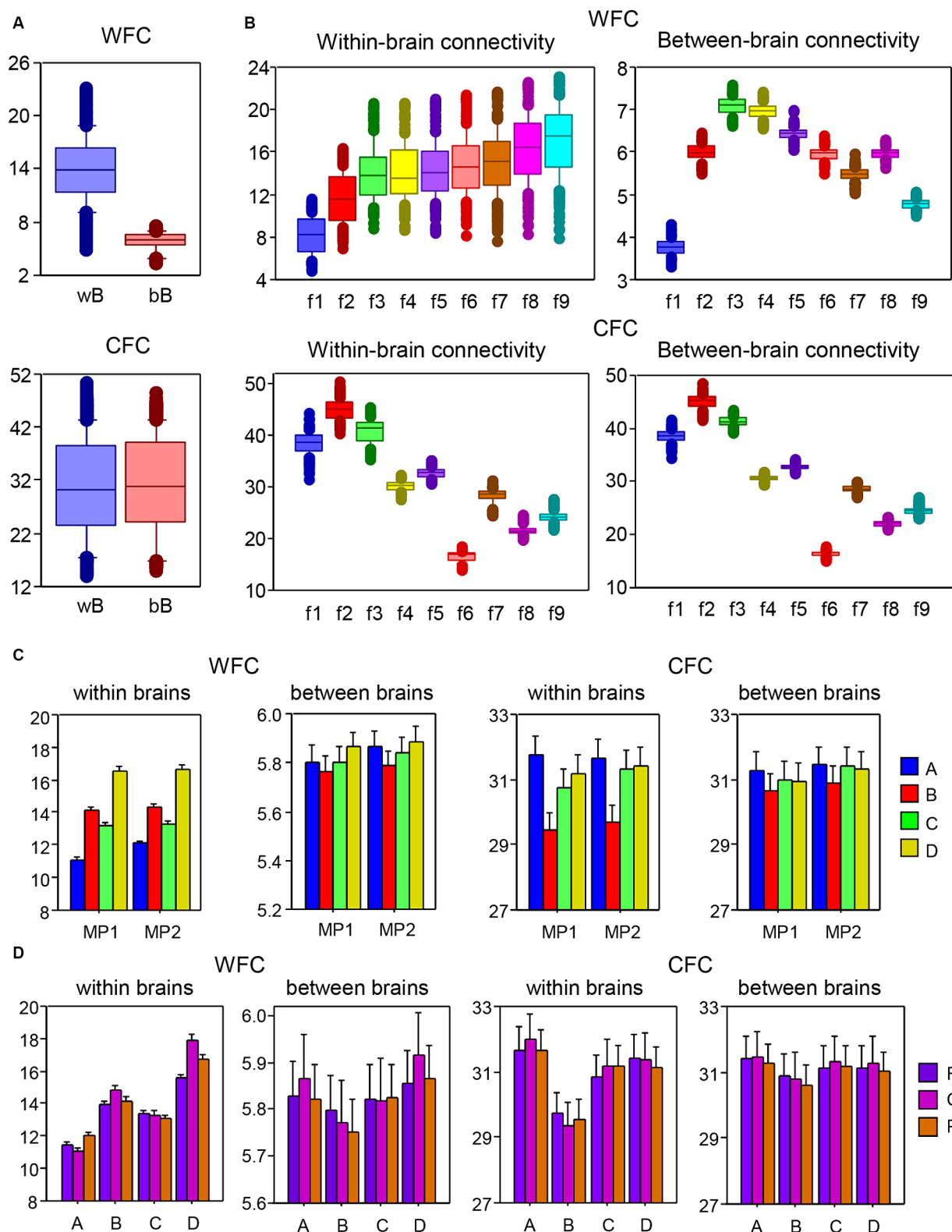


FIGURE 6

ANOVA results for mean values of within- and between-brain connectivity measured by WFC and CFC, respectively. **(A)** ANOVA results for the main effect of Coupling. The main effect of the factor Coupling (within vs. between brains) for WFC (top) and CFC (bottom) is presented in box plots. **(B)** ANOVA results for the main effect of Frequency. The main effect of the factor Frequency for WFC (top) and CFC (bottom) is presented in box plots. Note that within-brain (left) and between-brain (right) couplings are shown in two separate box plots. **(C)** ANOVA results for the interaction Guitarist by Music Piece (MP1: Libertango; MP2: Comme un tango). The interaction of Guitarist by Music Piece for WFC (left) and CFC (right) is presented for within-brain and between-brain couplings in two separate diagrams. **(D)** ANOVA results for the interaction of Guitarist by Site. The interaction of Guitarist by Site for WFC (left) and CFC (right) is presented for within-brain and between-brain couplings in two separate diagrams.

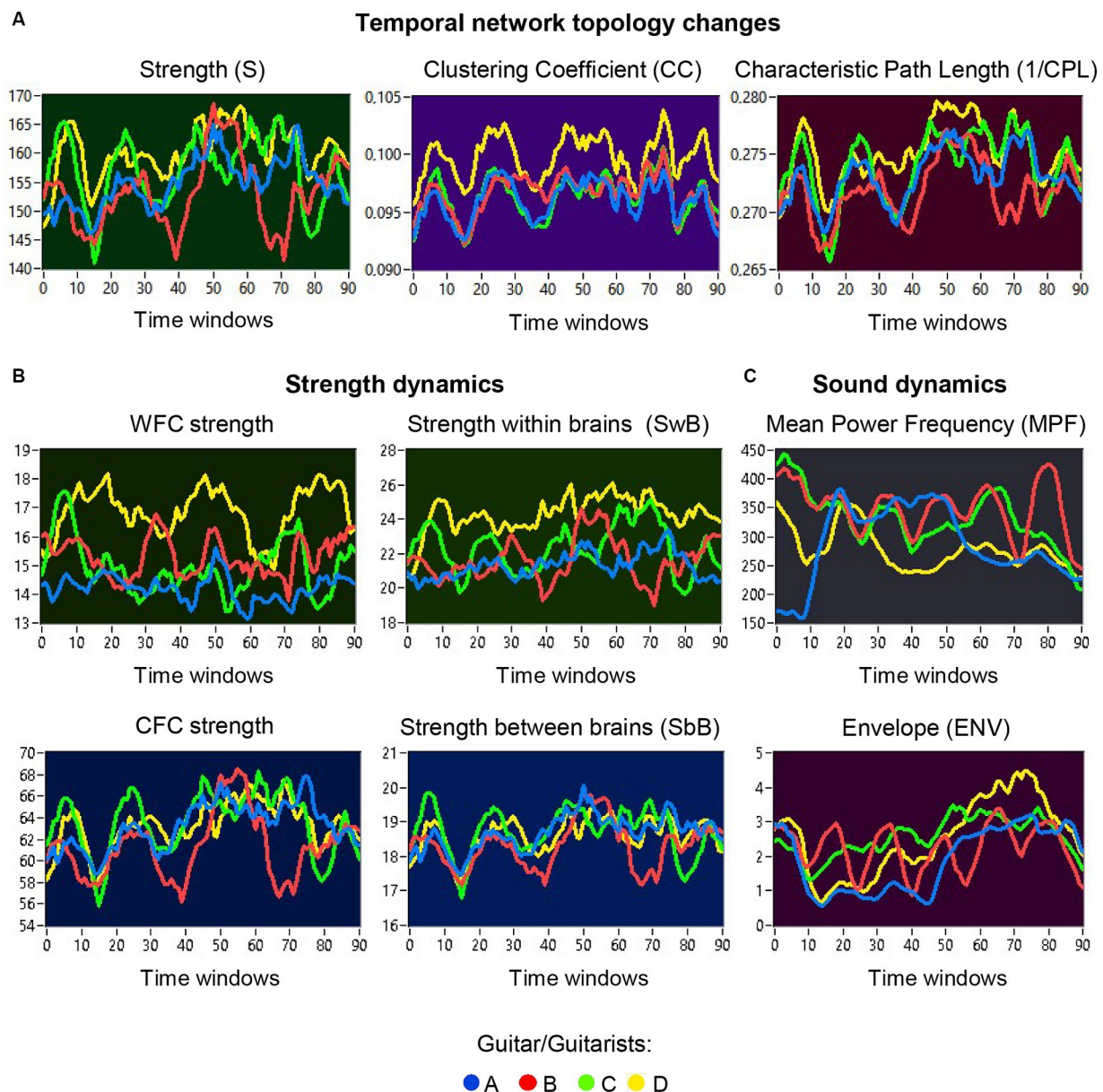


FIGURE 7

Temporal network topology changes and sound dynamics. **(A)** Examples of temporal changes in network topology within a music sequence, indicated by *S*, *CC*, and *CPL*. The temporal changes in the network topology are depicted separately for the four guitarists (guitarist A in blue, guitarist B in red, guitarist C in green, and guitarist D in yellow) across different time windows. **(B)** Examples of temporal changes in strengths within a music sequence, calculated separately for WFC and CFC, as well as for within- and between-brain coupling. The temporal changes in strengths are also depicted separately for the four guitarists across different time windows. **(C)** Examples of sound dynamics within a music sequence, indicated by *MPF* and *ENV*. Sound dynamics, as indicated by *MPF* (top) and *ENV* (bottom), are presented separately for the four guitar sounds (guitar A in blue, guitar B in red, guitar C in green, and guitar D in yellow) across different time windows.

regions, and most importantly, the network topology of guitarists differs in different music sequences and pieces of music, indicating that the network topology is nonstationary and contingent on musical situation. Moreover, these differences between guitarists also depend on the couplings type (WFC or CFC) and their properties (within or between the brains). The dependence of the guitarists' network topology on the musical situation as well as on coupling properties has also been demonstrated in our previous work (Sänger et al., 2012, 2013; Müller et al., 2013, 2018b; Müller and Lindenberger, 2019).

Ensemble performance has been conceived as a microcosm of social interaction in which the ensemble functions as a dynamic system and the individual musicians as processing units (D'Ausilio et al., 2015). We show here that this microcosm has a multi-layered structure and the musicians act differently at different organizational levels in terms of their neural connections, which collectively form the entire network and its constituent parts. It can also be seen that the strengths of nodes in the common HB-HFN decrease with high frequency, while *CC* and especially *CPL* increase. All the changes across the frequencies forming different layers in multilayer networks

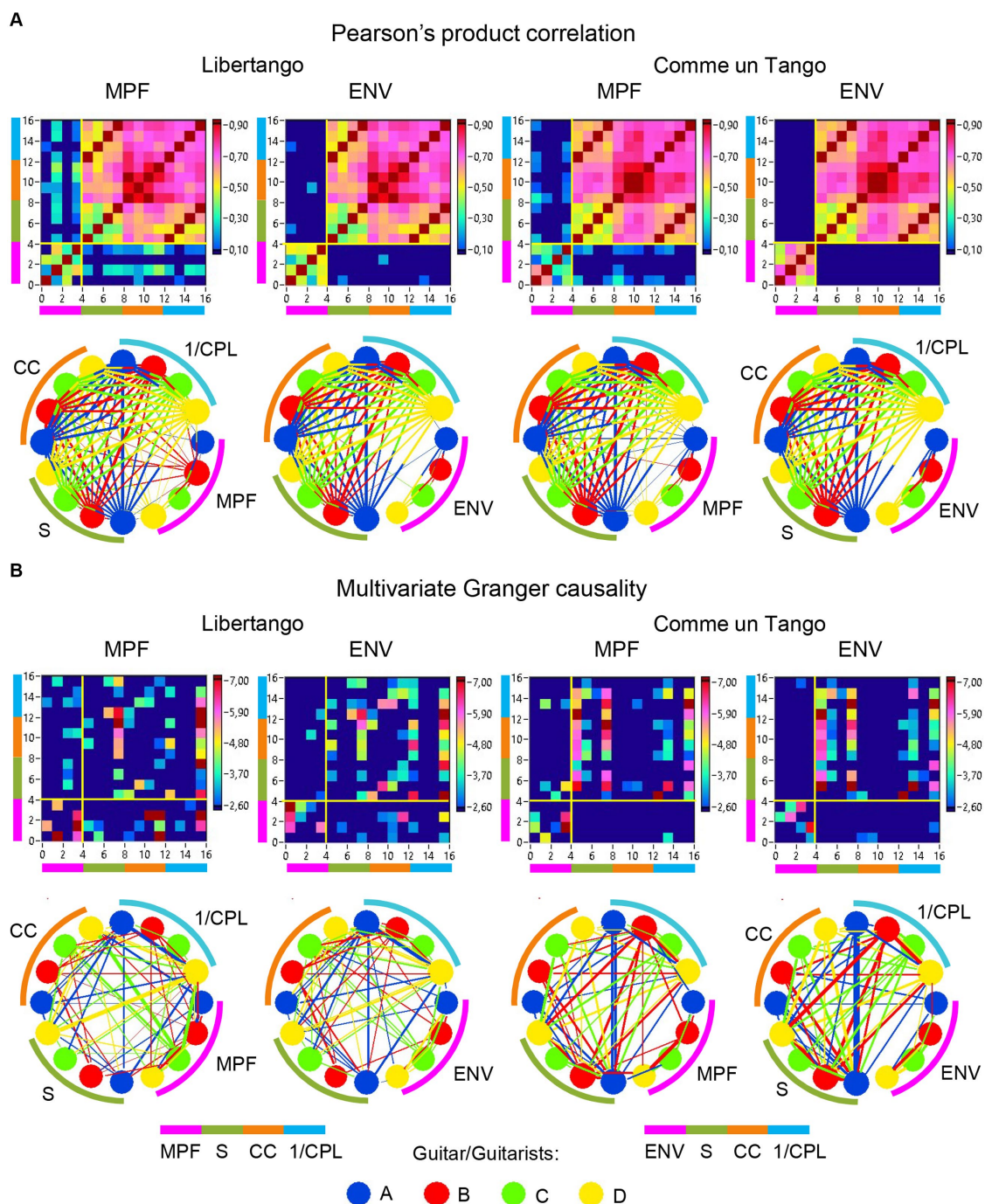


FIGURE 8

Linear and directional relationships between guitar sounds (MPF and ENV) and NTD indices (S, CC, and 1/CPL) for Libertango and Comme un Tango, respectively. **(A)** Linear relationships indicated by Pearson's product correlation. **(B)** Directional relationships indicated by multivariate Granger causality. The relationships are presented as matrices or heatmaps and circular connectivity maps. The different measures in the heatmaps and circular connectivity maps are highlighted by stripes or arcs of different colors: the pink stripe or arc indicates the four guitar sounds, determined by MPF or ENV (nodes 1–4), the green stripe or arc indicates the S in the four guitarists' brains (nodes 5–8), the light brown stripe or arc indicates the CC in the four guitarists' brains (nodes 9–12), and the light blue stripe or arc indicates the inverse CPL or 1/CPL in the four guitarists' brains (nodes 13–16). The four guitars or guitarists in the connectivity maps are indicated by color. The linear relationships are symmetric and the directional relationships are asymmetric. The direction of the links is coded by color. Note that the links in the directional connectivity maps are either unidirectional or bidirectional.

are highly significant and indicate different contributions of these frequencies to the network topology and functioning, with lower frequencies contributing to network integration (indicated by shorter

CPL) and higher frequencies providing or causing network segregation (indicated by higher CC) (Müller et al., 2018b). Interestingly, there is a discrepancy regarding WFC with respect to changes of within- and

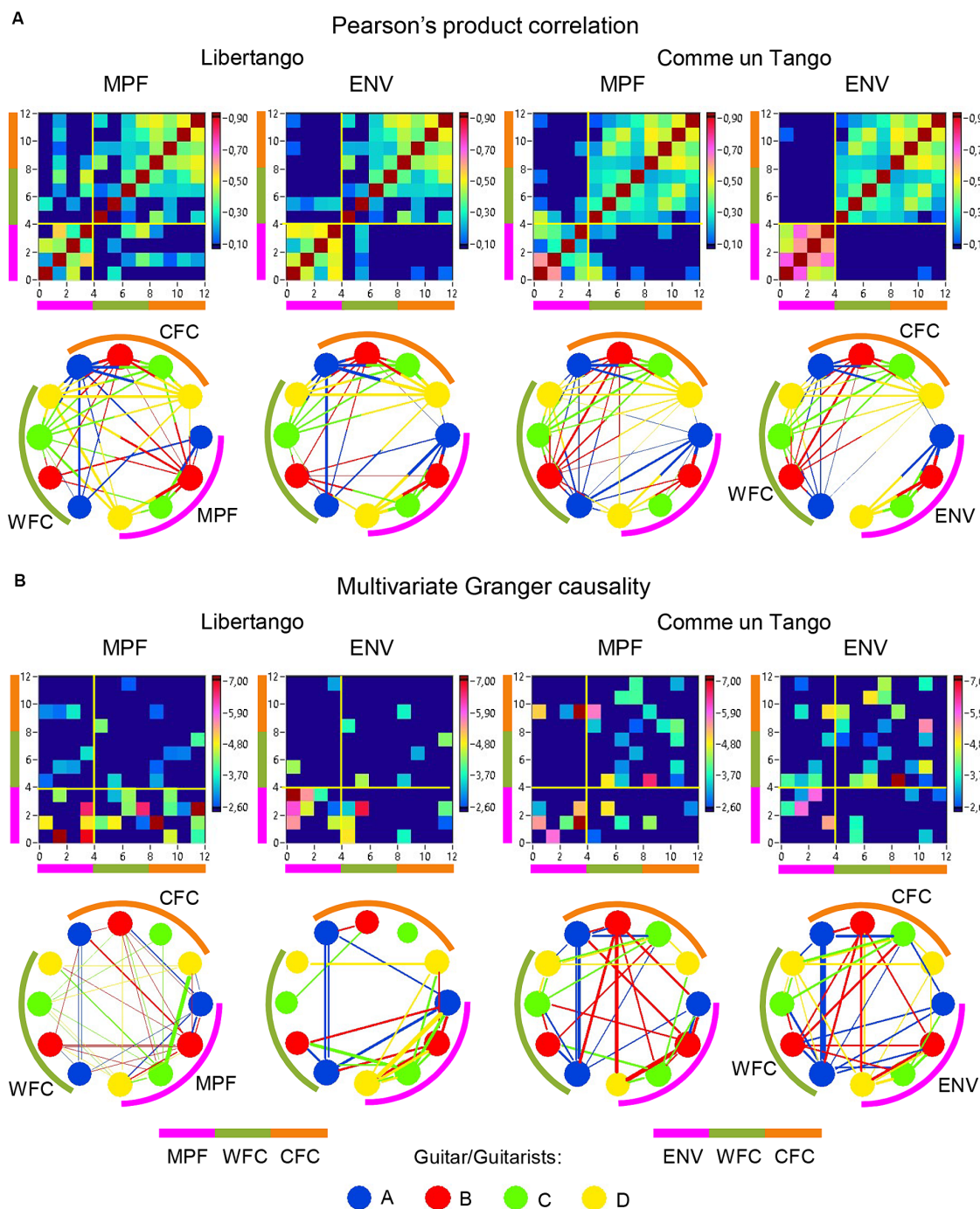


FIGURE 9

Linear and directional relationships between guitar sounds (*MPF* and *ENV*) and WFC and CFC strengths for Libertango and Comme un tango, respectively. **(A)** Linear relationships indicated by Pearson's product correlation. **(B)** Directional relationships indicated by multivariate Granger causality. The relationships are presented as matrices or heatmaps and circular connectivity maps. The different measures in the heatmaps and circular connectivity maps are highlighted by stripes or arcs of different colors: the pink stripe or arc indicates the four guitar sounds, determined by *MPF* or *ENV* (nodes 1–4), the green stripe or arc indicates the WFC strengths in the four guitarists' brains (nodes 5–8), and the light brown stripe or arc indicates the CFC strengths in the four guitarists' brains (nodes 9–12). The four guitars or guitarists in the connectivity maps are indicated by color. The linear relationships are symmetric and the directional relationships are asymmetric. The direction of the links is coded by color. Note that the links in the directional connectivity maps are either unidirectional or bidirectional.

between-brain coupling with advancing frequency: while the WFC within brains increases with higher frequency, WFC between the brains increases only up to 10 Hz and then gradually decreases. Similar coupling patterns were also found previously (Müller et al., 2013,

2018b). However, we show here that these patterns are characteristic only for the WFC, while CFC (both within and between brains) practically showed strong decrease with growing frequency. This indicates that CFC at low frequencies is of paramount importance

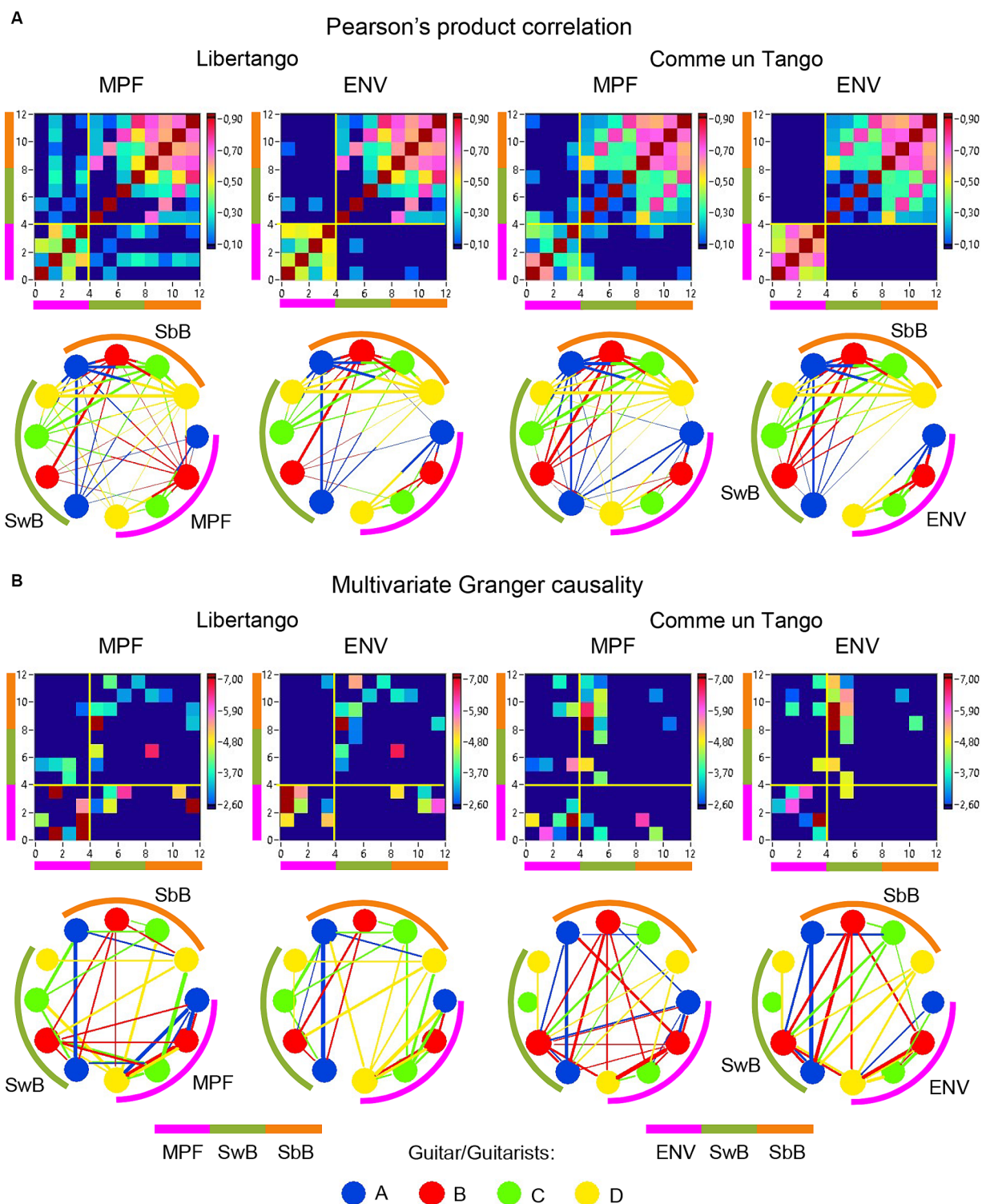


FIGURE 10

Linear and directional relationships between guitar sounds (MPF and ENV) and within- and between-brain strengths for Libertango and Comme un Tango, respectively. (A) Linear relationships indicated by Pearson's product correlation. (B) Directional relationships indicated by multivariate Granger causality. The relationships are presented as matrices or heatmaps and circular connectivity maps. The different measures in the heatmaps and circular connectivity maps are highlighted by stripes or arcs of different colors: the purple stripe or arc indicates the four guitar sounds, determined by MPF or ENV (nodes 1–4), the green stripe or arc indicates the within-brain strengths (wB) in the four guitarists' brains (nodes 5–8), and the light brown stripe or arc indicates the between-brain strengths (bB) in the four guitarists' brains (nodes 9–12). The four guitars or guitarists in the connectivity maps are indicated by color: guitar/guitarist A in blue, guitar/guitarist B in red, guitar/guitarist C in green, and guitar/guitarist D in yellow. The linear relationships are symmetric and the directional relationships are asymmetric. The direction of the links is coded by color. Note that the links in the directional connectivity maps are either unidirectional or bidirectional.

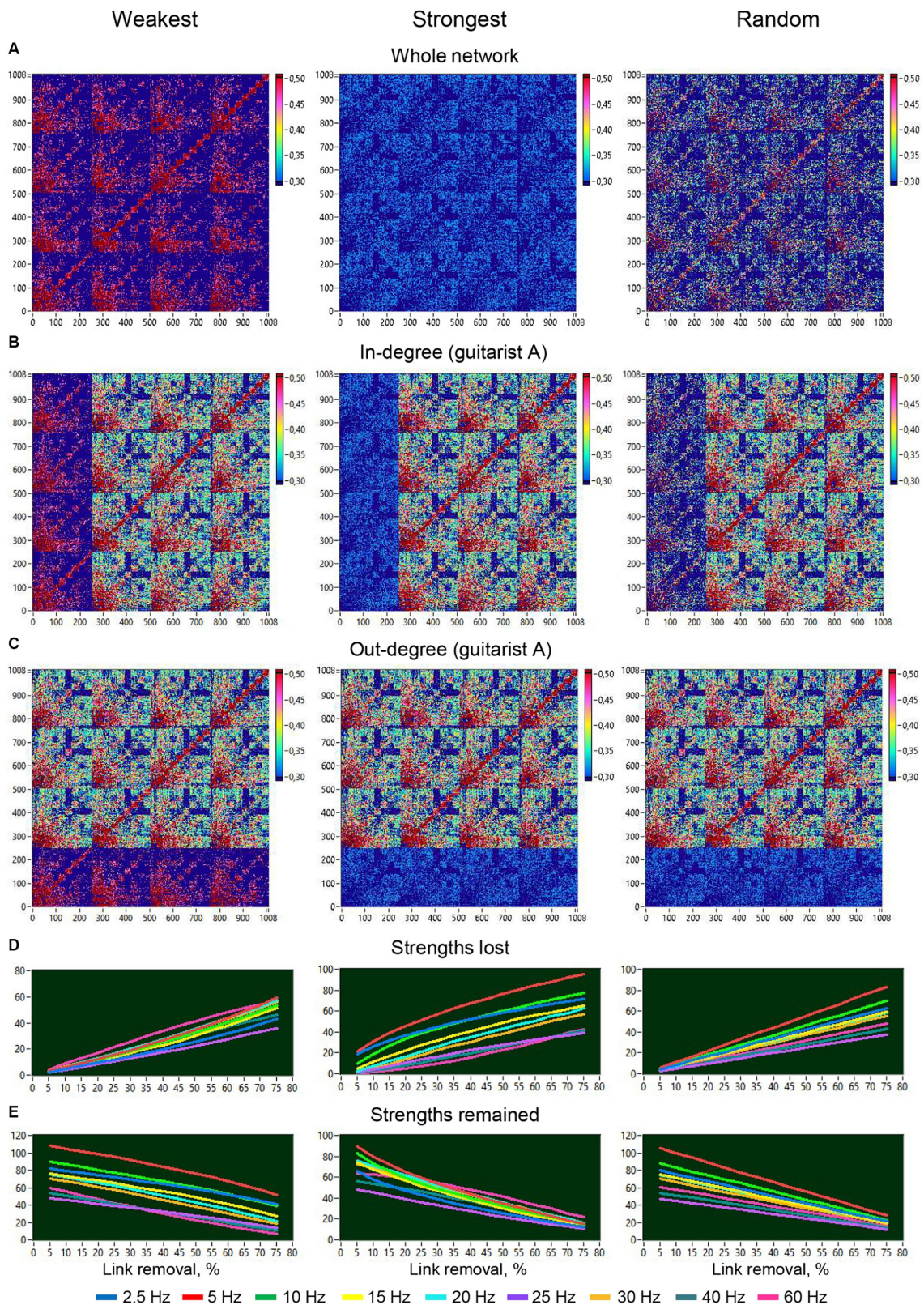


FIGURE 11

Removal of different types of links from the entire network or from one guitarist's brain and changes in strengths of different frequencies as a function of this removal. (A) Removal of different types of links from the entire network. (B) Removal of different types of links or in-degree manipulation in guitarist A. (C) Removal of different types of links or out-degree manipulation in guitarist A. (D) Changes in loss of strengths at different frequency nodes as a function of link removal from the entire network. (E) Changes in retaining strengths at different frequency nodes as a function of link removal from the entire network.

with respect to neuronal integration between different network structures and network layers. Similar results were found in a kissing study, where WFC and CFC were used for evaluation of the inter-brain synchrony, with theta–alpha hyper-brain subnetworks playing an essential role in the between-brain binding, and with alpha-frequency nodes serving a cleaving or pacemaker function in the HB-HFN (Müller and Lindenberger, 2014). Most interestingly, such a differentiation between WFC and CFC patterns (increasing WFC and decreasing CFC with advancing frequency) was also found in a superordinate physiological system with the respiratory, cardiac, and vocalizing subsystems in a choir in song, also including the motor subsystem of the choir conductor (Müller et al., 2018a). It can therefore be assumed that such system behaviors (with increasing WFC and decreasing CFC in relation to increasing frequency) are characteristic of biological systems and of organismic, but also social organizations. This is apparently due to the fact that WFC typically emphasizes the local features of complex systems, which operate relatively quickly and utilize faster frequencies for this purpose. In contrast, CFC tends to focus on the integrative capabilities of the system, which are better suited to slower or lower frequencies. These coordination dynamics are assumed to function as a superordinate system, or superorganism, based on the principles of self-organization and circular causality with upward and downward causation, which are emergent properties of the system (Müller et al., 2018a, 2019a; Delius and Müller, 2023).

Examining the dynamics within the music sequences showed that the variability in the network topology determined by the SD differs in the four guitarists and also varies with the electrode sites, oscillation frequency, and music sequences in the two pieces of music. Most interestingly, the SD decreased with higher frequency for all topology measures. This suggests that the low-frequency nodes, which exhibit most variability, may have adaptive capabilities to adequately adjust the system or HB-HFN to the changes that occur during guitar playing. Recent literature suggests that brain signal variability (i.e., transient temporal fluctuations in brain signal) can capture complex interactions between neuronal structures and cell assemblies and provide important information about network dynamics and brain states as well as cognitive performance and mental activity (McIntosh et al., 2008, 2014; Deco et al., 2011; Garrett et al., 2011, 2015; Sleimen-Malkoun et al., 2015). It has also been shown that the network structure and connectivity dynamics are non-stationary and reveal rich dynamic patterns, 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). In addition, analysis of the temporal variability of HFN structure has revealed specific NTD, i.e., temporal changes of different GTA measures such as strength, CC, CPL, and local and global efficiency determined for HFNs in different time windows (Müller et al., 2016, 2019b). Furthermore, the variability of these NTD metrics, as measured by the SD over time, was found to correlate positively with perceptual speed, suggesting that a more variable NTD increases performance on cognitive or at least perceptual speed functions and improves the adaptability of the system or individual (Müller et al., 2019b). Thus, the high variability or adaptability of low-frequency nodes in the HB-HFN is accompanied by the integrative properties of these nodes as indicated by the shorter CPL.

It has been suggested that the real-time exchange of information between musicians that the ensemble needs to maintain coordination and achieve its artistic goals is determined by the social dynamics and

constraints related to the musical material and instruments (Keller, 2014, 2023; Bishop, 2018; Bishop et al., 2021; Bishop and Keller, 2022). As mentioned above, the relationships between brains and instruments provide important evidence that inter-brain or hyper-brain synchrony has a specific relationship to the behavior of musicians (Müller and Lindenberger, 2023). Here we showed that different NTD measures exhibit linear and/or causal relationships with guitar sounds that vary in amplitude and frequency characteristics, with guitar sounds having a stronger influence on brain NTD than vice versa. These guitar-to-brain connections were also found for intra- and inter-brain strengths, especially during Libertango, but there were also connections going from brain to guitar, especially during Comme un tango. We also showed that high intra-brain strengths in a guitarist are strongly related to the inter-brain connectivity strengths from this guitarist to all others. Moreover, this relationship, when examined by multivariate GC, is mostly unidirectional and reaches from inter-brain to intra-brain strength, and may involve not only the same but also other guitarists. These influences from inter-brain to intra-brain strength presumably indicate that inter-brain synchrony can affect neural processes within the brains to achieve a stronger coordination of playing. In our previous study, we showed that these relationships between brains and instruments concern not only the guitarists' but also the audience members' brains during a concert (Müller and Lindenberger, 2023). In general, it can be concluded that the network topology of brains and the dynamical structure of guitar sounds are in permanent interplay and exhibit specific guitar–guitar, guitar–brain, and brain–brain bi- and unidirectional associations, indicating multilevel dynamics with upward and downward causation at all levels of dynamic organization.

We investigated the effect of edge or link removal in the entire HB-HFN or in its part concerning one guitarist's brain and examined how this removal would change the network topology within the whole HB-HFN and in individual guitarists' brains. We showed that the HB-HFN of the guitarist quartet is relatively robust against the loss of connections, especially when the strongest connections are preserved and especially when the loss of connections only affects one guitarist's brain. When the edge removal or the loss of connections is manipulated in one guitarist's brain, the topology measures (CC and CPL) change significantly only when the random and especially the strongest connections were lost, while the weakest connections mostly have no significant effect on the network topology. This indicates that the strongest connections play an essential role in the network topology and the loss of these connections may have detrimental consequences for topology and functioning. As mentioned above, network robustness is the ability of a network to maintain its integrity and functionality after the removal of nodes or edges, and is a prominent feature of most biological systems and social groups (Barabási and Pósfai, 2016; Liu et al., 2020; Bellingeri et al., 2020b). The fact that removing nodes according to weighted rank produces the highest damage in real-world complex networks is well known (Bellingeri and Cassi, 2018; Bellingeri et al., 2019, 2020a). Moreover, it has been found that the robustness of real-world complex networks against link removal is negatively correlated with link weights heterogeneity and that a small fraction of strong links removal can rapidly decrease the efficiency and the total flow in these systems (Bellingeri et al., 2019). All this indicates that removal of the strongest connections affects the functionality of a network not only because they are so strong, but

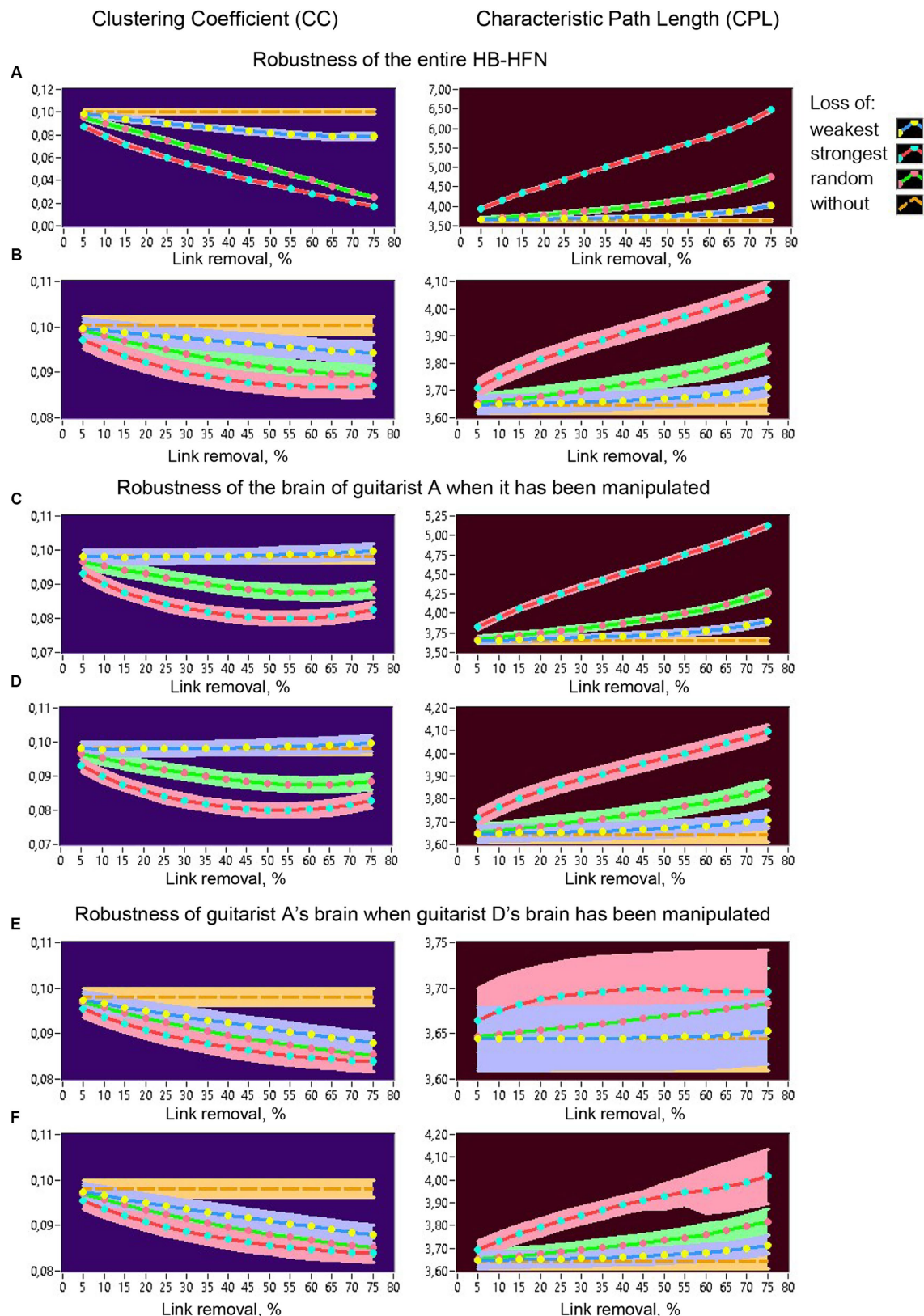


FIGURE 12

Robustness of the entire HB-HFN and of an individual guitarist's brain indicated by changes in *CC* and *CPL* as a function of link removal of different types. (A) Robustness of the entire HB-HFN when the entire HB-HFN has been manipulated. (B) Robustness of the entire HB-HFN when links have been removed only in one guitarist's brain (here guitarist A). (C) Robustness of one guitarist's brain (here guitarist A) as a part of the HB-HFN when in-degree in the same guitarist has been manipulated. (D) Robustness of the one guitarist's brain (here guitarist A) as a part of the HB-HFN when out-degree in the same guitarist has been manipulated. (E) Robustness of one guitarist's brain (here guitarist A) as a part of the HB-HFN when in-degree in

(Continued)

FIGURE 12 (Continued)

another guitarist (here guitarist D) has been manipulated. (F) Robustness of the one guitarist's brain (here guitarist A) as a part of the HB-HFN when out-degree in another guitarist (here guitarist D) has been manipulated. Changes in *CC* (left) and *CPL* (right) as a function of link removal across the 15 5%-steps are presented in all diagrams for different types of link removal: loss of weakest, strongest, and random connections, in comparison to without removal.

mainly because the strongest connections are highly relevant in terms of network structure and its topology. In HB-HFN of the guitarist quartet, the low-frequency nodes have the strongest connections and play an important role in the functioning of the network, which is mainly integrated by these connections or nodes. If one would imagine a situation in which the quartet is disturbed in its functionality (e.g., by any technical disturbances or other external circumstances), these low-frequency connections between the quartet participants would probably be the first to be disrupted, and the network could become disorganized or disintegrated. On the other hand, it has recently been shown that the coupling between the brains of pianists can increase during a disturbance, presumably as an adaptive compensatory effect of inter-brain synchronization (Lender et al., 2023). This indicates that our simulations of link removal are very important to understand how networks react, or can react, to such perturbations, but they are not sufficient to draw conclusions about living organisms or intact social groups and interactions, as different adaptive compensatory mechanisms can counteract the perturbations in such networks. Further studies are needed to better understand such processes and phenomena.

Limitations

The present study has limitations and leaves room for questions that should be addressed in future research. First, we considered the whole HB-HFN as a supra-adjacency matrix and computed the GTA measures for each individual node with respect to the whole network. The individual layers and the connections between them were only captured using WFC (as coupling within the layers) and CFC (as coupling between the layers) strengths. However, the multilayer structure could be assessed in an even more differentiated way. To do so, the GTA tools must be adapted or other tools must be used to differentiate between the layers. Furthermore, we only used three GTA measures (i.e., *S*, *CC*, and *CPL*). Other GTA measures could be helpful to capture other properties of these complex networks, such as assortativity, betweenness or closeness centrality, local and global efficiency, etc. Second, we analyzed the properties of the hyper-brain network within a single quartet. However, we observed consistent patterns of HB-HFN connectivity and network organization across different music sequences in two distinct pieces of music. While this may enhance the generalizability of the results, further research in this direction is warranted. Third, robustness of a complex network is an important property that has not yet been investigated in relation to hyper-brain networks. It may be useful to investigate such networks in a social interaction under perturbation conditions (cf. Lender et al., 2023) in order to verify and further develop the simulation assumptions. Furthermore, we investigated the

removal of links, but removal of nodes would broaden the perspective of robustness, allowing specific nodes and their role in the network to be investigated. Therefore, further sophisticated research is needed to shed light on the neural mechanisms of social interaction and interpersonal action coordination behavior.

Conclusion

Our results extend previous work on the reach of network interactions during interpersonal action coordination when playing the guitar in a quartet and highlight the way in which WFC and CFC, representing within- and between-layer communications in a complex multilayer HB-HFN, integrates different levels of network interaction with regard to its topology and functioning. We demonstrate linear and causal relationships between different characteristics of guitar sounds and GTA properties. We conclude that playing the guitar in a quartet is a dynamic process requiring tight interpersonal action coordination that is characterized by coupled brains and specific network topology dynamics, with high robustness of both network elements and underlying network structure. These findings align with studies investigating neural markers of interpersonal action coordination, particularly in the context of inter- or hyper-brain network activity (Sänger et al., 2012; Müller et al., 2013, 2018b; Müller and Lindenberger, 2014, 2019, 2023) and sensorimotor coupling in music and ensemble playing (Janata et al., 2012; Keller et al., 2014; van der Steen et al., 2015; Gallotti et al., 2017; Jacoby et al., 2021; Laroche et al., 2022). It is assumed that these coordination dynamics function as a superordinate system, or superorganism, based on the principles of self-organization and circular causality, which are emergent properties of system behavior. Our methods provide a versatile toolkit for studying interpersonal action coordination across various social interactions and behaviors.

Data availability statement

The data analyzed in this study is subject to the following licenses/restrictions: the dataset is intended for internal use only. Requests to access these datasets should be directed to vmueller@mpib-berlin.mpg.de.

Ethics statement

The studies involving humans were approved by the Ethics Committee of Max Planck Institute for Human Development approved the study. The studies were conducted in accordance with the local legislation and institutional requirements. The participants provided their written informed consent to participate in this study.

Author contributions

VM: Conceptualization, Investigation, Methodology, Project administration, Visualization, Writing – original draft, Writing – review & editing, Data curation, Supervision. UL: Writing – original draft, Writing – review & editing, Conceptualization, Supervision.

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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.2024.1416667/full#supplementary-material>

SUPPLEMENTARY VIDEO 1

This video contains a 30-second sequence from the quartet's performance of Libertango during the experiment.

SUPPLEMENTARY VIDEO 2

This video showcases real-time HB-HFN changes as the quartet performs a 5-second music sequence from Libertango.

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Measuring information alignment in hyperscanning research with representational analyses: moving beyond interbrain synchrony

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Hyperscanning, which enables the recording of brain activity from multiple individuals simultaneously, has been increasingly used to investigate the neuropsychological processes underpinning social interaction. Previous hyperscanning research has primarily focused on interbrain synchrony, demonstrating an enhanced alignment of brain waves across individuals during social interaction. However, using EEG hyperscanning simulations, we here show that interbrain synchrony has low sensitivity to information alignment across people. Surprisingly, interbrain synchrony remains largely unchanged despite manipulating whether two individuals are seeing same or different things at the same time. Furthermore, we show that hyperscanning recordings do contain indices of interpersonal information alignment and that they can be captured using representational analyses. These findings highlight major limitations of current hyperscanning research and offer a promising alternative for investigating interactive minds.

KEYWORDS

hyperscanning, EEG, interbrain synchrony, social interaction, representational alignment, information content

1 Introduction

Understanding how social interactions dynamically shape human mind and behavior and vice versa is a key question in cognitive neuroscience and psychology (Sebanz et al., 2006; Hari et al., 2015). Hyperscanning, which enables the recording of the brain activity of multiple individuals at the same time, has been increasingly used to address this question. Hyperscanning research revealed enhanced interbrain synchrony between individuals interacting socially, which has been argued to reflect resonant minds facilitating cooperation and communication (Dumas et al., 2010; Dikker et al., 2017; Pérez et al., 2017; Goldstein et al., 2018; Reindl et al., 2018). However, here we highlight an important limitation of interbrain synchrony measures by showing that these measures indexing the alignment of neural activity patterns across individuals have low sensitivity to their information content. We show that representational analyses, the framework of Representational Similarity Analysis (RSA) in particular, is a promising alternative to address this issue and better index information alignment across individuals in hyperscanning research.

2 Interbrain synchrony does not measure information alignment

Interbrain synchrony has been investigated in hyperscanning research using a range of neuroimaging techniques including Electroencephalography (EEG), Magnetoencephalography (MEG), functional Magnetic Resonance Imaging (fMRI), and functional Near-Infrared Spectroscopy (fNIRS). Numerous measures have been used to index interbrain synchrony in hyperscanning studies generally based on amplitude correlation and phase locking (Czeszumski et al., 2020). For EEG and MEG, enabling access to neural processing at faster time scales, these analyses have also focused on the amplitude and phase of neural oscillations, with larger emphases on activity in the alpha (8–12 Hz) and beta (13–30 Hz) bands (Dumas et al., 2010; Goldstein et al., 2018). See Czeszumski et al. (2020) for a comprehensive review of hyperscanning and interbrain synchrony measures.

While all these methods are relevant to measure synchrony in general, the processes captured by interbrain synchrony in the context of hyperscanning research remain unclear. The causal nature of this phenomenon has been the main source of concerns so far, whether interbrain synchrony directly drives synchronised mind and behavior or interbrain synchrony is simply caused by synchronised mind and behavior (Burgess, 2013; Hari et al., 2013; Hamilton, 2021; Novembre and Iannetti, 2021; Holroyd, 2022). If synchronised mind and behavior causes interbrain synchrony, then this suggests that there is no direct brain-to-brain coupling between individuals, and interbrain synchrony is the result of similar sensory and cognitive processes driven by shared environment and task. As pointed out by Hamilton (2021), a lack of direct brain-to-brain coupling may not be a critical issue because interbrain synchrony measures are still of interest for hyperscanning research if they provide insight into the alignment of sensory information and cognitive processes across individuals while socially interacting.

However, here we present results showing that interbrain synchrony measures do not effectively index information alignment between individuals because these measures are largely content agnostic. We leveraged a publicly available EEG dataset from the visual object recognition literature with 48 participants who were presented with 400 images from 40 categories (Shatek et al., 2022). All recordings were made individually with a 128-channel BrainVision actichamp EEG system. We used this dataset to run hyperscanning simulations to assess the sensitivity of interbrain synchrony to information alignment by comparing interbrain synchrony when two individuals see the same things (Same objects) vs. different things (Different objects) at the same time (Figures 1, 2).

We ran 10,000 hyperscanning simulations with 24 pseudo pairs randomly drawn from the 48 subjects available (Figure 2). Interbrain synchrony was computed for a wide range of frequencies as amplitude correlation and phase locking across subjects for all possible combinations of channels (Czeszumski et al., 2020). Results were averaged across all possible combinations of channels to capture any potential changes in interbrain synchrony. With optimal control of the timing and content of the presented stimuli, the results from the simulations revealed that interbrain synchrony has low sensitivity to information alignment across individuals. Amplitude correlation and phase locking values remained largely unchanged whether people were seeing the same object or not (Figure 2D). t -values after stimulus

presentation across all frequencies obtained from the 10,000 simulations show that difference between Same objects and Different objects would in most cases be statistically undetectable despite a sample size at least similar (i.e., 24 pairs) to those generally used in the literature (Figure 2F). Figure 2F depicting t -values on averaged amplitude and phase values across frequencies within 180 and 220 ms after image presentation – time window yielding highest percentages of significant t -values and peak decoding accuracy in object literature in general (Grootswagers et al., 2019; Shatek et al., 2022) – shows that barely 50% of the simulations reached statistical significance for interbrain synchrony (IBS). See legend of Figure 2 and publicly available code at <https://osf.io/etx64/> for further methodological details.

3 Interbrain representational similarity analysis to effectively measure information alignment

The Representational Similarity Analysis (RSA) framework has received significant interest in the field of cognitive neuroscience (Kriegeskorte et al., 2008; Haxby et al., 2014), including more recently in social neuroscience and the intersubject correlation community (Nastase et al., 2019; Popal et al., 2019), but has not been used yet in hyperscanning research. This analysis is based on the computation of Representational (Dis)similarity Matrices (RDMs) to abstract from the patterns of neural activity themselves and characterise their informational content, allowing testing how two different systems quantitatively relate to each other by comparing their RDMs. RSA makes it possible to compare the responses from different systems, including responses recorded with different neuroimaging systems, neuroimaging and behavioral responses, as well as responses from different individuals, as shown here.

We computed Interbrain RSA (IRSA) using the same amplitude and phase data as IBS (Figure 2E). RDMs that encode information content and abstract from activity patterns were first computed separately for each subject and channel by calculating the amplitude correlation and phase locking for all pairs of stimuli. This approach based on (dis)similar temporal patterns in time-frequency data separately for each channel differs from other approaches often used with RSA (Kriegeskorte et al., 2008; e.g., Grootswagers et al., 2017; Shatek et al., 2022), but allows here to directly compare between IRSA and IBS. The results of the simulations show that information alignment can be captured in EEG hyperscanning with better sensitivity using IRSA. IRSA values decrease dramatically when shuffling the stimuli (Figure 2E), as reflected in differences between Same object vs. Different objects being statistically detected more consistently than IBS with statistical significance being reached in most simulations (Figure 2F). See legend of Figure 2 and publicly available code at <https://osf.io/etx64/> for further methodological details.

4 IBS vs. IRSA: statistical comparison

Statistical analyses on the 10,000 simulations indicated that t -values testing differences between Same vs. Different objects in the 180–220 ms selected time window, as depicted in Figure 2F, were significantly higher for IRSA than IBS for both amplitude, $t(19998) = 117.22$, $p < 0.0001$,

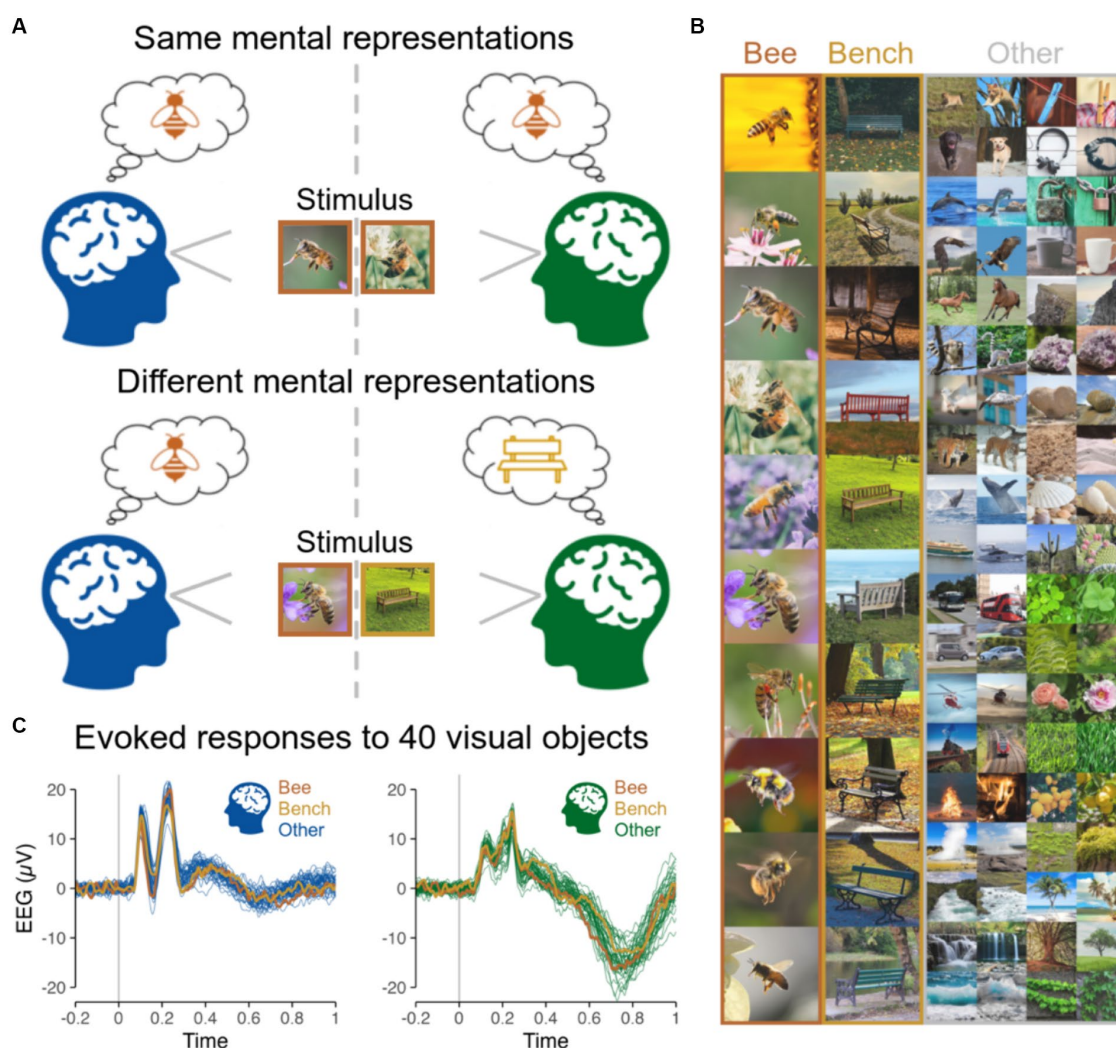


FIGURE 1

(A) Same vs. different mental representations across two subjects induced by the presentation of same vs. different objects at the same time. (B) Stimuli presented to subjects individually in Shatek et al. (2022), including 40 different categories of objects, each with 10 different images presented 10 times, while EEG used here to run hyperscanning simulations was recorded. The 10 images are shown for the categories Bee and Bench, and 2 out of the 10 images for each of the remaining 38 categories are shown in the 'Other' column. (C) EEG evoked responses for two representative subjects (at channel POz) for the 40 categories of objects averaged across all images and repetitions highlighting the low magnitude of variations related to image content.

$d = 1.66$, $BF_{10} > 1,000$, and phase, $t(19998) = 109.31$, $p < 0.0001$, $d = 1.55$, $BF_{10} > 1,000$, showing that IRSA has higher sensitivity to content shuffling than IBS. These effects held beyond the selected time window as indicated by significantly higher t -values for IRSA than IBS for both amplitude, $t(19998) = 139.21$, $p < 0.0001$, $d = 1.97$, $BF_{10} > 1,000$, and phase, $t(19998) = 95.87$, $p < 0.0001$, $d = 1.36$, $BF_{10} > 1,000$, when conducting these analyses on a larger time interval from 0 to 500 ms after stimulus presentation. Large effect sizes observed here demonstrate a critical advantage of IRSA over IBS to index information alignment from amplitude and phase data in hyperscanning research.

5 Perspectives and challenges

Using hyperscanning simulations with well-controlled visual stimuli, our work shows that content-related information in

hyperscanning research is not effectively captured by interbrain synchrony measures. This contrasts with previous research that found reliable decrease in interbrain synchrony when shuffling data across trials and/or pairs (Zamm et al., 2021, 2024; Reindl et al., 2022), which our results suggest might most likely be due to breaking the alignment of the timing of sensory and cognitive processes occurring in shared tasks and environments rather than the alignment of their information content. Shuffling information content while keeping timing constant in our simulations only marginally decreased interbrain synchrony whereas changes in timing resulting in large variations in neural signals would have a strong influence (Burgess, 2013; Holroyd, 2022). Examining and controlling for timing (dis)alignment of sensory, cognitive, and motor responses when shuffling across pairs and/or trials will be essential in future research to better understand the processes reflected by interbrain synchrony.

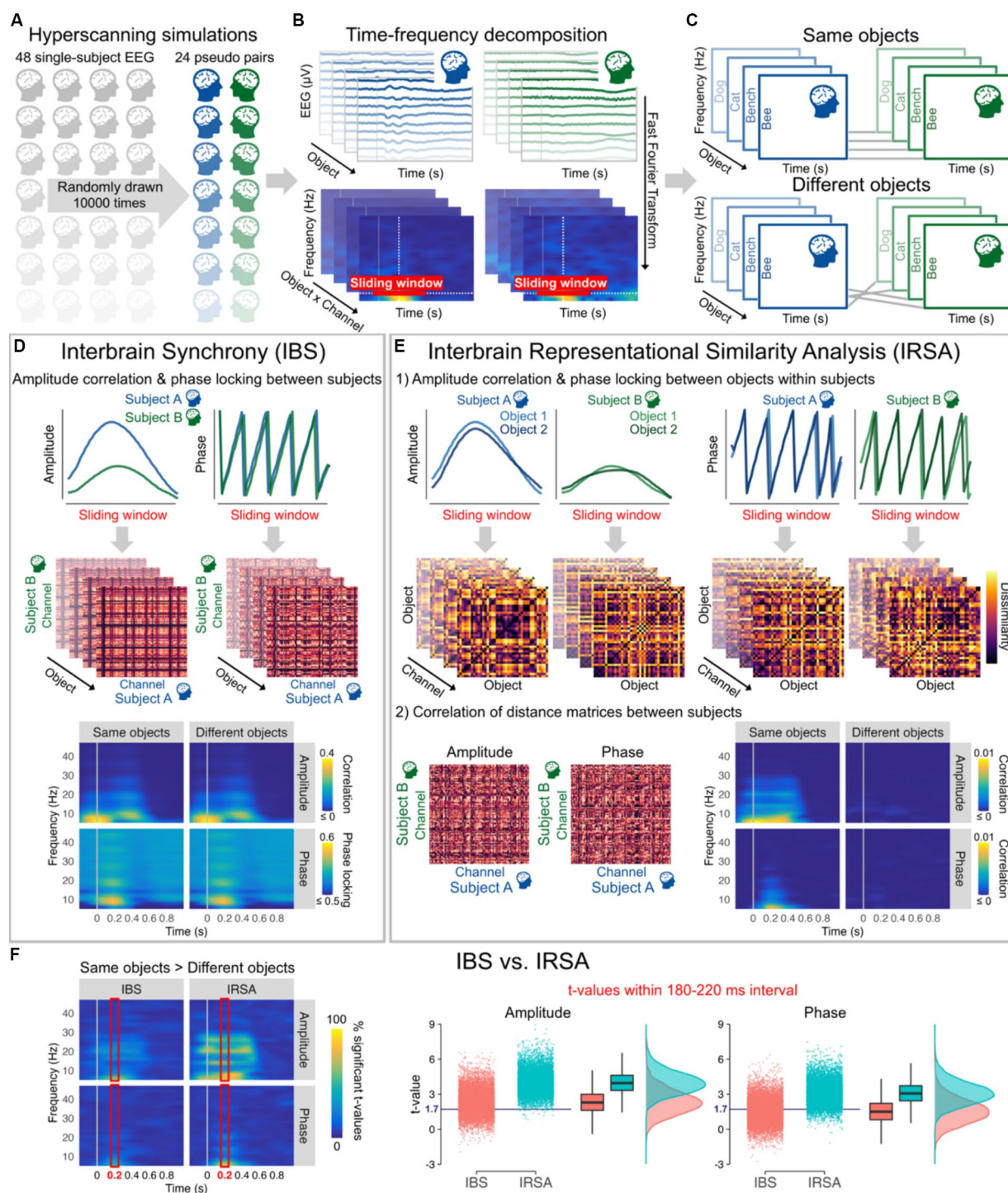


FIGURE 2

(A) 10,000 hyperscanning simulations based on individual 128-channel EEG recordings from Shatek et al. (2022), each simulation including 24 pseudo pairs randomly drawn from the 48 subjects available. (B) EEG data were average referenced, bandpass filtered between 0.1 and 100 Hz, and downsampled to 250 Hz. Amplitude and phase were then estimated for each channel and all 40 objects (averaged across all stimuli and repetitions within categories) from 6 to 46 Hz every 10 ms using a 500 ms sliding Hanning window yielding a 2 Hz frequency resolution (Oostenveld et al., 2011). (C) Objects presented to the two subjects of each pair were either kept the same (Same objects) or made different by shuffling their order (Different objects). (D) Interbrain synchrony (IBS) was computed at each 10 ms time step and frequency bin as the amplitude (Pearson) correlation and phase locking (relative phase mean vector length) between the two subjects of the pairs for all combinations of channels within a 510 ms sliding window from 0.2 to 1 s before/after stimulus onset. The resulting 128×128 channel interbrain connectivity matrices for each object were then averaged to obtain a single amplitude correlation and phase locking value at each time step and frequency bin for Same objects and Different objects. Interbrain connectivity matrices are from a representative pseudo pair (at 10 Hz and 200 ms after stimulus onset) and time-frequency maps correspond to the grand average of all pseudo pairs and simulations. (E) For Interbrain Representational Similarity Analysis (IRSA), amplitude correlation and phase locking

(Continued)

FIGURE 2 (Continued)

were first calculated between all pairs of objects within a 510 ms sliding window from 0.2 to 1 s before/after stimulus onset to obtain dissimilarity matrices. Amplitude dissimilarity was calculated as $1 - \text{Pearson correlation}$ and phase dissimilarity was calculated as $1 - \text{phase locking (relative phase mean vector length)}$. We then computed the (Spearman) correlation between dissimilarity matrices across the two subjects for all combinations of channels. The resulting 128×128 channel interbrain connectivity matrices were averaged to obtain a single correlation value at each time step and frequency bin for Same objects and Different objects. The figure shows example dissimilarity matrices and interbrain connectivity matrices from a representative pseudo pair (at 10 Hz and 200 ms after stimulus onset, channel POz for the dissimilarity matrices). Time-frequency maps correspond to the grand average of all pseudo pairs and simulations. (F) Time-frequency maps (averaged across all possible combinations of channels) represent the percentage of significant t -values from the 10,000 simulations for Same objects vs. Different objects (t -values >1.714 , critical t -value for one-tailed t -tests with 24 observations, $\alpha = 0.05$) for amplitude and phase data as a function of IBS and IRSA, with brighter colours indicating that large proportions of simulations yielded significant differences. The right panels represent the mean t -values within 180–220 ms (time interval showing highest percentages of significant t -values in line with peak decoding accuracy in object literature) from the 10,000 simulations for Same objects vs. Different objects after averaging correlation and phase locking data across all frequency bins. The blue horizontal line indicates the critical t -value. These plots show that the same vs. different objects differences were observed only in around 50% of simulations using IBS, but in more than 80% of simulations when using IRSA.

More generally, these results support the hypothesis that interbrain synchrony is caused by synchronised mind and behavior rather than the opposite, interbrain synchrony causing synchronised mind and behavior. Showing that interbrain synchrony does not uniquely capture sensory and cognitive processes supporting social interactions, our results suggest that interbrain synchrony cannot be a causal mechanism (underpinned by direct brain-to-brain coupling), and importantly, might be at best a poor proxy of synchronised sensory and cognitive processes supporting social interactions (Hamilton, 2021; Novembre and Iannetti, 2021). To be an effective top-down mechanism enabling the myriads of social behaviors observed every day, interbrain synchrony would not only require reflecting reliable timing information but also content information, which is not supported by our hyperscanning simulations.

The lack of unique and direct relationship between interbrain synchrony and synchronised sensory and cognitive processes during social interactions might explain part of the discrepancies in hyperscanning literature, including interbrain synchrony not being observed in some studies despite participants interacting and synchronising with each other (Liu et al., 2018; Czeszumski et al., 2020; Newman et al., 2024). While further research with a wider range of sensory and cognitive processes and neuroimaging techniques will be needed to expand our work beyond EEG visual evoked responses, the limitations of interbrain synchrony revealed here add to the growing concerns having been expressed in the field (Burgess, 2013; Hari et al., 2013; Hamilton, 2021; Novembre and Iannetti, 2021; Holroyd, 2022).

Our results highlight representational analyses as a powerful alternative to synchrony measures to better index information alignment between individuals. Enabling information content to be compared across individuals, even while obtained from different (neuroimaging) systems, these analyses will have critical advantages for future hyperscanning research. While implementing representational analyses is relatively straightforward when having time-locked trials with many different stimuli, moving into the representational space in more naturalistic tasks as often used in hyperscanning research will be more challenging. Advancing representational analyses methods for non-time locked data will be needed to reach full capacity of hyperscanning and enable a step change in understanding the sensory and cognitive processes supporting real-time social interactions.

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/etx64/>.

Ethics statement

The studies involving humans were approved by University of Sydney Human Research Ethics Committee. The studies were conducted in accordance with the local legislation and institutional requirements. The participants provided their written informed consent to participate in this study.

Author contributions

MV: Conceptualization, Methodology, Writing – original draft. TG: Conceptualization, Methodology, Writing – review & editing.

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Pleasantness makes a good time: musical consonance shapes interpersonal synchronization in dyadic joint action

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Introduction: Music making is a process by which humans across cultures come together to create patterns of sounds that are aesthetically pleasing. What remains unclear is how this aesthetic outcome affects the sensorimotor interaction between participants.

Method: Here we approach this question using an interpersonal sensorimotor synchronization paradigm to test whether the quality of a jointly created chord (consonant vs. dissonant) affects movement coordination. We recruited non-musician participants in dyads to perform a dyadic synchronization-continuation task (dSCT): on each trial, participants first synchronized their movements to a metronome (synchronization phase) and then continued tapping together at the same tempo without the metronome (continuation phase). Each tap yielded a note and participants heard both their own and that of their partner, thus creating a chord that was varied to be either consonant (Perf5 or Maj6) or dissonant (Min2 or Maj2). For each trial, participants also rated the pleasure they felt in creating the sounds together. Additionally, they completed questionnaires about social closeness to the other participant, musical reward sensitivity and musical training.

Results: Results showed that participants' taps were closer in time when they jointly created consonant (high pleasure) vs. dissonant (low pleasure) chords, and that pleasure experienced by the dyad in each trial predicted interpersonal synchronization. However, consonance did not affect individual synchronization with the metronome or individual tapping when the metronome was discontinued. The effect of consonance on synchronization was greater in dyads who reported feeling less close prior to the task.

Discussion: Together, these results highlight the role of consonance in shaping the temporal coordination of our actions with others. More broadly, this work shows that the aesthetic outcome of what we create together affects joint behaviors.

KEYWORDS

joint action, interpersonal synchronization, musical pleasantness, consonance, joint outcome

1 Introduction

Human cultures across the globe engage in music making: people come together and sing, play flutes, or beat drums to create aesthetically pleasing sounds. This process involves interpersonal synchronization, which entails the coordination of actions, emotions, thoughts, and even physiological rhythms among two or more people

(Bernieri and Rosenthal, 1991; Ackerman and Bargh, 2010; Palumbo et al., 2017). To achieve such coordination, individuals must understand each other's intentions, adapt to different environments, take others' perspectives, and make quick decisions to synchronize effectively (Hasson et al., 2004; D'Ausilio et al., 2015; Sacheli et al., 2018). What remains unclear is the extent to which the aesthetic quality of what is jointly created affects this coordination of action.

Joint music-making provides a unique channel to study humans' ability to precisely synchronize movements in time (Repp, 2005; Repp and Su, 2013; Keller et al., 2014; Abalde et al., 2024). When playing together, musicians must adapt their production of tone sequences based on auditory information from themselves and their partners in order to synchronize effectively (Goebel and Palmer, 2009; Wing et al., 2014). Rhythmic interpersonal coordination can be measured by calculating the asynchrony between the onsets of sounds that are supposed to occur simultaneously in a piece. While some studies explored temporally precise rhythmic interpersonal coordination during naturalistic, expressive ensemble performance (Keller and Appel, 2010; Ragert et al., 2013; Keller et al., 2014; Colley et al., 2018; Laroche et al., 2022; Proksch et al., 2022), most relevant research has been conducted using sensorimotor synchronization tasks, where participants are required to perform simple movements, such as finger taps (Mates et al., 1992; Konvalinka et al., 2009, 2010; Nowicki et al., 2013; Schultz and Palmer, 2019). This task allows researchers to manipulate various conditions, providing insights into social and prosocial behaviors, as well as synchronization and cooperation processes (Konvalinka et al., 2010; D'Ausilio et al., 2015). Indeed, rhythmic joint action can be affected by factors that are related to musical expression (Keller, 2013), including tempo (Rasch, 1988; Konvalinka et al., 2010), metrical structure (Large et al., 2002; Keller and Repp, 2005; Snyder et al., 2006; Rankin et al., 2009), intensity (Goodman, 2002), and timbre (Ternström and Karna, 2002; Ternström, 2003; Sundberg, 2006). Intonation, the accurate control of pitch, is crucial for achieving consonance in music ensembles (Keller, 2013). Selective adjustments in intonation are fundamental to achieve harmonic consonance for the overall sound (Papiotis et al., 2011, 2012). However, research on interpersonal synchronization has primarily focused on the temporal aspects of coordination, neglecting the potential influence of the aesthetic quality of the joint outcome (e.g., Konvalinka et al., 2010; D'Ausilio et al., 2015).

One principal aesthetic dimension of music is consonance. Based on the work of Helmholtz (1913) and Terhardt (1984) identified sensory consonance and harmony as the two main roots of consonance. The former operates at the auditory sensation level and is linked to frequency relations, while the latter relies on pitch relationships and involves a more sophisticated cognitive process. Consonance has been investigated in literature from different perspectives, including arithmetical, psychoacoustic, neurophysiological, and cultural (for a comprehensive review, see Di Stefano et al., 2022). However, due to contrasting evidence, there is still no general consensus on how consonance is governed in music (Di Stefano et al., 2022). Nonetheless, consonant sounds are generally perceived as pleasant, while dissonant sounds as unpleasant (Trainor et al., 2002; Bendor and Wang, 2005; Di Stefano et al., 2022). This preference for consonance is observed

in infants and appears to be a universal trait (Vos and Troost, 1989; Zentner and Kagan, 1998; Trainor et al., 2002; Masataka, 2006; Fritz et al., 2009).

We conjecture that the aesthetic quality of the joint outcome, particularly its consonance, might affect performance during sensorimotor tasks. One reason for this is the overlap in neural underpinnings of consonance processing and joint motor action. Specifically, Minati et al. (2009) found that consonant sounds elicited activation in the right hemisphere premotor cortex and inferior parietal lobe, among others. These brain regions are also implicated in auditory-motor integration at the individual level (Chen et al., 2008; Giovannelli et al., 2014; Lega et al., 2016; Siman-Tov et al., 2022) and in understanding others' action intentions (Ortigue et al., 2010). Based on this neural overlap, one might hypothesize that consonance influences joint action, as investigated in our study. Additionally, research with adults has shown that the learning of rules is easier when conveyed through consonant intervals compared to dissonant ones, indicating that consonance has a positive effect on higher-level cognitive abilities (Crespo-Bojorque and Toro, 2016; Di Stefano et al., 2022). To our knowledge, Komeilipoor et al. (2015) is the only study to have investigated the role of consonance in a sensorimotor synchronization task. They had individual participants perform sliding movements with their fingers to the sound of a metronome consisting of a consonant or dissonant chord. They found that consonance did not affect synchronization of movements while the metronome was present. But, puzzlingly, when the metronome was removed and participants were asked to continue moving in the same tempo, they did so less precisely and with greater variability in the dissonant (vs. consonant) condition. This result suggests that consonance has an effect on individual sensorimotor synchronization. However, it is important to recognize that in that study, participants did not themselves participate in the creation of the sound and the consonance was instead driven by an external stimulus beyond their control. Thus, it remains unclear whether sensorimotor synchronization is affected by the aesthetic quality of an individual or a jointly created outcome.

The aim of this study was to test whether the consonance of a jointly created chord affects the synchronization of movements between participants. We reasoned that when participants tap together and each person creates a sound, forming a chord, the timing of their movements would be more synchronized if the chord is consonant. We expected this effect might arise from a mutual adaptation of movement (Konvalinka et al., 2010; Nowicki et al., 2013; Van Der Steen and Keller, 2013; Keller et al., 2014; Uccelli et al., 2023), as well as from processing advantages for consonance and aesthetic pleasant chords (Bones et al., 2014; Tabas et al., 2019). If we follow this line of reasoning, we might also expect that individuals who are more sensitive to the aesthetic outcome should exhibit a greater difference between consonant and dissonant sounds. As a proxy for sensitivity to aesthetic outcome we used the extended Barcelona Music Reward Questionnaire (eBMRQ; Cardona et al., 2022). The original version of this questionnaire (BMRQ, Mas-Herrero et al., 2014) is correlated with the aesthetic facet of "Openness to Experience" section of the NEO-PI-R (Costa and McCrae, 1992), indicating that higher aesthetic sensitivity for art and beauty correlates with higher BMRQ scores. Indeed, some studies have employed the BMRQ to investigate

aesthetic reward sensitivity in the music domain and beyond (Mas-Herrero et al., 2018; Hernández et al., 2019; Witek et al., 2023). Given this questionnaire's relevance for assessing aesthetic sensitivity, we used it to explore our hypothesis that those who are more sensitive to aesthetic outcome may show a greater effect of consonance. Additionally, we might expect individuals who are more socially close to show higher consonance effect. Our reasoning is that if individuals are socially close, they likely perceive themselves as part of the same group. Thus, the outcomes of a joint action matter more than if they belonged to different groups. From an evolutionary perspective, people in the same group may have more frequent interactions with each other rather than with outsiders ("shadow of the future" effects, Axelrod, 1984). Hence, we expect that the greater the social closeness between individuals, the more they will care about the quality of their joint outcomes, resulting in a stronger impact of consonance on their interpersonal synchronization.

When testing the effect of the joint outcome on rhythmic interpersonal synchronization, it is important to take into account not only the intrinsic acoustic properties of the auditory stimulus (Goodman, 2002; Ternström and Karna, 2002; Ternström, 2003; Sundberg, 2006), but also social and psychological factors (Keller et al., 2014), and individual expertise. For instance, musical expertise is known to promote proficiency in action–effect anticipation, leading to smaller asynchronies in such interpersonal tapping task (Aschersleben and Prinz, 1995; Aschersleben, 2002; Keller and Koch, 2008; Vuust et al., 2009; Pecenka and Keller, 2011; Schultz and Palmer, 2019), and maintaining a more consistent metronome rate when receiving other feedback (Schultz and Palmer, 2019). Social skills and personality traits, such as social competence and empathy, also affect coordination timing. For example, children with higher social skills synchronize better in dyadic drumming tasks (Kleinspehn, 2008), while autistic traits are linked to deficits in interpersonal motor coordination (Curioni et al., 2017) and synchronization difficulties (Kasten et al., 2023). Investigating the effect of consonance on these aspects could provide deeper insights into how aesthetical and pleasant stimuli influences motor coordination in a population with varying levels of social skills and autistic traits. Additionally, inter-dyadic differences in spontaneous rhythm production behaviors (e.g., speech, gait, and dance) influence synchrony in joint tasks, with greater synchrony predicted by smaller differences in spontaneous production rates (Zamm et al., 2016; Palmer et al., 2019; Tranchant et al., 2022).

In the present study, we recruited non-musician participants in a dyadic synchronization-continuation task (dSCT), in which they first synchronized their movements to a metronome together (synchronization phase) and then continued tapping at the same tempo without the metronome (continuation phase). Each participant heard the auditory feedback (notes) from themselves and their partner, and we varied these sounds so that the chord they jointly created was either consonant or dissonant. If the consonance of the joint outcome and the subjective pleasure derived from it affect how paired participants synchronize their movements, we expect that consonance as well as the subjective pleasure of each chord influence the precision of the tapping coordination, both during synchronization and continuation phase (aim 1). To rule out that this effect was due to overall effects on synchronization, we

also tested whether the two participants' individual synchronization to the metronome was affected by consonance (aim 2). Further, we reasoned that if the aesthetic quality of the metronome affects movement, this effect should be stronger in those who are more sensitive to the aesthetic quality of music, i.e., more sensitive to musical reward (aim 3). We also hypothesized that dyads who feel socially closer would show a greater effect of consonance on synchronization (aim 4). Finally, to confirm the validity of the measure of interpersonal synchronization, we tested whether participants who have greater musical training achieve, as expected, greater synchronization.

2 Method

2.1 Participants

Forty-two volunteers took part in the study (mean age = 23.64 ± 3.20 years; 21 men and 21 women). Participants were pseudorandomly divided into 21 dyads, ensuring they were unfamiliar with their assigned partner prior to the experiment. The dyads included seven male-male, seven female-female, and seven mixed-gender dyads (as done in Nowicki et al., 2013). All participants were neurologically healthy and did not report any hearing impairments. Most of them were right-handed ($N = 38$), while 4 were left-handed. Participants were non-musicians, defined as having received <2 years of formal or informal musical training, assessed using the Musical Training subscale of the Gold-MSI questionnaire (Müllensiefen et al., 2014). The experimental protocol was approved by the local ethics committee of the University of Pavia (Ethical Committee Prot. # 132/23) and participants were treated in accordance with the Declaration of Helsinki.

2.2 Materials

The whole experimental procedure is charted in Figure 1A. With regard to the dyadic synchronization task, participants were positioned facing each other on opposite sides of the table, with a panel placed in the center to obstruct their view of the other participant during the task (Figure 1B). Each participant tapped on a computer keyboard placed in front of them. The two keyboards used by participants in the dyad were linked to the same computer. During the task, one participant pressed the A key on one keyboard while the other pressed the L key on the other keyboard. To receive the sound feedback as well as to ensure participants could not hear the sounds produced by clicking the keys, they were equipped with noise-canceling earphones (see Figure 1B). Taps were recorded by a custom Python interface running Pygame (a set of bindings to Simple DirectMedia Layer, SDL, connected to the two keyboards), which also created the sound of feedback and the click of the metronome, as well as the final gong indicating the end of each trial (see Figure 1D). The metronome sound was a woodblock sound wave file of 30 ms duration, included by default in the Teensy Python interface (Van Vugt, 2020; see also Schultz and Van Vugt, 2016), while the duration of the tap feedback sound was either 150, 200, or 400 ms (held constant within each trial). Each participant received auditory

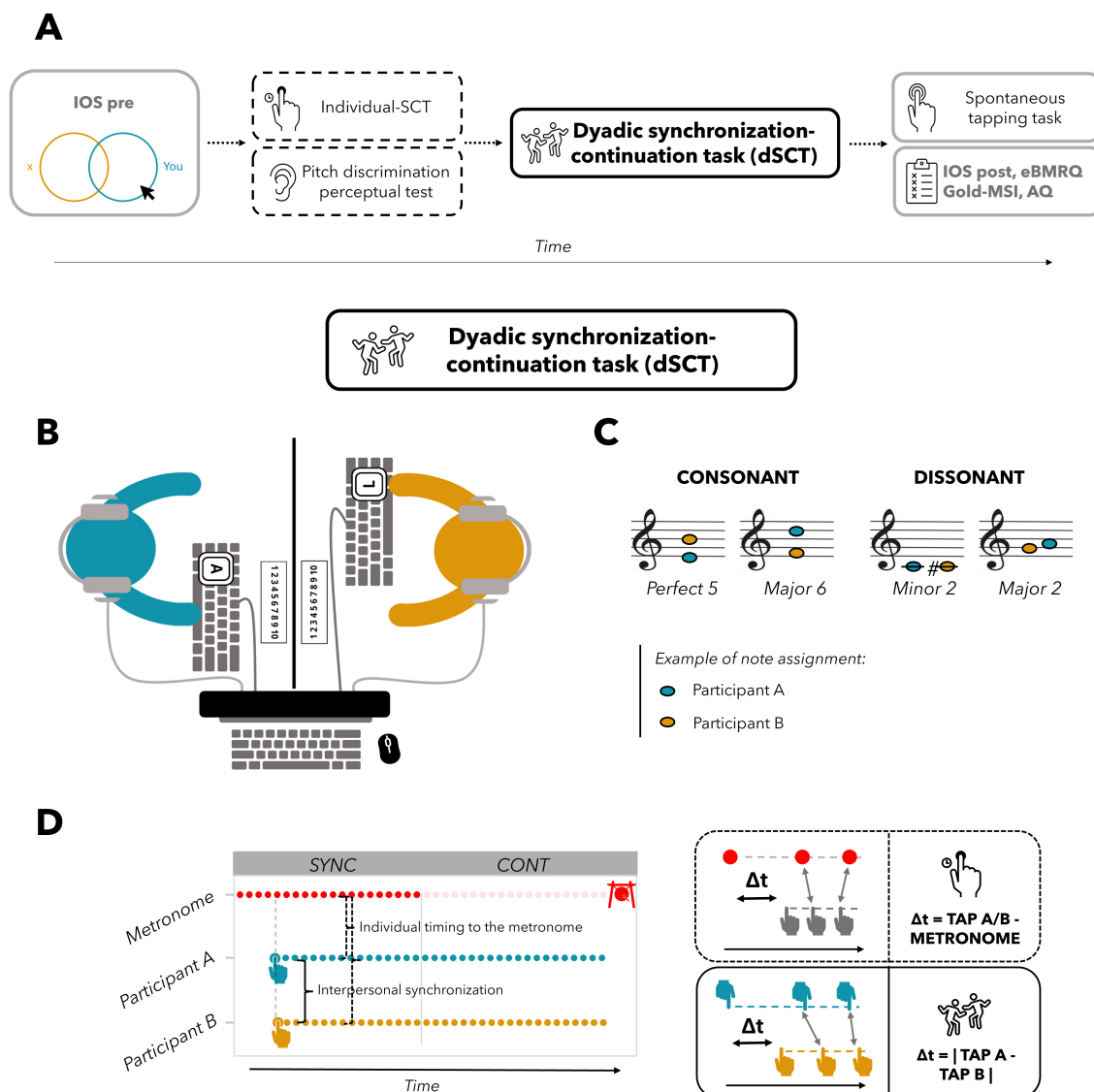


FIGURE 1

(A) Flow chart of the procedure. IOS, Inclusion of Other in Self scale, administered once before (pre) and once after (post) the dSCT; Individual-SCT, individual synchronization-continuation task; dSCT, dyadic synchronization-continuation task; eBMRQ, extended Barcelona Music Reward Questionnaire; Gold-MSI, Goldsmith Musical Sophistication Index; AQ, Autism Quotient Questionnaire. Assessment of inter-individual differences is outlined in gray, while the assessment of pitch discrimination and synchronization abilities with a dashed line. (B) Top view of the experimental setup. Participants sat facing each other on opposite sides of the table, with a central panel preventing them from seeing each other; they wore noise-canceling earphones. Participant A of the dyad (in blue) taps on the “A” key of one keyboard, while participant B (in yellow) on the “L” key of the other. Keyboards and earphones were linked to the same computer. (C) The four musical chords employed in the experiment, divided into consonant and dissonant ones. (D) Dyadic synchronization-continuation task (dSCT) structure. Red dots indicate clicks of the metronome, which is discontinued in the continuation phase, while blue (Participant A) and yellow (Participant B) dots refer to participants’ taps. A gong (depicted on top right corner) indicates the end of each trial. Time differences between each participant’s tap and the closest metronome click ($\Delta t = \text{tap A/B} - \text{metronome}$) were calculated for the individual timing in the synchronization phase, while time differences between participant A and B closest taps were computed for the interpersonal synchronization ($\Delta t = |\text{tap A} - \text{tap B}|$) in both synchronization and continuation phase, bottom right corner of the Figure.

feedback in the form of one of eight distinct tones synthesized as pure sine waves with a 5 ms linear fade in and one of the following frequencies: C (261 Hz), C# (277.18 Hz), E (329.63 Hz), F (349.23 Hz), G (392 Hz), A (440 Hz), B (493.88 Hz), and D (587.33 Hz). During the dyadic synchronization-continuation task (see details below), each participant heard the auditory feedback from themselves and the other, thus creating a chord, which could be either consonant (Perf5 or Maj6) or dissonant (Min2 or Maj2). We use “chord” here to refer to two notes played simultaneously,

as shown in Table 1 and Figure 1C. The selection of these chords was based on previous studies (Krumhansl and Cuddy, 2010; McDermott et al., 2010). These studies revealed that Perf5 and Maj6 chords received high pleasure ratings. Conversely, Min2 and Maj2 chords were associated with low ratings of pleasure. These results were obtained when participants rated chords from very unpleasant to very pleasant (McDermott et al., 2010), as well as when indicated how effectively a tone completed an unfinished scale, such as how well the C note concluded the ascending scale

TABLE 1 Auditory stimuli employed in the experiment.

	Note assigned to participant A of the dyad	Note assigned to participant B of the dyad	Chord	Nominal consonance
1	C	C#	Min2	Dissonant
2	C#	C	Min2	Dissonant
3	G	A	Maj2	Dissonant
4	A	G	Maj2	Dissonant
5	E	B	Perf5	Consonant
6	B	E	Perf5	Consonant
7	D	F	Maj6	Consonant
8	F	D	Maj6	Consonant

C-D-E-F-G-A-B (from very badly to very well, Krumhansl and Cuddy, 2010). The onset of each tap of both participants as well as metronome timings were written to a file for offline analysis (see Van Vugt, 2020).

2.3 Procedure

After participants arrived in the lab, they responded to questionnaires, underwent perceptual testing, and performed individual and joint tapping tasks, as illustrated in Figure 1A. Comprehensively, the procedure lasted 2 h.

2.3.1 Perceived social closeness

Participants were asked to indicate the perceived social closeness to the other participant of the dyad using the *Inclusion of Self in the Other scale* (IOS; Aron et al., 1992), implemented via the jsPsych plugin (see Kinley and Van Vugt, 2023). Participants were asked to indicate their perceived closeness to their partner in the dyad by adjusting the amount of overlap of two circles (see example in Figure 1A), where greater overlap indicated higher perceived closeness. This test was conducted both before (pre) and after (post) the collaborative tasks to measure changes in closeness (see Figure 1A). We are interested in the effects of previously existing closeness, uncontaminated by changes that might happen as a result of the experiment, on the interpersonal synchronization and on the consonance effects. Additionally, we aim to look at the changes between the two measures' timing. To mitigate the influence of social desirability bias, participants completed the test privately on both occasions, ensuring their responses remained undisclosed to their pairs.

2.3.2 Assessment of pitch discrimination and synchronization abilities

We reasoned that two prerequisites for adequately performing the dyadic synchronization-continuation task (dSCT) are I) the perceptual ability to discriminate between the chords used in the experiment and II) the ability to motorically synchronize with the metronome. Thus, prior to the dSCT, participants performed two preliminary tasks, evaluating pitch discrimination (*pitch*

discrimination perceptual test) and sensorimotor synchronization abilities (*individual synchronization-continuation task*, SCT; see Figure 1A). The *pitch discrimination perceptual test* aimed to assess that participants could accurately distinguish between the chords used in the dSCT. Participants listened to a total of 10 chord pairings, consisting of combinations of the chords listed in Table 1, thus creating 6 pairings with different and 4 with the same chords. Participants were required to indicate whether chords in each pair were identical or different by pressing either the A or L key on the computer (counterbalanced across participants). The software OpenSesame (Mathôt et al., 2012) was used for stimuli presentation and data collection. The individual sensorimotor synchronization abilities of each participant of the dyad were assessed through an *individual-SCT*. In this task, participants were instructed to synchronize their tapping with the metronome (synchronization phase), starting at the fifth click, using their dominant hand on the assigned key (A or L, counterbalanced across participants). After this phase, consisting of 20 metronome clicks, the metronome stopped, and participants were told to continue tapping for a duration equivalent to 20 clicks, maintaining the same tempo (continuation phase). At each tap, participants received auditory feedback in the form of A note (440 Hz). Each trial concluded with the sound of a gong. Participants underwent a total of nine trials, determined by the random combination of three metronome tempo (Inter-Onset Intervals, IOI; 450, 550, or 650 ms) x 3 auditory feedback durations (150, 200, and 400 ms).

2.3.3 Dyadic synchronization-continuation task

The materials and the procedure employed in this task are similar to the individual-SCT. Participants were instructed not only to synchronize their taps with the metronome, as they did in the individual-SCT, but also to align their taps with each other. While tapping, participants received auditory feedback (i.e., a note) from both themselves and their partner. If they tapped simultaneously, they jointly created a chord, which could be either consonant or dissonant (see Figure 1C). Based on which note was assigned to each participant in each trial, the dyad could create a total of eight different chords (refer to Table 1). These instructions were chosen so that they could apply to both the synchronization and continuation phases equally. The dyads completed 72 trials, which were randomly determined by combining three metronome IOI (450, 550, or 650 ms), three auditory feedback durations (150, 200, and 400 ms) and eight chords (see Table 1). A break was offered when half of the trials were completed. At the end of each trial, participants were asked to rate how much they liked the chord they produced together on that trial (*subjective ratings of pleasure*) on a scale from 1 to 10. We instructed participants to consider this range from very unpleasant to highly pleasant sounds, to use the entire rating scale, and to rate independently of their synchronization with the other. To provide their ratings, participants indicated with their hand the chosen number on a paper sheet, hidden from the view of the other (Figure 1B).

2.3.4 Individual spontaneous tapping rate

Each participant engaged in a *spontaneous tapping task* to assess their spontaneous tapping rate individually without a pacing stimulus (see Figure 1A). Participants A and B of each dyad

performed this task separately. They were asked to tap as regularly as possible for about 1 min at a comfortable, self-chosen pace (Wing and Kristofferson, 1973; Hammerschmidt et al., 2021; Pfordresher et al., 2021), while the other participant waited. This test aimed to be able to control for spontaneous tapping rates in joint synchronization tasks (see Zamm et al., 2016; Tranchant et al., 2022). Since this analysis was not directly relevant to our aims the results are included in the [Supplementary Section 4](#).

2.3.5 Music reward sensitivity

Furthermore, participants completed the *extended* version of the *Barcelona Music Reward Questionnaire* (eBMRQ; Cardona et al., 2022) to measure their music reward sensitivity. This questionnaire consists of 24 items, divided into six subscales: Music Seeking, Emotion Evocation, Mood Regulation, Sensorimotor, Social, and Musical Absorption, with four items per subscale. Each item (e.g., “When I share music with someone, I feel a special connection with that person.”) requires responses on a 5-point Likert scale, ranging from “completely disagree” to “completely agree.”

2.3.6 Musical training and perceptual abilities

Then, each participant filled out the *Musical Training and Perceptual Abilities* subscales of the *Goldsmith Musical Sophistication Index* (Gold-MSI; Müllensiefen et al., 2014) to evaluate the influence of musical expertise on interpersonal tapping abilities. The Musical Training subscale comprises 7 items, such as “I engaged in regular, daily practice of a musical instrument (including voice) for N years,” with N varying across a 7-point scale for each item (e.g., 0, 1, 2, 3, 4–5, 6–9, 10+). Responses are then scored from 1 to 7, based on the position of the number of years within the scale (for instance, 0 years is scored as 1, 1 year as 2, 2 as 3, and so on, up to 10+ scored as 7). The *Perceptual Abilities* subscale includes 9 items (e.g., “I am able to judge whether someone is a good singer or not”) and require responses on a 7-point Likert scale, ranging from “totally disagree” to “totally agree.”

2.3.7 Autism

Lastly, participants completed the *Autism Quotient Questionnaire* (AQ; Ashwood et al., 2016) to investigate autistic-like traits influence (Tryfon et al., 2017; Bloch et al., 2019; Granner-Shuman et al., 2021; Carnevali et al., 2024) on sensorimotor synchronization abilities. This 50-item questionnaire offers four response options, ranging from “totally agree” to “totally disagree.” For some items, points are given for disagreeing (e.g., “I prefer to do things with others rather than on my own”), while in others for agreeing (e.g., “I prefer to do things the same way over and over again”).

2.4 Data analysis

2.4.1 Assessment of pitch discrimination and synchronization abilities

In the *pitch discrimination perceptual test*, we computed the mean and standard deviation of correct responses (out of ten)

to verify participants’ ability to distinguish sounds. Additionally, this task enabled us to screen participants for amusia (Peretz et al., 2002; Liu et al., 2017; Whiteford and Oxenham, 2017). We observed a mean of 8.95 correct responses, with a standard deviation of 1.03. All participants performed above chance level ($X = 5$), as indicated by the significant one-sample *t*-test against the hypothesis $\mu = 5$ [$t_{(41)} = 24.75$, $p < 0.001$], confirming adequate ability in distinguishing between the chosen chords. We then analyze the *individual synchronization-continuation task* (SCT) as follows: we computed the signed timing difference between each tap and the nearest metronome click (in ms) and then we aggregated these differences within each of the nine trials for each participant, to determine the mean and SD (in ms). The distribution of the means and SDs across participants had the following parameters: Skewness_M = 0.08, Kurtosis_M = 3.72; Skewness_{SD} = 0.84, Kurtosis_{SD} = 2.42. The mean values ranged from a minimum of −181.90 ms to a maximum of 225.81 ms. As a result, we determined that all participants have normal proficiency in both pitch discrimination and sensorimotor synchronization abilities. Consequently, we decided to retain the entire sample for further analysis.

2.4.2 Dyadic synchronization-continuation task

We analyzed the *subjective ratings of pleasure* performing a within-participants ANOVA with consonance of the chords (two levels: consonant vs. dissonant), auditory feedback duration (three levels: 150, 200, and 400 ms) and metronome tempo (three levels of IOI: 450, 550, and 650 ms) as factors, to assess whether the consonant chords were rated higher than dissonant ones (see Krumhansl and Cuddy, 2010; McDermott et al., 2010), as well as to see differences in pleasure rating based on the duration of the sound and the metronome tempo. Then, we analyzed tapping data inspecting *interpersonal synchronization* and *individual tapping precision*. Both synchronization and continuation phases were included in the analyses. For *interpersonal synchronization*, we analyzed both phases (synchronization and continuation) in the same way: by measuring the time difference between the taps of the two participants. We incorporated the factor “Task Phase” in the ANOVA model. For *individual tapping precision*, we conducted different analyses for the two phases: during the synchronization phase, we analyzed the time difference between the participant’s taps and the metronome, while for the continuation phase, when the metronome was discontinued, we examined the Inter-Tap Intervals (ITIs). Thus, we performed two different ANOVA models, one for each phase. Specifically, when investigating participants’ *interpersonal synchronization*, we firstly excluded a few trials ($n = 6$, 0.39% of all trials) in which, due to a technical glitch, only one participant’s taps were recorded. Then, we paired each tap from participant A with the tap from participant B that was closest in time, and we calculated the absolute time difference (in ms) between the two taps ($\Delta t = |\text{tap A} - \text{tap B}|$; see [Figure 1D](#)). We excluded taps after the end-of-trial sound signal and, to avoid incorrect tap matching (e.g., participant B started tapping later compared to participant A, thus the dyad has not started synchronizing yet), we also removed absolute difference values $> 80\%$ metronome IOI. Following this criterion, 1.05% of matching pairs were excluded. We aggregated these absolute taps differences within each of the 72 trials for each dyad to determine the mean of

absolute tap time difference (in ms), both for the synchronization and the continuation phase, using the formula $mean(\Delta t)$, where Δt is the time difference calculated above. The distribution of the means of absolute taps difference showed considerable departure from normality (Skewness = 2.36, Kurtosis = 10.73), so we applied a logarithmic transformation (transformed scores Skewness = 0.55, Kurtosis = 3.17). These log transformed means, calculated within each trial, were then averaged across the trials of the same dyad, separately for each task phase, tempo, auditory feedback duration and consonance of the sound (36 values per dyad). After this data pre-processing, we performed a within-dyads ANOVA on log transformed means with consonance of the chords (two levels: consonant vs. dissonant), tempo (three levels of metronome IOI: 450, 550, and 650 ms), auditory feedback duration (three levels: 150, 200, and 400 ms) and task phase (two levels: synchronization vs. continuation) as factors.

To examine the *individual tapping precision* and determine whether this measure is affected by consonance, for the synchronization phase we analyzed each individual's timing deviation from the metronome. We matched each tap with the closest (in time) click of the metronome, and we calculated the signed time difference (in ms) between the metronome click and the nearest participant's tap for this phase ($\Delta t = \text{tap A/B} - \text{metronome}$; see Figure 1D). We then calculated the mean and variability of these signed time differences (in ms), with the formulas $mean(\Delta t)$ and $sd(\Delta t)$. Due to the presence of negative values and the adherence to the normality assumption for the means' and SDs' distributions (Skewness_M = -0.17, Kurtosis_M = 3.39, Skewness_{SD} = 1.09, Kurtosis_{SD} = 2.95), we opted not to apply a logarithmic transformation to the variables. Consequently, the values will be reported in their original scale. The means and SDs of signed time differences calculated within each trial were then averaged across the trials of the same participant (18 values per participant). Thus, we performed two within-participant ANOVAs with mean and variability (SD) of signed time differences as dependent variables, and the same set of variables described above as factors, except for task phase. For the continuation phase, where the metronome is discontinued, we analyzed the consonance effect on the Inter-Tap Intervals (ITIs). We calculated ITIs between consecutive taps of the same participant, and then averaged them across trials to determine the mean and standard deviation of ITIs (18 values per participant). Thus, we performed two within-participant ANOVAs with mean ITI and standard deviation ITI as the dependent variables (in ms), and the same set of factors described above.

All the ANOVA models were performed using the *ez* package (Lawrence, 2016) in the R statistical language (R Core Team, 2023). *Post-hoc* comparisons were computed using the package *rstatix* (Kassambara, 2019) with Holm correction method. Following the recommendation of Bakeman (2005), we reported generalized effect sizes (η^2_G ; Olejnik and Algina, 2003).

Lastly, regardless of the consonant/dissonant properties of the auditory stimuli, we investigated if dyadic pleasure influences how participants synchronize their movements (*pleasure and interpersonal synchronization relationship*). For each dyad, we collected all trials, and we computed a per-dyad regression slope between pleasure (calculated as the average score between participant A and participant B for each trial) and the mean absolute tap differences (in log ms). We then tested whether these

regression slopes were significantly different from zero on the group level using a *t*-test.

2.4.3 Assessment of psychological constructs

We calculated the difference between post-experimental and pre-experimental closeness (IOS) scores for each dyad, hence yielding a change in closeness rating. For clarity, we expressed IOS scores as a percentage. To examine whether the effect of consonance correlates with closeness or musical reward sensitivity, we first averaged the mean absolute tap differences (in log ms) for both consonant and dissonant trials for each dyad and we calculated an estimate of the dyad's consonance effect by subtracting the mean dissonant score from the mean consonant score for each dyad. Then we computed the correlation between this dyad consonant effect and the dyad-summed musical reward and closeness scores (two separate correlations).

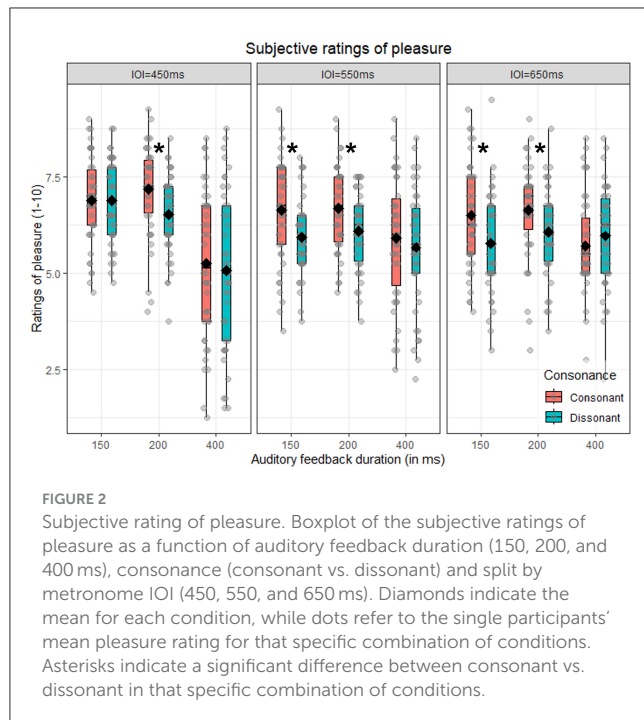
Additionally, we conducted an exploratory analysis investigating whether dyadic differences in social factors (i.e., social closeness and autism), musical experience and music reward sensitivity correlate with interpersonal synchronization. We summed the scores of participant A and participant B for each questionnaire (IOS pre, eBMRQ, AQ, Musical Training, and Perceptual Abilities) and we employed these dyadic scores sum in a correlation analysis with the mean of absolute taps difference (in log ms) aggregated for each dyad. We performed the correlation analyses using package *stats* in the R statistical language (R Core Team, 2023).

3 Results

3.1 Dyadic synchronization-continuation task

3.1.1 Subjective rating of pleasure

The main aim of this analysis is to confirm that subjective pleasure is predicted by consonance. Additionally, we investigated whether this effect interacted with both feedback duration and metronome IOI. Thus, we performed a repeated-measure ANOVA with consonance, auditory feedback duration and metronome IOI as within-subjects factors. As expected, we found a significant main effect of consonance [$F_{(1,41)} = 7.61, p = 0.009, \eta^2_G = 0.02$]: consonant chords were rated significantly higher ($M = 6.37, SD = 1.50$) compared to dissonant ones ($M = 6.00, SD = 1.39$), as illustrated in Figure 4A. This effect significantly interacted with both feedback duration and metronome IOI, as indicated by the significant three-way interaction consonance x metronome IOI x auditory feedback duration [$F_{(4,164)} = 2.77, p = 0.029, \eta^2_G = 0.01$]. To further explore this interaction, we analyzed pleasure ratings separately by metronome IOI and auditory feedback duration, to test in which combination of conditions consonant chords were rated higher than dissonant ones. This was true for the IOI = 550 ms [$t_{(41)} = 2.97, p = 0.028$] and IOI = 650 ms [$t_{(41)} = 3.80, p = 0.004$] in the 150 ms auditory feedback duration, and for all the metronome IOI conditions in the 200 ms auditory feedback duration condition [450 ms: $t_{(41)} = 3.50, p = 0.008$; 550 ms: $t_{(41)} = 3.03, p = 0.028$; 650 ms: $t_{(41)} = 3.05, p = 0.028$], as illustrated in Figure 2. In sum, consonant trials are overall associated with



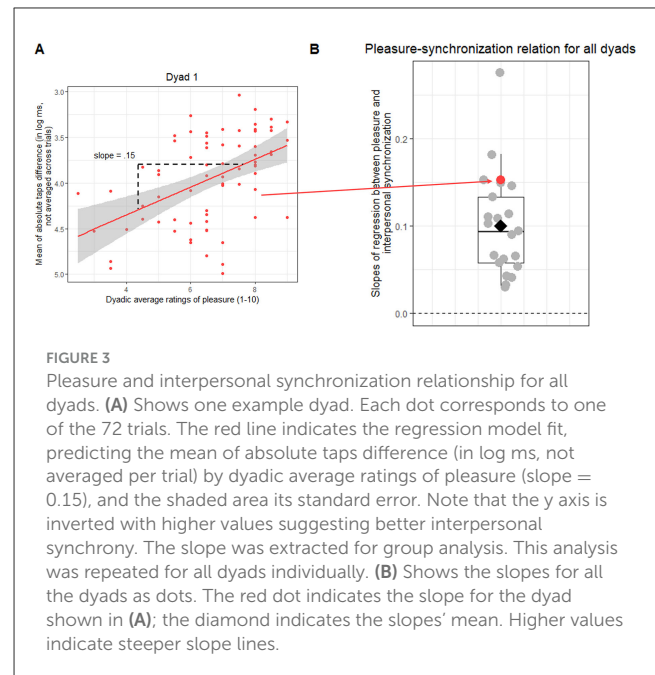
higher pleasure (main consonance effect), although the pattern is not significant across all combinations of metronome tempo and auditory feedback duration (interaction). Since the main interest of this analysis was the effect of consonance on subjective pleasure, the interactions that do not involve consonance have been moved to [Supplementary Section 1](#).

3.1.2 Interpersonal synchronization (dSCT)

To test whether consonance affected interpersonal synchronization (aim 1), we performed an ANOVA on the interpersonal synchronization (calculated as mean of absolute taps difference in log ms), which revealed a main significant effect of consonance [$F_{(1,20)} = 7.99$, $p = 0.010$, $\eta_G^2 = 0.01$]. Crucially, participants demonstrated better synchronization with each other when they produced a consonant chord (3.73 log ms, 48.55 ms) compared to a dissonant one (3.78 log ms, 51.89 ms), as illustrated in [Figure 4B](#). None of the interaction effects with consonance were significant (all $F_s < 2.37$, $p_s > 0.107$). Since the main interest of our study was on the effect of consonance, all the other main or interaction effects that do not involve consonance have been moved to [Supplementary Section 2](#).

3.1.3 Pleasure and interpersonal synchronization

When analyzing the correlation between dyadic pleasure rating and interpersonal synchronization (aim 1), we found a positive slope in all dyads (mean = 0.10, SD = 0.06), indicating that the higher the pleasure, the higher is the interpersonal synchronization. This slope was significantly different from zero on the group level [$t_{(20)} = 7.78$, $p < 0.001$; [Figure 3B](#)]. We conclude that, independently from the metronome IOI and the auditory feedback duration, dyads tended to tap more closely together on trials that were rated as more pleasant (see [Figures 3A, B](#)).



3.1.4 Individual tapping precision (dSCT)

To test whether consonance affected individual timing relative to metronome (aim 2), we performed an ANOVA on the mean of signed time differences (in ms) during the synchronization phase. No significant main effect of consonance emerged [$F_{(1,41)} = 2.42$, $p = 0.127$, $\eta_G^2 = 0.003$; $M_{\text{Consonant}} = -39.53$ ms; $M_{\text{Dissonant}} = -37.37$ ms], as shown in [Figure 4C](#). None of the other interaction effects with consonance reached significance either (all $F_s < 1.65$, $p_s > 0.164$). Additionally, we performed the same analysis on the variability (SD) of signed time differences (in ms). This analysis indicated again no significant main effect of consonance [$F_{(1,41)} = 3.32$, $p = 0.076$, $\eta_G^2 = 0.003$; $SD_{\text{Consonant}} = 63.47$ ms; $SD_{\text{Dissonant}} = 61.06$ ms]. None of the interaction effects with consonance reached the significance (all $F_s < 1.61$, $p_s > 0.173$). Since the main interest of our study was on the effect of consonance, the interaction effects not involving consonance have been included in [Supplementary Section 3A](#). In the continuation phase, when investigating the effect of consonance, the ANOVA on the mean inter-tap interval (ITIs) indicated no significant main effect of consonance [$F_{(1,41)} = 0.07$, $p = 0.789$, $\eta_G^2 < 0.001$; $M_{\text{Consonant}} = 525.72$ ms; $M_{\text{Dissonant}} = 525.94$ ms], see [Figure 4D](#). The interaction between auditory feedback duration and consonance [$F_{(2,82)} = 3.83$, $p = 0.026$, $\eta_G^2 = 0.01$] was statistically significant. However, corrected *post-hoc* comparisons testing for consonance vs. dissonance differences within each auditory feedback duration did not reveal any significant differences [all $t_{(41)} < 2.15$, $p_s > 0.114$; [Supplementary Section 3B](#), [Supplementary Figure 3B](#)]. No other interactions with consonance were significant (all $F_s < 1.62$, $p_s > 0.173$). Looking at the variability (SD) in the ITIs as a function of consonance, the ANOVA revealed only a trend toward a significant consonance effect [$F_{(1,41)} = 3.81$, $p = 0.058$, $\eta_G^2 = 0.003$; $SD_{\text{Consonant}} = 30.88$ ms; $SD_{\text{Dissonant}} = 32.30$ ms]. None of the interaction effects with consonance reached significance (all $F_s < 1.47$, p_s

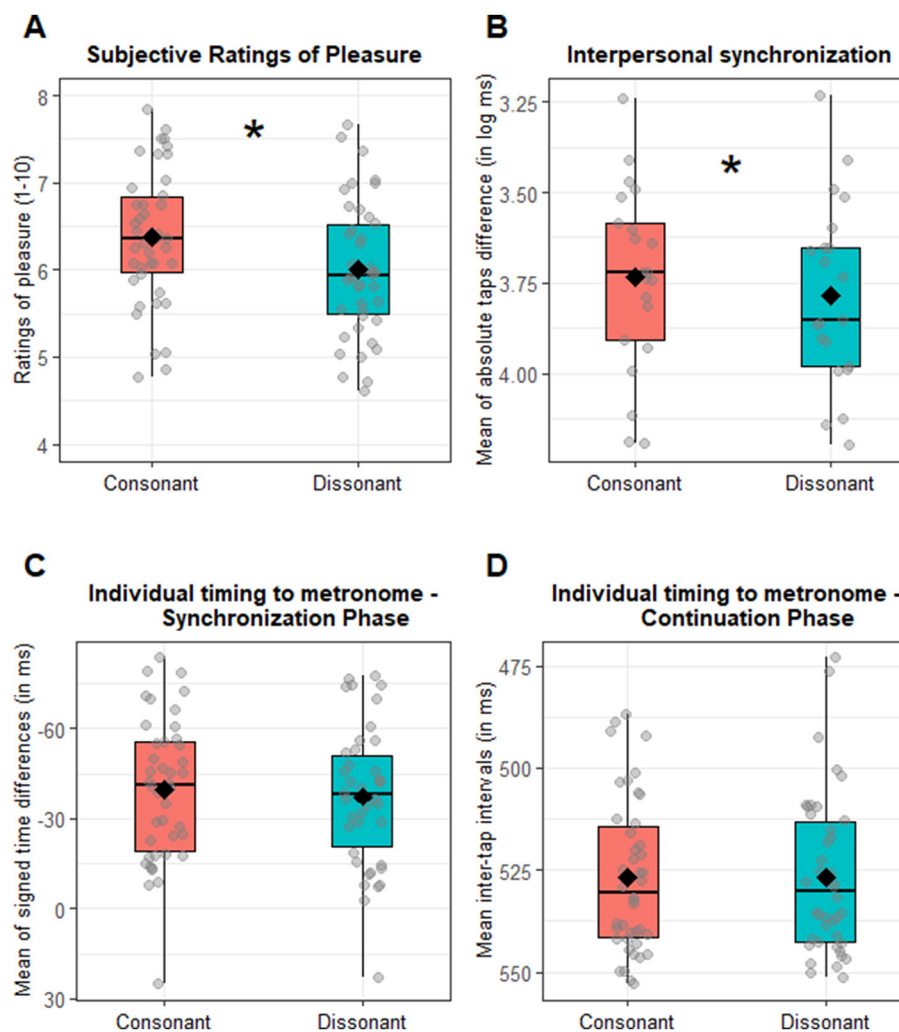


FIGURE 4

Consonance effect. (A) Boxplot of the subjective ratings of pleasure as a function of consonance (consonant vs. dissonant). Dots refer to the individual participants' mean rating of pleasure for each condition. (B) Boxplot of the consonance effect on interpersonal synchronization (measured as the mean of absolute taps difference log transformed). Diamonds indicate the general consonant and dissonant means, while dots refer to the dyadic mean of absolute taps difference for each condition. Note that the y axis is inverted so that higher values suggest better interpersonal synchrony. (C) Boxplot of the consonance effect on the individual tapping precision (tap timing relative to the metronome) in the synchronization phase (measured as the mean of signed time differences in ms). Diamonds indicate the general consonant and dissonant means, while dots refer to the individual mean of signed difference for each condition. Zero suggests perfect synchronization with the metronome. (D) Boxplot of the consonance effect on individual tapping precision in the continuation phase (measured as mean inter-tap interval, mean ITI). Diamonds indicate consonant and dissonant mean ITI, while dots refer to the individual mean ITI for each condition. Asterisks indicate a significant difference between consonant vs. dissonant condition.

> 0.213). Since the main interest of our study was on the effect of consonance, the interaction effects not involving consonance have been included in [Supplementary Section 3B](#). In sum, we found no overall significant effects of consonance on individual tapping performance, neither in terms of synchronization to the metronome nor in terms of tapping continuation without the metronome.

3.2 Assessment of psychological constructs

[Table 2](#) reports the general mean, SD and maximum value for each questionnaire. IOS values, expressed as a percentage, were

significantly higher after the experiment than before [$t_{(41)} = -4.26$, $p < 0.001$], demonstrating an increased perceived closeness after the experiment.

3.2.1 Inter-dyadic differences on consonance effect

To investigate the effect of musical reward sensitivity (aim 3) and perceived closeness (aim 4) on consonance, we performed a correlation analysis between the consonance effect (calculated for each dyad as the interpersonal synchronization in the consonant minus the dissonant trials) and both eBMRQ dyadic scoring sum and IOS pre dyadic sum. The dyadic music reward sensitivity scores did not significantly correlate with the consonance effect

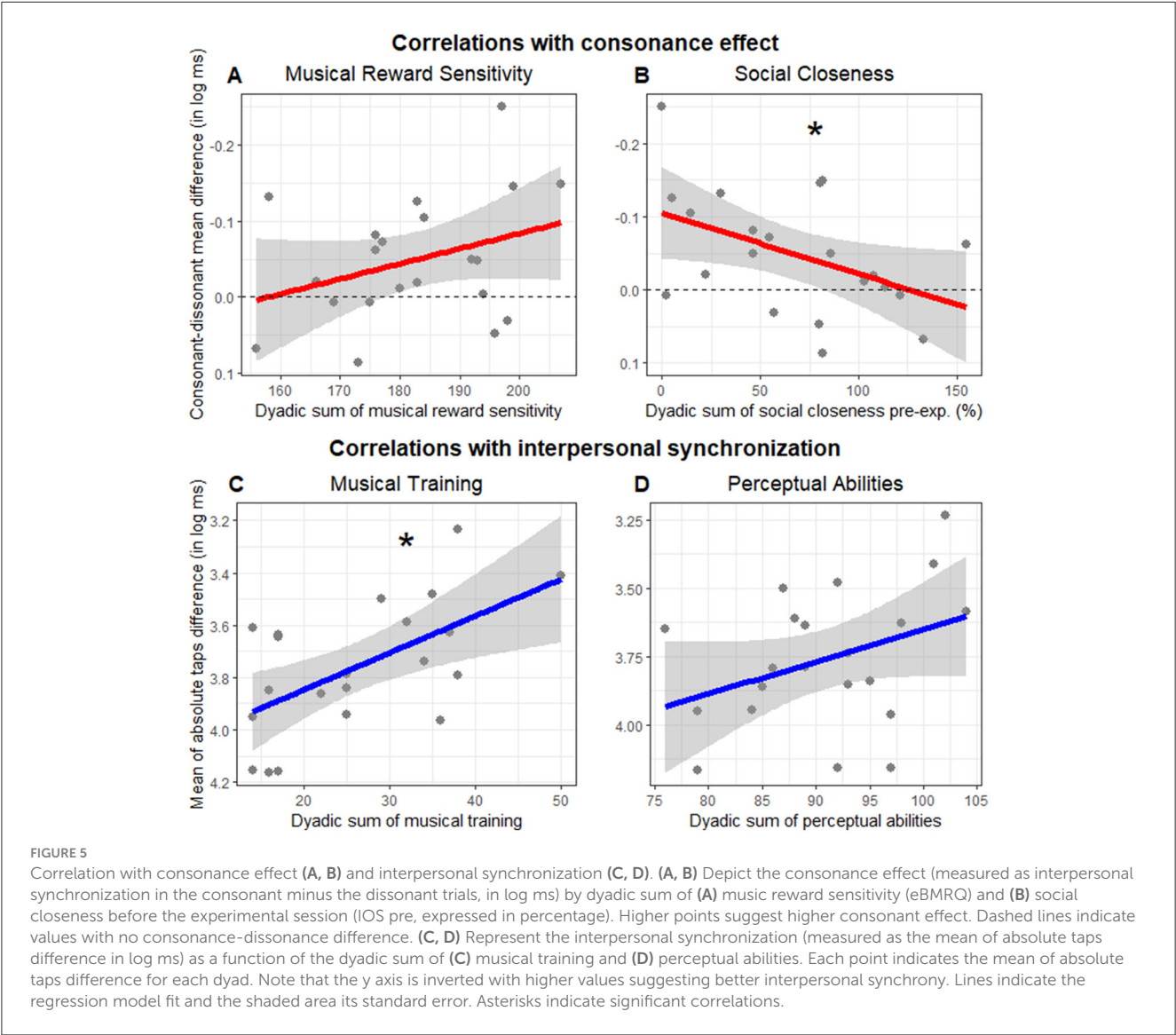
TABLE 2 Mean, SD, and maximum value for each questionnaire.

	General mean	SD	Questionnaire maximum value
Closeness (IOS pre)	33.8%	32.5%	100%
Closeness (IOS post)	51.4%	29.2%	100%
Closeness change (post—pre IOS)	17.6%	26.8%	100%
Music reward sensitivity (eBMRQ)	91.2	11.3	120
Musical training (Gold-MSI)	13.1	7.01	49
Perceptual abilities (Gold-MSI)	45.4	6.53	63
Autism quotient (AQ)	14.9	6.06	50

($r = -0.33$, $p = 0.139$; Figure 5A). The perceived closeness, uncontaminated by changes that might happen as a result of the experiment (IOS pre), significantly correlated with the consonance effect ($r = 0.46$, $p = 0.038$), but the direction of this effect was opposite to what we had hypothesized: the higher the perceived closeness before the experiment, the *smaller* the effect of consonance during dSCT (Figure 5B). Since we did not have hypotheses about the relationships between the consonance effect and the other questionnaire scores, we have moved these to the [Supplementary Section 6A](#).

3.2.2 Inter-dyadic differences on interpersonal synchronization

We performed an exploratory correlation analysis to investigate the relationships between dyadic scoring sum of each questionnaire and interpersonal synchronization (measured as the mean of



absolute taps difference in log ms). Only the dyadic musical training sum showed a significant correlation with interpersonal synchronization ($r = -0.59$, $p = 0.005$, **Figure 5C**). In contrast, the correlation with perceptual abilities was not significant ($r = -0.36$, $p = 0.105$, **Figure 5D**). These results indicated that the higher the dyadic musical training sum, the higher their interpersonal synchronization. Social factors (IOS pre: $r = -0.04$, $p = 0.864$; AQ: $r = -0.27$, $p = 0.232$), as well as eBMRQ dyadic scores sum ($r = -0.19$, $p = 0.415$) did not correlate significantly with interpersonal synchronization. We reported all the correlations between questionnaire dyadic scoring sum and interpersonal synchronization in **Supplementary Section 6B**.

4 Discussion

The present study investigated whether the quality of a joint outcome can shape the dynamics of interpersonal movement synchronization between individuals. Paired non-musician participants performed a dyadic synchronization-continuation task (dSCT). Each participant heard the auditory feedback from themselves and their partner, thus creating a chord, which could be either consonant (Perf5 or Maj6) or dissonant (Min2 or Maj2). Results showed that interpersonal synchronization accuracy was higher when participants produced consonant chords together (high pleasure), compared to dissonant ones (low pleasure). Since the consonant and dissonant conditions (varied within dyads) only differed in the pitch content, with no differences in auditory feedback duration and metronome tempo, we argue that the interpersonal sensorimotor timing differences observed are driven by the consonance created by the dyad. Supporting this finding, we also found that the dyad's subjective rating of pleasure from the chord they produced together predicted interpersonal synchronization on a per-trial basis. Therefore, both an objective intrinsic property of the auditory stimulus (i.e., the consonance), as well as a subjective measure of pleasure of the joint outcome significantly influences how participants synchronize their movements to each other, affecting the temporal coordination of their actions. Interestingly, the effect of consonance was stronger for dyads that reported feeling less close at the beginning of the experiment. Finally, we corroborate previous findings, by demonstrating a significant effect of musical training (even in non-musician participants) on interpersonal synchronization (**Pecenka and Keller, 2011**), thus supporting the validity of our measure in accurately assessing tapping production abilities in an interpersonal context. Together these findings suggest that the pleasantness of the joint auditory outcomes positively influences the accuracy of interpersonal synchronization, highlighting the importance of perceptual and aesthetic emotional factors in collaborative motor tasks.

Our findings indicate a significant relationship between the acoustic properties of the joint outcome and interpersonal synchronization (aim 1). The observed greater dyadic synchronization accuracy for consonant chords compared to dissonant ones suggests that the sensory-driven quality of what we produce together directly influences interpersonal motor coordination. Indeed, in our case, predictions about the quality of the joint outcome are purely driven by incoming perceptual

information, since participants were unaware of the chords in advance, ruling out top-down expectations or strategic influences on their behavior. These results can be interpreted in light of the processing advantages for consonance compared to dissonance (**Bones et al., 2014; Tabas et al., 2019**; for a review, see **Di Stefano et al., 2022**). At the neural level, data has shown that consonant vs. dissonant stimuli are processed differently at both subcortical (**Fishman et al., 2001; McKinney et al., 2001; Tramo et al., 2001; Bidelman and Krishnan, 2009**) and cortical levels (**Itoh et al., 2003, 2010; Bidelman and Grall, 2014**) of the auditory system. These neurobiological studies have demonstrated that consonance processing begins early in the human auditory cortex and that additional neural resources are recruited to encode and discriminate dissonant chords compared to consonant ones (**Tervaniemi et al., 2011; Virtala et al., 2013; Crespo-Bojorquez et al., 2018**). Interestingly, this distinctive activation pattern is observed in both humans and monkeys, suggesting a shared evolutionary trait (**Fishman et al., 2001; Kadia and Wang, 2003; Bendor and Wang, 2005**). The advantages of consonance extend beyond perceptual processing to impact higher-level cognitive abilities and motor performance. **Crespo-Bojorquez and Toro (2016)** found that learning of stimulus-response association rules is facilitated when conveyed through consonant rather than dissonant intervals, while **Komeilipoor et al. (2015)** demonstrated that individual movement performance is less variable and more precise following exposure to a consonant as compared to a dissonant metronome. Our results align with these findings, showing that creating consonance together affects how we motorically synchronize with partners, thereby extending previous research to highlight the social impact of consonance. **Minati et al. (2009)** also observed strong right hemisphere activation (including premotor cortex and inferior parietal lobe) in response to consonant sounds. These brain regions are part of the dorsal auditory stream, which integrates auditory and motor information (**Rauschecker, 2011; Lega et al., 2016**). This neural pathway is particularly active in the right hemisphere for both rhythm perception (**Chen et al., 2008; Siman-Tov et al., 2022**) and production (**Giovannelli et al., 2014**). Moreover, other brain areas activated by consonant sounds, such as the orbitofrontal cortex, amygdala, and anterior cingulate gyrus (**Dellacherie et al., 2009; Omigie et al., 2015**), coincide with regions engaged in social behavior during interpersonal task (**Beer et al., 2006; Cacioppo et al., 2014**, see also aim 4). Taken together, this neural overlap between areas involved in consonance processing and interpersonal interaction bolsters the picture emerging from our study that these processes are linked.

Building upon the established link between consonance and enhanced synchronization, our findings underscore the significance of subjective pleasure in shaping interpersonal coordination. The observation that dyads' self-reported pleasure rating of the joint outcome predicts synchronization accuracy on a trial-by-trial basis highlights the interplay between perception and aesthetic pleasure in motor control. Previous studies have shown that negative interpersonal perception disrupts mutual motor adjustments (**Sacheli et al., 2012**) while improving synchronization (lower movement correction and variability). This suggests that partners who report a negative interpersonal bond execute a cooperative task more individually, less adapting to each other's motor behavior. Similarly, recent studies have experimentally

manipulated emotional states (positive, negative, or neutral) and demonstrated that individuals induced with positive emotions, as opposed to negative emotions or a neutral state, maintained behavioral synchrony with other group members for a longer period of time (Smykovskyi et al., 2022). In contrast, inducing negative emotions significantly reduced the time spent in synchrony and decreased levels of synchronization (Smykovskyi et al., 2024). We speculate a similar mechanism may be at work in the present study, where the positive affective experience plausibly generated by consonant chords may promote more precise interpersonal movement coordination (i.e., mutual adaptation), but not necessarily improve the precision of the performance itself (i.e., individual synchronization with the metronome). Following this reasoning, we might hypothesize that consonance acts as a mediator of a pleasant affective experience, which in turn affects interpersonal motor coordination. Indeed, we showed that consonant chords received higher ratings of pleasure compared to dissonant ones, in line with a host of prior studies (Koelsch et al., 2006; Sammler et al., 2007; Krumhansl and Cuddy, 2010; McDermott et al., 2010; Komeilipoor et al., 2015). However, it is important to note that the present study design does not allow us to definitively disentangle the specific contributions of low-level perceptual features (consonance) and higher-level aesthetic experiences to the observed effects. Future studies employing more complex musical stimuli are necessary to test the selective contribution of these factors and to further explore the causal relationship between pleasure and interpersonal synchronization. Indeed, although we confirm that consonant chords were rated higher than dissonant ones, the levels of pleasure experienced by the presentation of single chords composed by pure tones are limited, as demonstrated also by the low variability of chord ratings of pleasure. Future studies could investigate full-fledged musical stimuli that presumably evoke more intense experiences of pleasure (see Blood and Zatorre, 2001; Salimpoor et al., 2011).

Interestingly, consonance affects synchronization between individuals but not individual tapping metrics, suggesting that the effect of consonance is primarily social in nature (aim 2). This result may seem to contradict the study by Komeilipoor et al. (2015), which demonstrated that individual motor synchronization performance, when the metronome was discontinued, was less precise and showed greater variability in the dissonant (vs. consonant) condition. In our study, consonance effects during individual tapping in the continuation phase did not reach significance, and, despite the significant interaction between consonance and auditory feedback duration, no consonant vs. dissonant differences were found in any feedback duration conditions. Thus, consonance did not affect overall individual synchronization with the metronome. Indeed, in our study participants were explicitly instructed to synchronize with each other, emphasizing the interpersonal aspect over individual synchronization, which may lead to the different outcomes compared to Komeilipoor et al. (2015), where participants tested alone were instructed to synchronize to a metronome. Previous studies have shown that when people engage in joint actions, top-down rule-based mechanisms can regulate bottom-up sensory-driven processes (Konvalinka et al., 2010). Specifically, when participants are instructed to perform a joint action, they mutually

and continuously adapt their tap intervals, employing a “mutual adaptation” strategy (Konvalinka et al., 2010; Nowicki et al., 2013; Van Der Steen and Keller, 2013; Keller et al., 2014; Uccelli et al., 2023). Furthermore, in the study by Komeilipoor et al. (2015), consonance was not generated by the participants’ movements but was instead delivered by an external stimulus beyond their control, a crucial difference that may help explain the divergent outcomes between their study and ours.

When investigating if reward sensitivity affects consonance, we anticipated that individuals more sensitive to aesthetic outcomes would show a more pronounced difference between consonant and dissonant sounds (aim 3). Although we did not find a significant correlation, the direction of the effect followed our expectations. Future research could delve further into this relationship, particularly examining which stages of the interaction between joint outcome and interpersonal synchronicity are most influenced by reward sensitivity (e.g., consonance, pleasantness, or beauty in general).

Our results indicate that the effect of consonance has a social component, as it is significantly modulated by the quality of the dyadic relationship prior to the experiment (aim 4). The direction of this relation was opposite to what we had hypothesized. Specifically, we demonstrated that the impact of consonance on interpersonal synchronization is greater in dyads that reported feeling less close before the task. We do not have a definitive explanation for this finding, and given that it was opposite to our hypothesis, we think further confirmatory experiments are needed to decide if this effect is robust. However, we might speculate on a potential underlying mechanism: individuals who already feel closer rely less on their joint outcomes to guide their behaviors, because the prior closeness buffers the need for a pleasurable outcome. By analogy, close friends may feel more at ease to have tough (not pleasurable) conversations because of the strength of their social bond. A limitation of this explanation is that the participants in our study were recruited specifically to not know each other beforehand, and hence the level of closeness would be limited. Individuals with less close interpersonal relationships may benefit more from positive external stimuli, such as consonant and pleasant interactions, to improve their emotional state and sense of connectedness (Lee et al., 2013; Taruffi and Koelsch, 2014; Schäfer et al., 2020). While the bidirectional relationship between perceived closeness and interpersonal synchronization has been previously established (Hove and Risen, 2009; Basile et al., 2022; Hu et al., 2022; Bégel et al., 2024), our results raise a possibility that this relationship could be mediated by the aesthetic experience of what is created together. Future studies should further explore these interactions and their causal direction, such as by manipulating the quality of the dyadic relationship and examining the effect of consonance on dyadic synchronization tasks.

5 Conclusion

In conclusion, our study demonstrates that the aesthetic quality of collaboratively produced sounds significantly influences the precision of interpersonal motor synchronization. These findings build on previous research examining factors such as tempo,

timbre, and intensity in rhythmic joint actions, and highlight the importance of considering aesthetic and consonant elements in collaborative motor tasks. From a clinical perspective, these results are particularly valuable. If consonant musical pitch intervals can enhance movement synchronization more effectively than dissonant intervals, future research could leverage these stimuli for treating neurological and psychiatric disorders. By promoting the joint creation of pleasant sounds and synchronized movements, these techniques could improve movement performance in patients with sensory-motor deficits, such as Parkinson's disease (Rodger et al., 2014; Komeilipoor et al., 2015). Additionally, considering that schizophrenic patients often exhibit reduced synchronous behaviors, impaired movement and gestures, and social-affective disorders, pitch-based interpersonal synchronization tasks could help improve movement synchronization, foster feelings of closeness, and enhance social interactions (Varlet et al., 2012; Lavelle et al., 2014; Raffard et al., 2015; Dean et al., 2021).

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/y2aeh/?view_only=9e5991a23b414881a39cc678e7678ba9.

Ethics statement

The studies involving humans were approved by University of Pavia (Ethical Committee Prot. # 132/23). The studies were conducted in accordance with the local legislation and institutional requirements. The participants provided their written informed consent to participate in this study.

Author contributions

GL: Data curation, Formal analysis, Investigation, Visualization, Writing – original draft. LS: Conceptualization, Methodology, Writing – review & editing. C-EB: Conceptualization, Methodology, Writing – review & editing. CL: Conceptualization, Methodology, Project administration, Supervision, Writing – original draft, Writing – review & editing.

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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.2024.1472632/full#supplementary-material>

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Hyperscanning: from inter-brain coupling to causality

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In hyperscanning studies, participants perform a joint task while their brain activation is simultaneously recorded. Evidence of inter-brain coupling is examined, in these studies, as a predictor of behavioral change. While the field of hyperscanning has made significant strides in unraveling the associations between inter-brain coupling and changes in social interactions, drawing causal conclusions between brain and behavior remains challenging. This difficulty arises from factors like the inherently different timescales of behavioral responses and measured cerebral activity, as well as the predominant focus of existing methods on associations rather than causality. Specifically, a question remains as to whether inter-brain coupling between specific brain regions leads to changes in behavioral synchrony, or vice-versa. We propose two novel approaches to addressing this question. The first method involves using dyadic neurofeedback, wherein instances of inter-brain coupling are directly reinforced. Such a system could examine if continuous changes of inter-brain coupling are the result of deliberate mutual attempts to synchronize. The second method employs statistical approaches, including Granger causality and Structural Equation Modeling (SEM). Granger causality assesses the predictive influence of one time series on another, enabling the identification of directional neural interactions that drive behavior. SEM allows for detailed modeling of both direct and indirect effects of inter-brain coupling on behavior. We provide an example of data analysis with the SEM approach, discuss the advantages and limitations of each approach and posit that applying these approaches could provide significant insights into how inter-brain coupling supports crucial processes that occur in social interactions.

KEYWORDS

hyperscanning, structural equation model, causality - causal modeling, neurofeedback, functional near infrared spectroscopy (fNIRS)

Introduction

Neuroscience is largely dedicated to studying the brain's structure and function, with a primary focus on understanding how neural processes influence behavior, cognition, and overall mental health. To this aim, traditional neuroimaging studies have relied on assessing activation estimates within specific regions of interest (ROIs) and examining their relationship with behavior (e.g., [Molenberghs et al., 2016](#)). As cognitive processes are often the result of complex interactions between multiple regions, not the activity of single areas in isolation ([Bullmore and Sporns, 2009](#); [Damoiseaux et al., 2006](#);

Smith et al., 2009), research has shifted toward utilizing network-level brain variables to explore brain-behavior relationships, reflecting the interdependent nature of neural processes (Bassett and Sporns, 2017).

A recent approach in the field of social neuroscience has extended the network approach to social interactions, suggesting that brain activity is not only coupled within an individual brain but is also coupled between brains during social communication. According to the hyper-brain cell assembly hypothesis, neural cell assemblies may form not only within individual brains but also across brains, operating under principles similar to Hebbian learning within a single brain (Müller, 2022). Within this framework, inter-brain coupling refers to the correlation of time series of brain signals originating from regions of two or more interacting brains (Dikker et al., 2021). The technique of measuring inter-brain coupling is called hyperscanning, an approach that allows simultaneous scanning of multiple brains (Montague et al., 2002). Hyperscanning employs neuroimaging techniques such as Electroencephalography (EEG), functional Magnetic Resonance Imaging (fMRI), and functional Near-Infrared Spectroscopy (fNIRS) and it is increasingly used to examine joint brain activity in individuals within social interactions in various social paradigms. For example, in typical hyperscanning fNIRS studies participants are assigned into dyads or groups and are asked to perform a joint task, while inter-brain coupling in fNIRS signals are taken from all participants. Given the relatively mobile, robust and unintrusive nature of the available portable fNIRS systems, a wide range of interactive tasks can be used in ecologically valid environments, including motor, emotional and cognitive tasks, as well as creativity and problem-solving tasks. Inter-brain coupling values from the obtained fNIRS data are calculated post-recording, and often compared against other, concurrently obtained, task-related data, such as synchrony in speech, eye-movements or motor activity.

The findings of inter-brain coupling during social interactions have greatly advanced neuroscience by demonstrating that multiple brains of interacting individuals can be viewed as components of an extended network (Shamay-Tsoory, 2022). With this approach studies have shown for example that inter-brain coupling in the inferior frontal gyrus (IFG) is increased during face-to-face interaction compared to no-interaction (Jiang et al., 2012), during synchronized movement (Gamliel et al., 2021) and during song learning (Pan et al., 2018). Other brain regions including the dorsolateral prefrontal cortex and the temporoparietal regions were shown to be highly coupled during tasks of group creativity (Mayseless et al., 2019; Pick et al., 2024) and group collaboration (Xie et al., 2020).

However, the initial enthusiasm from hyperscanning was tempered by concerns that inter-brain coupling might merely be an epiphenomenon of performing the same activity simultaneously (Hamilton, 2021). To address this issue, new statistical approaches have been developed, including demonstrating that inter-brain coupling is stronger in real interacting pairs compared to pseudo-pairs [non-interacting pairs performing the same task (Marton-Alper et al., 2023)] or showing that inter-brain coupling is not entirely explained by motor synchrony (Pérez et al., 2017). In a study with dyads of rodents, it was demonstrated that inter-brain coupling emerges from two neuronal populations that separately encode one's own behaviors and those of the interaction partner,

providing evidence that inter-brain coupling arises from ongoing exchange of social signals (Kingsbury et al., 2019). Furthermore, inter-brain coupling has been shown to yield higher predictive power for learning outcomes during social learning compared to single-brain measures (Davidesco et al., 2023), emphasizing the importance of incorporating these measures into models of social behavior.

Despite these exciting developments, a critical question remains regarding the causal relationship between inter-brain coupling and behavioral change. While hyperscanning studies to date have examined the association between inter-brain coupling and behavior, it is not yet clear whether inter-brain coupling triggers behavioral changes or if dyadic behavior creates inter-brain coupling (Hamilton, 2021). It could be the case that during coordinated activities (e.g., joint actions), individuals are exposed to the same sensory stimuli, such as visual or auditory cues. These shared inputs can result in similar neural responses in the brains of the individuals involved, leading to coupled neural activity. Furthermore, during coordinated behavior, individuals often predict each other's actions and adjust their own actions accordingly. This anticipatory mechanism involves neural processes that align the timing of neural activity between brains and could lead to inter-brain coupling. Yet, another possibility is that inter-brain coupling modulates behavior, with fluctuations in coupling levels driving the dynamics of communication during social interactions. Given that social interactions inherently involve a continuous feedback loop of reciprocal exchanges, this bidirectional interaction may underlie the causal relationship between inter-brain coupling and behavioral outcomes. Here, we emphasize the importance of examining the causal pathways between brain activity and behavior, as understanding this relationship is crucial for elucidating the neural mechanisms underpinning inter-brain coupling. Such an investigation could reveal how neural coupling promotes effective communication and facilitates social coordination. We propose here two approaches for testing causality: The first approach relates to manipulating the brain with neurofeedback and involves providing real-time feedback to participants based on their inter-brain coupling. The second approach offers statistical methods for assessing causality. We discuss these two options including the advantages and limitations of each approach and their feasibility in addressing mechanistic explanation of social behavior.

Dyadic neurofeedback

While emerging studies with brain stimulation targeting the IFG show a causal relationship between simultaneous dyadic IFG stimulation and increased coupling (Novembre et al., 2017), it is unclear whether inter-brain coupling could be trained and to what extent training is translated into behavioral change.

Neurofeedback is a technique that provides real-time information about the current level of brain activity, to which we otherwise do not have conscious access. Such information can be used to learn volitional regulation of brain activity. The feedback is visual or auditory (e.g., an animated fish swimming in the sea), in which changes in certain parameters (e.g., the fish's movement) reflect changes in certain features of the measured brain activity.

Neurofeedback leverages the brain's ability to reorganize itself following operant conditioning (Paret et al., 2019) and Hebbian-like plasticity (Coscia et al., 2019) by selectively reinforcing specific neuronal changes.

In the same manner that neurofeedback can regulate the activity of specific brain regions, training with a dyadic neurofeedback platform may allow participants to control their inter-brain coupling by providing feedback on this coupling. Such a setup could involve reinforcement via a visual signal following increased inter-brain coupling between selected regions (see Figure 1). Initial attempts have demonstrated the feasibility of connecting two participants in a single feedback loop. For example, using EEG, Chen et al. (2021) showed an association between social closeness and inter-brain coupling in a dyadic neurofeedback protocol. While no study to date has demonstrated long-term behavioral changes following dyadic neurofeedback training, the growing efforts to develop such protocols demonstrate significant potential.

A dyadic neurofeedback setup may include simultaneous synchronized fNIRS data collection from two participants. The data obtained from each participant are pre-processed in real-time by application of frequency filtering, motion artifact removal, and common component removal using Short Separation channels (Gagnon et al., 2012) or other statistical methods (e.g., Zhang et al., 2016). The filtered data is then separated into temporal windows of 30 s or more, and inter-brain coupling values are extracted from each window using the Wavelet Transform Coherence (WTC) technique (Grinsted et al., 2004) that enables transforming a time series into a function of time and frequency. This process repeats in intervals of approximately 1 s, with each output value representing the brain synchrony within the preceding window, with a large degree of overlap. These values may be used to adjust the motion speed of an animated fish on a screen, which the participants in the study can observe. Participants are randomly assigned to dyads and instructed to observe a computer screen displaying a virtual task involving a swimming fish (Figure 1). Their goal is to increase the speed of the fish's movement. The speed of the fish is contingent upon the participants' ability to enhance their inter-brain coupling, providing real-time reinforcement of their increasing interbrain coupling. This feedback loop is designed to promote enhanced synchronization between the participants' brain activity, thereby facilitating functional inter-brain connectivity. If indeed it will be possible to measure noticeable behavioral change following training in dyadic neurofeedback, it will provide initial evidence that indeed inter-brain coupling supports behavioral change. The changes could be observed at the individual level, for example increased empathic capacities of a participant following dyadic training, or changes at the level of the dyad, such as improved motor synchronization or enhanced cooperation.

The application of dyadic neurofeedback offers several distinct advantages. Unlike neurostimulation, neurofeedback is a non-invasive technique, making it a safer and more accessible option for modulating brain activity. In addition to its potential for testing causal inferences in neural circuits, successful implementation of dyadic neurofeedback could lead to a wide range of clinical applications aimed at enhancing social behavior in various populations.

Despite the potential of dyadic neurofeedback for establishing causal links between inter-brain coupling and behavioral changes,

significant challenges remain in developing appropriate control conditions to effectively rule out placebo effects and expectation biases. Additionally, there are unresolved questions regarding the specific brain regions that are most relevant for these dyadic neurofeedback protocols. While a recent meta-analysis found the largest effects size for inter-brain coupling in the frontal cortex and temporoparietal junction (Czeszumski et al., 2022), it is possible that other brain regions may also have potential for training inter-brain coupling. In addition, the process of learning to control brain activity within dyadic neurofeedback is inherently slow and complex. Finally, variability in individual learning abilities within the dyad can significantly influence the overall effectiveness of achieving and maintaining enhancements in inter-brain coupling. Nonetheless, demonstrating that modifications in inter-brain coupling can lead to measurable behavioral changes would provide compelling evidence of causality, reinforcing the potential impact of such interventions on social and cognitive processes.

Statistical approach for testing causality

Various statistical tools have been employed to address the challenge of causality in neuroimaging studies, including Granger causality and structural equation modeling (SEM). These methodologies can be applied to explore the causal dynamics of inter-brain coupling and its impact on social interactions, thereby providing insights into the neural mechanisms underlying social behavior.

The Granger causality approach relies on the principle of comparing the predictive power of a past value of a variable Y on its current value (autoregression) to the predictive power of autoregression and the values of a second variable X. If the latter is significantly higher than the former, X can be said to be G-causing Y (Seth et al., 2015). Importantly, Granger causality tests can be performed in the opposite direction – i.e., whether Y is G-causing X. Significance in both cases is not mutually exclusive. If changes in the neural activity of one brain can be shown to G-cause changes in another brain's activity, and this neural interaction correlates with specific social behaviors, it becomes possible to predict how changes in inter-brain coupling may influence or correspond to future behaviors in social interactions. G-causality has been extensively utilized in neuroimaging studies, particularly within the framework of ordinary linear autoregressive (AR) models of stochastic processes (Goebel et al., 2003; Roebroeck et al., 2005), and it may therefore become valuable in understanding and forecasting the dynamics of social behavior based on inter-brain coupling. One possibility is employing Granger causality to investigate the directionality between inter-brain and intra-brain coupling. Indeed, Müller and Lindenberger (2024) showed that the dynamics of both inter-brain and intra-brain connections are critical for understanding interpersonally coordinated actions. If it is found that inter-brain coupling influences intra-brain connectivity, this would suggest that changes in inter-brain dynamics may drive alterations in individual neural processes, ultimately leading to behavioral modifications.

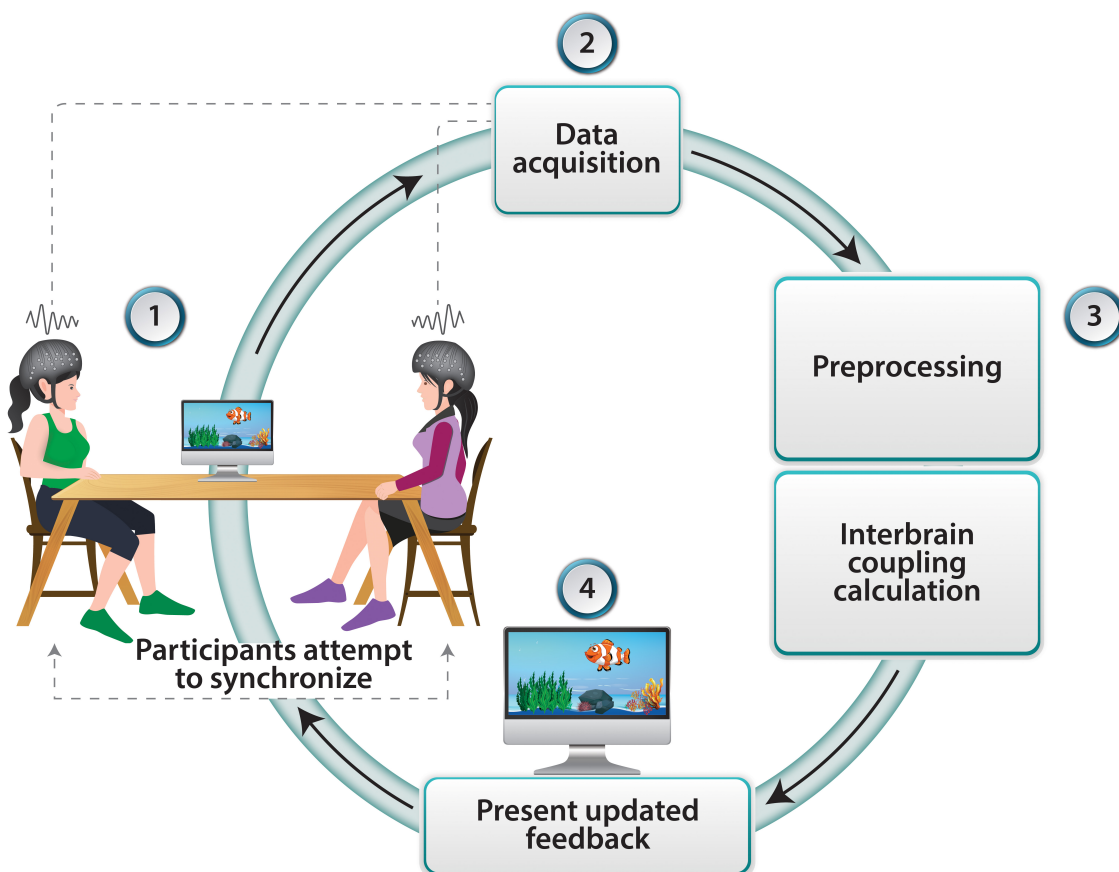


FIGURE 1

Neurofeedback loop in dyadic interaction using fNIRS. Two participants observe a swimming fish that and its velocity represents their levels of inter-brain coupling. fNIRS data is collected from both participants in real-time as they perform the task. The recorded fNIRS data undergo preprocessing to remove artifacts and noise. Interbrain coupling is then calculated and the real-time inter-brain coupling information is presented back to the participants through updated movement of the fish, thus completing the neurofeedback loop.

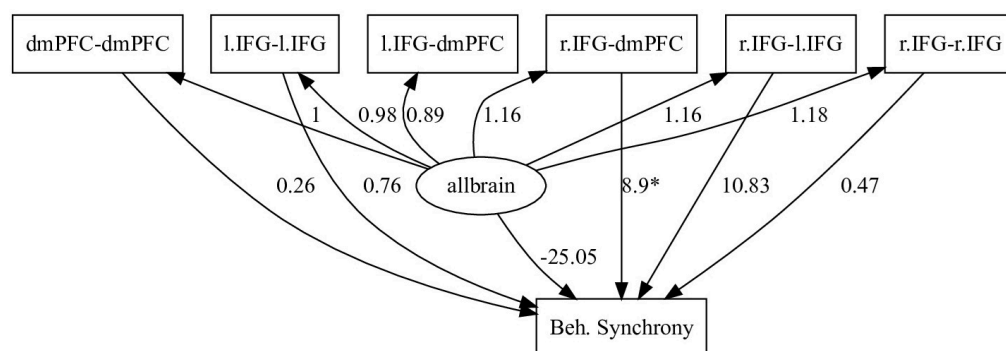


FIGURE 2

Example SEM model. Predicting behavioral synchrony by the measured activity of several ROI couplings and the computed combined activity of the interbrain network as a whole (allbrain). Here, only couplings including r.IFG and dmPFC were used to predict behavior, according to previous findings. The loading values are indicated by the numbers, while significance is indicated by the asterisk. Only the r.IFG-dmPFC coupling was shown to significantly positively predict behavioral synchrony.

To establish causal link between inter-brain coupling and behavior, Koul et al. (2023) used synchronized EEG recordings from dyads engaged in a nonverbal task. The authors applied G-causality explore the directional relations between inter-brain coupling and behavioral measures (e.g., synchrony in facial

expressions). To this end, participants were placed at either a short (1 m) or long (3 m) distances from each-other under conditions where they could or could not see each-other, under no specific instructions to interact. During each block, EEG, movements and eye-tracking recordings were obtained. Inter-brain

coupling emerged spontaneously when participants were looking at each-other regardless of distance. The authors first analyzed the power spectra across several EEG frequency bands. They then used computational model, which relied on contemporaneous power increase in these frequency bands within dyads, to identify instances of inter-brain coupling. Behavioral recordings were analyzed to produce a matching timeline, representing synchronous behavior. These timelines were then used to construct a Bayesian model, which was then fitted to a vector autoregressive (VAR) model, which, in turn, was used to calculate multivariate G-causality values. G-causality was found significant in both directions, although the predictive effects of behavioral synchrony on inter-brain coupling were reported to be stronger than the opposite (Koul et al., 2023). The latter finding raises questions about the specific mechanism of this reciprocity. It may be hypothesized, for example, that inter-brain coupling between specific ROIs may causally affect behavioral coupling, and vice-versa for other ROI pairs. Exploration of this topic is somewhat hampered by the difficulty in source localization inherent in EEG recordings (e.g., Bradley et al., 2016; Jatoi et al., 2014). In contrast, techniques relying on cerebral haemodynamic response, such as fMRI and fNIRS, which are relatively accurate in their spatial resolution, may lack the required temporal resolution for G-causality analyses. For example, in a typical study using fNIRS for measuring brain activity, the haemodynamic response may be trailing the underlying neural activity by several seconds (Cinciate, 2019), thus leading to the possibility of the resulting behavior taking place before the haemodynamic response can be recorded. One possibility is to use simultaneous recordings of fNIRS and EEG data which may allow identifying causal relationships between specific ROI pair coactivation and behavioral synchrony in more detail.

Another potential approach toward establishing and testing network-based models of brain and behavior may be based on structural equation modeling (SEM). In SEM parameters are represented by connection strengths or path coefficients between variables, analogous to effective connectivity in a neural network model. Each path within the model is directional, reflecting hypothesized causal influences between variables. The parameters in SEM are estimated by minimizing the discrepancy between the observed covariance matrix and the covariance matrix predicted by the proposed structural model. This estimation process enables SEM to solve the entire path model simultaneously, providing insights into the causal directionality among multiple ROIs. In a study modeling both brain and behavior, Bolt et al. (2018) conducted a study on data from a large pool of participants, who performed tasks from three cognitive domains (working memory, relational processing, and arithmetic processing), with each task having a respective control condition. fMRI recordings were taken during the tasks' completion. The authors then used SEM to construct a network model, based on the collected data, which included several ROIs in the brain as well as behavioral responses. A regression equation was constructed to represent the activity of each ROI as a function consisting of a network activation component, an ROI activation component unrelated to the network, and a residual component. The behavioral outcome was then estimated as a regression function including the activity within the network, the network-independent activity in each ROI, and a random component. The resulting model was then pruned to remove ROIs with low loadings. Using this method,

only individual ROIs were shown to affect behavior independently of the network as a whole. This approach is highly promising for application in inter-brain coupling. In particular, it allows for testing of specific hypothetical models, such as models that include inter-brain coupling between specific regions and behavior.

We tested this approach using an fNIRS dataset published by Marton-Alper et al. (2023), where we previously found that interbrain coupling in the right inferior frontal gyrus (rIFG) and dorsomedial prefrontal cortex (dmPFC) positively predicted movement synchronization during a 3D movement task. In this study, dyad members were handed a RAZER 3D motion sensor and instructed to move their arms in synchrony. The 3D position data of the participants' arms were recorded, and fNIRS inter-brain coupling data were obtained from each participant's dmPFC and IFG areas, bilaterally. The levels of motion synchrony were calculated as a timeseries throughout each task block by means of Cosine Velocity Vector (CVV) calculation (Reiss et al., 2019), which allows or detection of lagged and unlagged synchronized 3D motion. fNIRS data were preprocessed by frequency filtering, motion artifact removal, PCA-based spatial filtering (Zhang et al., 2016), and converting to relative oxygenated and deoxygenated hemoglobin concentrations. Inter-brain coupling was calculated on the oxygenated hemoglobin values using the WTC toolbox for Matlab (Grinsted et al., 2004) between all ROI combinations. This method of detecting inter-brain coupling is based on a two-stage process, wherein the hemoglobin concentrations are first subjected to wavelet transformation (WT) using a seed Morlet wavelet, which serves the functional purpose of detecting single-brain activity across time and wavelength. We used the wavelengths of 6–66 s. In the second stage, coherence between the two WT series is calculated, to derive WTC values between the two brains. Whereas in the Marton-Alper et al. (2023) study we used LME-type analyses, here we constructed an SEM model using the same data, in which we sought to examine the effects of inter-brain coupling between all measured pairs of ROIs on motion synchrony. The simple assumption behind this model, provided as a feasibility example, was that coupling between some ROIs are likely to be correlated to behavioral synchrony, while inter-brain coupling between others might not. For our purposes, we considered two sets of ROI pairs – each set related to one hemisphere. In our model, overall interbrain connectivity network was represented by a latent variable (allbrain), representing joint effect of all ROI pairs' activation on behavior, and consisting of the coupling values of all ROIs (lIFG-lIFG, lIFG-dmPFC, lIFG-rIFG, rIFG-dmPFC, rIFG-rIFG, dmPFC-dmPFC), and the level of behavioral synchrony (movement synchronization) was predicted by the computed activity of the allbrain variable, and by each of the ROI couplings including rIFG and dmPFC. As shown in Figure 2, the model indicated that only the rIFG-dmPFC coupling significantly ($p < 0.05$) predicted behavioral synchrony. A similar model using lIFG and dmPFC couplings to predict behavioral synchrony levels was tested and yielded no significant predictions. These findings not only corroborate the original findings of Marton-Alper et al. (2023) but also offer a model that includes directionality interdependencies between multiple observed and latent variables.

While we use this as a simple example of using SEMs to describe the relationship between inter-brain and behavioral synchrony, it is possible that data of neural activity as well as social behaviors collected from multiple individuals could be tested by means of

multilevel structural equation modeling (mSEM), as proposed by Rabe-Hesketh et al. (2004). In this type of model, ROIs from each individual in a group would be treated as clusters on the lower level of the model, whereas the upper level of the model would represent the group as a whole. Behavioral outcomes can then be factored into such a model in two ways: individual behavior can be factored in as related to the lower-level clusters, respectively; group behavioral measures, such as motor synchrony levels, can be related to both levels of the model.

When comparing the two approaches, the advantage of Granger causality (G-causality) is its ability to provide direct statistical evidence of causality, including the direction of the causal relationship, between continuous time series data. Yet, on its own it provides a fairly narrow view individual connections within the wider network of ROIs involved in inter-brain coupling and the concurrent behavior. In contrast, SEM-based models provide an excellent potential tool for testing the structure of this network as a whole, albeit somewhat limited in inferring causality, in the sense that the direction of causality needs to be hypothesized a-priori in the model being tested. The latter is especially relevant for social interactions which occur in relatively naturalistic settings, as opposed to highly structured trial-based fMRI tasks. We propose that the way forward may be in combining the two approaches.

Conclusion

Overall, the latest literature on hyperscanning is converging toward the networked approach and much work is being done to devise statistical and experimental methods to validate an overall network model of social interaction. An important aspect of this kind of modeling is the question of causality between groups of ROIs constituting the inter-brain network, and between these groups and the concurrent behavior. Although dyadic neurofeedback studies provide preliminary evidence of causality in neural coupling and its effects, more robust methods are required to thoroughly examine the causal link between inter-brain coupling and behavioral outcomes. Approaches such as Granger causality and SEM offer powerful tools to test the directional influence of inter-brain coupling on behavior. Granger causality is particularly useful for identifying causality of temporal relationship between inter-brain coupling and subsequent behavioral changes. On the other hand, SEM enables researchers to model complex relationships between multiple observed and latent variables, allowing for the simultaneous testing of neural and behavioral dynamics. By applying these techniques, future research could move beyond correlational observations and establish more definitive causal mechanisms linking inter-brain coupling with social and cognitive behavior.

While inferring causal relationships between intra- and inter-brain coupling levels can be achieved using well-established statistical techniques, such as G-causality and SEM, doing the same at the brain-behavior level is more challenging. We propose that application of mSEM modeling together with measures of causality estimation may be highly beneficial for understanding the brain and behavioral dynamics of synchronous behavior. Working from a vantage point of a specific theoretical model of interpersonal interaction, it should be possible to construct and validate its

structure and components by examining a statistical mSEM model based on it. Behavioral components may be integrated into this model on multiple levels by means of attributing specific behavioral changes to ROIs that are established as causing behavior directly.

Data availability statement

Publicly available datasets were analyzed in this study. This data can be found here: <https://doi.org/10.17632/xd9zr7hh3z.1>.

Ethics statement

Ethical approval was not required for the studies involving humans because this is a purely theoretical paper. It includes analyses of previously published study with human subjects, which was approved by the ethics committee. The studies were conducted in accordance with the local legislation and institutional requirements. The human samples used in this study were acquired from primarily isolated as part of your previous study for which ethical approval was obtained. Written informed consent to participate in this study was not required from the participants or the participants' legal guardians/next of kin in accordance with the national legislation and the institutional requirements.

Author contributions

AM: Formal analysis, Methodology, Software, Visualization, Writing – original draft, Writing – review and editing. SS-T: Conceptualization, Formal analysis, Funding acquisition, Methodology, Supervision, Visualization, Writing – original draft, Writing – review and editing.

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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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Modeling dynamics on the dance floor with directional swarmalators

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Understanding collective behavior in both biological and social contexts, such as human interactions on dance floors, is a growing field of interest. Spatiotemporal dynamics of collective behavior have previously been modeled, for instance, with swarmalators, which are dynamical units that exhibit both swarming behavior and synchronization, combining spatial movement and entrainment. In our current study, we have expanded the swarmalator concept to encompass gaze direction as a representation of visual attention. We employ the newly developed directional swarmalator model for simulating the complex spatiotemporal dynamics observed on dance floors. Our model aims to reflect the complex dynamics of collective movement, as well as rhythmic synchronization and gaze alignment. It establishes a quantitative framework to dissect how individuals on dance floors self-organize and generate emergent patterns in response to both musical stimuli and visual perception of other dancers. The inclusion of gaze direction allows for the simulation of realistic scenarios on dance floors, mirroring the dynamic interplay of human movement in rhythm-driven environments. The model is initially tested against motion capture recordings of two groups dancing in a silent disco, however, it is theoretically adaptable to a variety of scenarios, including varying group sizes, adjustable degrees of auditory and visual coupling, as well as modifiable interaction ranges, making it a generic tool for exploring collective behavior in musical settings. The development of the directional swarmalator model contributes to understanding social dynamics in shared music and dance experiences.

KEYWORDS

dance and movement, interaction, complex dynamics, swarmalators, entrainment

1 Introduction

Humans display a wide array of coordination behaviors of varying complexity. Collaborative work, sports, music, and dance all require interpersonal coordination to perform successfully, whether coordinating through behavior matching (imitation) or through behavioral synchrony and rhythmic entrainment (Bernieri and Rosenthal, 1991). A lot of joint action research has focused on simple, dyadic interactions.

These are relatively easy to study in the lab, with two participants coordinating on a task, such as rowing, drumming, tapping, or dancing (Cuijpers et al., 2015; Dotov et al., 2022). In these instances, relatively simple measures of synchrony (e.g., cross-correlation) may be used to assess the extent of coordination. However, real social interactions are often more complex than two people moving in synchrony, and may involve large groups of people, which requires more complex means of modeling social dynamics.

According to McMahon and Isik (2023), there are three social primitives to any social interaction: contingent motion, distance, and facingness. These are the basic visual features that one may observe to determine the extent to which any two or more agents are interacting, and all three have been used to measure social interactions in dance.

Previous dance research has examined each of these social primitives. For example, contingent motion, often operationalized as a form of synchrony (Hartmann et al., 2023), has been found to predict perceived similarity between the dancers (Hartmann et al., 2019). Interpersonal distance has been measured as a proxy for social affiliation on the dance floor (Bamford et al., 2023). Finally, facingness, whether measured through head or torso orientation relative to other dancers, has been used to predict perceived interaction (Hartmann et al., 2019), or as a measure of social attention (Bamford et al., 2023; Woolhouse and Lai, 2014).

Dance provides a useful platform for studying large-scale, coordination dynamics. Although there are many examples of partner dances (Kaminsky, 2020), dance is often performed in groups in many cultures (Brown, 2022). However, most of these previous studies have focused on dyadic interactions or, in some cases, very small groups with limited spatial movement. Agent based modeling is a useful way of understanding complex behavior in humans and other animals, and some existing models may be applied to studying dance as a dynamic system.

Existing models have been used to study swarming behavior in birds, bees and other organisms. Collective behavior between individuals in a swarm can produce an emergent superorganism. For instance, Okubo (1986) model can be used to simulate a flock of birds (Reynolds et al., 2022). Models such as this may simulate the translational movement dynamics of individuals within a collective, however, they do not include the oscillatory dynamics featured in dance movements.

Other models have been used to study the behavior of two or more oscillators. The Kuramoto model describes the behavior of coupled oscillators, such that when there is sufficient coupling strength synchrony spontaneously emerges (Acebrón et al., 2005). This has since been applied to a wide range of biological phenomena, such as frogs chorusing (Aihara et al., 2008) and humans clapping at a concert (Néda et al., 2000). Another is the Haken-Kelso-Bunz (HKB) model, which was developed for modeling intraindividual synchrony between limbs, but has since been extended to interpersonal synchrony, and is notable for accommodating asymmetry, i.e., antiphase synchrony is treated as a stable state in the HKB model (Kelso, 2021). One other example, the ADaptation and Anticipation Model (ADAM), aims to simulate synchrony between individuals, while also modeling the internal adaptation and anticipation processes

required for sensorimotor synchronization (SMS) in humans (Van Der Steen and Keller, 2013). This makes ADAM more specific to modeling the interactions between agents with human-like SMS abilities, while the Kuromoto and HKB models are suitable for any interactions between coupled oscillators. However, all of these models are limited to oscillatory dynamics.

Social interactions on the dancefloor involve both oscillation within and between individuals, as well as movement or spatial translation across the dancefloor, and directed attention. Swarmalators provide a potential solution to incorporate the oscillatory and translational dynamics into a single model (O’Keefe et al., 2017). Each agent within the model is both an oscillator and a member of a swarm, which enables the study of contingent motion and interagent distance, as two social primitives. However, swarmalators still neglect the “facingness” component of any social interaction between humans.

Humans do not have an infinite attentional capacity, nor do they have eyes on the back of their head. Wirth et al. (2023) highlight the importance of visual heading in collective dynamics, emphasizing that the neighbourhood of interaction in human crowds is best explained by a visual model, where interactions are governed by optical motions and the visibility of neighbors. Keller (2023) in his theoretical model of ensemble coordination proposes three abilities that are required for SMS: attention, anticipation, and adaptation. Anticipation and adaptation are built into ADAM as discussed above (Van Der Steen and Keller, 2013), however, attention has not been incorporated. Similarly, swarmalators, in their current form, assume 360° vision (O’Keefe et al., 2017), which limits their applicability to humans interacting on a dance floor, in which the orientation of dancers is crucial to their successful coordination (Bamford et al., 2023).

The novel solution developed in this paper is to introduce a directional swarmalator model. This maintains the oscillatory and translational dynamics of typical swarmalators (O’Keefe et al., 2017), but also includes rotational dynamics, acknowledging the role of “facingness” in a social interaction. Each agent oscillates, can move around in a defined space, and can also change the orientation of its gaze. In addition, within this model, there is an external driving oscillation to which the agents are entrained. Within the model specified below, agents will be attracted to others that oscillate with a beat aligned to their own, and attraction can happen through both moving toward a target, and rotating to face it. An agent may also become entrained to other agents in the space, but only those within its field-of-view. Consequently, directional swarmalators offer an opportunity to study all three social primitives in large groups of dancers.

This paper specifies the directional swarmalator model with its three dynamics: translation, rotation, and oscillation. It then outlines measurements for each of these dynamics.

As circles are common formations in many dance cultures worldwide (Chauvigné et al., 2019; Sachs, 1965), we developed measures of self-organization to quantify the degree of circularity within the group, as well as centroidal alignment—the extent to which all group members were oriented toward the group’s midpoint. Finally, a phase coherence measure was used to quantify phase locking between swarmalators. Results for each of these measures were compared between simulated data from the directional swarmalator model, and real-world motion capture data from a silent disco.

2 Directional swarmalator model

Let the swarm consist of swarmalators s_j , $j = 1, \dots, N$. The instantaneous state of s_j is defined by five state variables. These are the position $\mathbf{x}_j \in \mathbb{R}^2$, oscillation phase θ_j , azimuth of gaze direction δ_j , spontaneous oscillation frequency ω_j , and phase of external stimulus φ_j .

For future purposes, we define the *proximity* between s_i and s_j as the inverse of their mutual Euclidean distance, $w_{jk} := 1/|\mathbf{x}_j - \mathbf{x}_k|$.

2.1 Translational dynamics

The translational dynamics of the model comprise three parts, those of global attraction, repulsion, and phase-and-gaze-dependent attraction. Consequently, the instantaneous velocity of s_j , denoted by $\dot{\mathbf{x}}_j$, consists of three components. First, overall attraction component constrains its distance from the origin, and is defined by

$$\dot{\mathbf{x}}_{Aj} = -A\mathbf{x}_j|\mathbf{x}_j|^{a-1} \quad (1)$$

Here A determines the strength of attraction and a defines its degree of exponential increase with distance. Second, the repulsion component prevents s_i from coalescing with other swarmalators, and is defined by

$$\dot{\mathbf{x}}_{Rj} = -\frac{R}{N} \sum_{k \neq j} w_{kj}^r (\mathbf{x}_k - \mathbf{x}_j) / |\mathbf{x}_k - \mathbf{x}_j| \quad (2)$$

Here R determines the overall strength of repulsion and the spatial decay exponent r dictates how the force or interaction decays with increasing distance to another swarmalators.

Third, phase-and-gaze-dependent spatial coupling is defined by

$$\dot{\mathbf{x}}_{pj} = \frac{P}{N} \sum_{k \neq j} w_{kj}^p \Omega(\theta_k - \theta_j) \Upsilon(\alpha_{kj} - \delta_j) (\mathbf{x}_k - \mathbf{x}_j) / |\mathbf{x}_k - \mathbf{x}_j| \quad (3)$$

where P and p determine the strength and spatial decay of the interaction, respectively, Ω denotes the phase coupling function, Υ the gaze coupling function, and $\alpha_{kj} := \angle(\mathbf{x}_k - \mathbf{x}_j)$ the azimuth angle of the vector pointing from s_j to s_k . The phase and gaze coupling functions should be defined so that s_j is maximally attracted by s_k when the two are similar in phase, and the gaze of s_j is pointing toward s_k . In the present instance of the model, we define the phase coupling function to be

$$\Omega(\theta) = \frac{1 + \cos(\theta)}{2} \quad (4)$$

Similarly, in the present instance of the model we define the gaze coupling function by

$$\Upsilon(\theta) = \left(\frac{1 + \cos(\theta)}{2} \right)^c / \int_{-\pi}^{\pi} \left(\frac{1 + \cos(\theta)}{2} \right)^c d\theta \quad (5)$$

Parameter c affects the width of the modeled visual field and is referred to as constriction. The denominator in Eq. 5 is a normalization parameter that makes the average value of Υ independent of c . The constriction parameter defines the width of a swarmalator's visual field, determining the angular region in

which interactions are strongest. Higher values of narrow the visual field, making the swarmalator less sensitive to individuals outside a forward-facing region. This models the limited visual attention of real-world agents, such as dancers, who primarily interact with those within their line of sight. See Figure 1 for an example of the effect of constriction.

Finally, the total instantaneous velocity of s_j is defined as the sum of the three previous terms:

$$\dot{\mathbf{x}}_j = \dot{\mathbf{x}}_{Aj} + \dot{\mathbf{x}}_{Rj} + \dot{\mathbf{x}}_{pj}. \quad (6)$$

2.2 Rotational dynamics

The gaze direction of swarmalators is attracted by other swarmalators, most strongly by those that are proximal and similar in phase. Formally, the time derivative of the gaze direction of s_j is defined as

$$\dot{\delta}_j = \frac{D}{N} \sum_{k \neq j} w_{kj}^d \Upsilon'(\alpha_{kj} - \delta_j) \Omega(\theta_k - \theta_j) \quad (7)$$

Here D and d determine the strength and spatial decay of rotational interaction, respectively, and $\Upsilon'(\theta) = \frac{d\Upsilon}{d\theta}$. Using the gaze coupling function of Eq. (5), we get

$$\Upsilon'(\theta) = \frac{c \sin \theta}{2} \left(\frac{1 + \cos(\theta)}{2} \right)^{c-1} \quad (8)$$

2.3 Oscillatory dynamics

The oscillatory dynamics of s_i comprises three components: spontaneous frequency, auditory entrainment to external stimulus, and visual entrainment to other swarmalators. Spontaneous frequency can, for instance, be drawn from a normal distribution centered at a mean spontaneous moving rate, $\omega_j \mathcal{N}(\mu, \sigma)$. The auditory entrainment component is expressed by

$$\dot{\theta}_{aj} = U \sin(\varphi_j - \theta_j) \quad (9)$$

where U denotes the strength of auditory coupling and φ_j the phase of the external stimulus.

Visual entrainment, in turn, is expressed by

$$\dot{\theta}_{vj} = \frac{V}{N} \sum_{k \neq j} w_{kj}^v \Upsilon(\alpha_{kj} - \delta_j) \sin(\theta_k - \theta_j) \quad (10)$$

where V and v determine the strength and spatial decay of the interaction. According to this equation, visual entrainment is strongest to other swarmalators that are proximal and similar in phase. Finally, the time derivative of the oscillation phase is expressed as the sum of the three abovementioned terms:

$$\dot{\theta}_j = \omega_j + \dot{\theta}_{aj} + \dot{\theta}_{vj} \quad (11)$$

3 Group-level measures of self-organization

Swarmalators manifest self-organization in terms of their location, direction, and oscillation phase. In the following, we

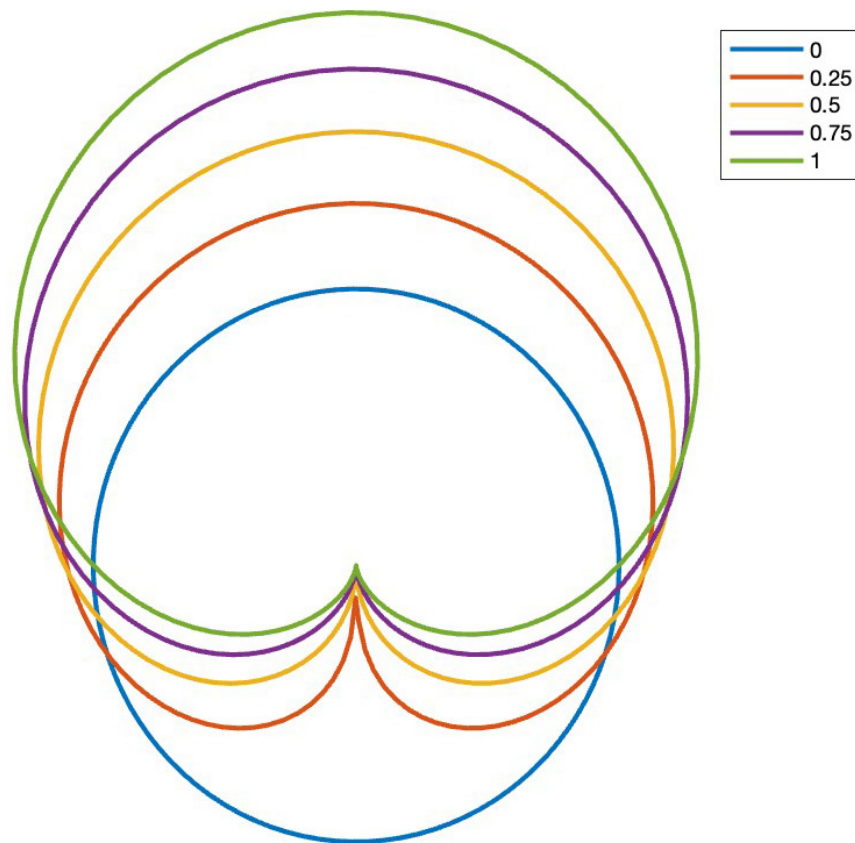


FIGURE 1
Effect of constriction parameter c on the gaze coupling function. Front view is on the top of this figure.

propose measures that can be used to quantify the degree of self-organization as a function of time in each of these three domains. In settings where groups of swarmalators are fed with different external stimuli, such as in a silent disco, all these measures can be calculated on both global and group levels.

3.1 Translational self-organization

Circularity κ measures the degree to which the swarmalators form a circular configuration, and is operationalized as standard deviation of distances from group centroid:

$$\kappa = \sigma(|\mathbf{x}_j - \langle \mathbf{x} \rangle|) \quad (12)$$

where $\langle \mathbf{x} \rangle = \frac{1}{N} \sum_j \mathbf{x}_j$ denotes the position of the group mean. The value $\kappa = 0$ indicates that the swarmalators are organized in a perfect circle.

Grouping coefficient ρ measures the extent to which swarmalators driven by the same stimulus are grouped together. It is operationalized as the intracluster correlation coefficient

$$\rho = \frac{\sigma_b^2}{\sigma_b^2 + \sigma_w^2} \quad (13)$$

where σ_b^2 and σ_w^2 are the between- and within-cluster variances, respectively, and ranges between 0 and 1. A cluster is defined based

on the auditory stimulus received by each swarmalator, with each unique stimulus corresponding to a distinct group.

3.2 Rotational self-organization

Gaze locking coefficient γ measures the degree to which swarmalators are facing at each other. It is defined by

$$\gamma = \frac{1}{N(N-1)} \sum_{k \neq j} \cos(\alpha_{kj} - \delta_j) \quad (14)$$

and ranges between -1 and 1 .

Centroidal alignment χ measures the degree to which swarmalators are facing at the group centroid, and is defined by

$$\chi = \frac{1}{N} \sum_j \cos(\varepsilon_j - \delta_j) \quad (15)$$

where ε_j denotes the azimuth angle from $\mathbf{x}_j$ to $\langle \mathbf{x} \rangle$, $\varepsilon_j = \angle((\mathbf{x}) - \mathbf{x}_j)$. Again, χ ranges between -1 and 1 .

3.3 Oscillatory self-organization

Phase coherence R measures the degree of phase locking between the swarmalators, and is calculated as the norm of the

Kuramoto order parameter

$$R = \frac{1}{N} \left| \sum_{i=1}^N e^{i\theta_i} \right| \quad (16)$$

To measure local phase coherence, we first define the *individual local phase coherence* of swarmalator j by

$$R_j^\sigma = \frac{\left| \sum_k K_{jk}^\sigma e^{i\theta_k} \right|}{\sum_k K_{jk}^\sigma} \quad (17)$$

where

$$K_{jk}^\sigma = e^{-|\mathbf{x}_j - \mathbf{x}_k|^2 / 2\sigma^2} \quad (18)$$

is the spatial kernel and σ the kernel width. The index R_j^σ thus weights the contribution of each swarmalator so that the weight decreases with increasing distance, and the value of σ determines the degree of locality in the measure. Subsequently, the *local phase coherence* R^σ is calculated as the mean of R_j^σ across all swarmalators:

$$R^\sigma = \frac{1}{N} \sum_j R_j^\sigma \quad (19)$$

It is straightforward to see that when σ increases, R^σ approaches the global phase synchronization measure:

$$\lim_{\sigma \rightarrow \infty} R^\sigma = R \quad (20)$$

4 Estimating state parameters from empirical data

When the participants in a silent disco experiment have been motion-captured with, for instance, two markers on the head, achieving the position and gaze direction is straightforward. As regards the oscillation phase, it has been found in several studies that in spontaneous dance the vertical velocity of the head tends to be synchronized to the tactus-level beat of music (Toiviainen et al., 2010; Toiviainen and Carlson, 2022; Burger et al., 2014). Consequently, the oscillation phase θ_i can be estimated from the vertical velocity component of head marker, $\dot{\mathbf{x}}_{iZ}$, by means of the analytical signal using

$$\theta_i = \angle (\dot{\mathbf{x}}_{iZ} + iH(\dot{\mathbf{x}}_{iZ})) \quad (21)$$

where $\angle$ denotes the argument (direction angle in complex plane), and H the Hilbert transform.

5 Simulations

5.1 Silent disco experiment

A silent disco was organized in an optical motion capture lab. Twelve participants (11 females, mean age = 22.9, $SD = 1.83$) were outfitted with silent disco headsets (Silent Disco King),¹ which had been fitted with reflective markers.

¹ <https://www.silentdiscoking.com/equipment>

The participants were asked to move in 20 conditions while listening to either metronome sequences or excerpts of real music stimuli through the silent disco headsets, however, only two were included in the current analysis due to their relevance for testing the directional swarmalator model. The first eight conditions involved participants bouncing to auditory stimuli (metronome or music) with varying phase or frequency shifts, without any specific instructions about grouping. The next eight conditions instructed participants to form groups based on visual information while listening to the same types of stimuli. In the final four conditions, participants were asked to dance freely without specific instructions. The sequence of conditions was randomized to minimize order effects. Each condition was motion-captured using the Qualisys Oqus cameras, capturing the movements of the markers affixed to the headsets at 120° Hz.

Recruitment was conducted via advertisements to Musicology and Music Education student associations at the University of Jyväskylä, and all participants were students of the Department of Music, Arts and Culture Studies. The study complied with ethical standards, including approval from the university's ethical review board.

In the conditions included in the present paper, the participants were randomly put into two different groups (Group 1 and Group 2). Group 1 heard the original version of the auditory stimuli, while Group 2 heard the stimuli with either a phase difference (90° or 180°) or a frequency difference (sped up) version of the stimuli. The groups were identified according to the number of markers affixed to the headsets (Group 1 headsets had three markers on the left side, while Group 2 headsets had two markers on the left side). A “dummy” marker was placed on the left side of the Group 2 markers so the participants would not be able to discern which group they were in Figure 2.

The instructions given during the conditions were either to move freely or bounce to the auditory stimuli's main beat (tactus). Moving freely was instructed as being dance-like movements and bouncing was defined as vertical movement caused primarily by knee flexions and extensions. In some conditions participants were tasked with finding members of their groups by identifying similar or synchronous movements. Visual inspection of the motion capture data revealed that the groups swarmed more easily in the bouncing conditions than those where they were dancing.

For the sake of the current study's modeling focus, four bouncing conditions are selected for analysis: Metronome 120 BPM with 90° and 180° phase shifts, and two musical excerpts (Girls and Boys by Blur with a 90° and Bad Romance by Lady Gaga with a 180° phase shift). The musical stimuli were time stretched to have a bpm of 120.

5.2 Model optimization

5.2.1 Parameters to be optimized

We used the motion capture data collected in the silent disco experiment described above to perform parameter fitting for our swarmalator model. The primary goal of this fitting was to align the final configurations of the swarmalators after one minute of simulation with the observed configurations from the silent disco data as closely as possible. Due to the complexity of the model and

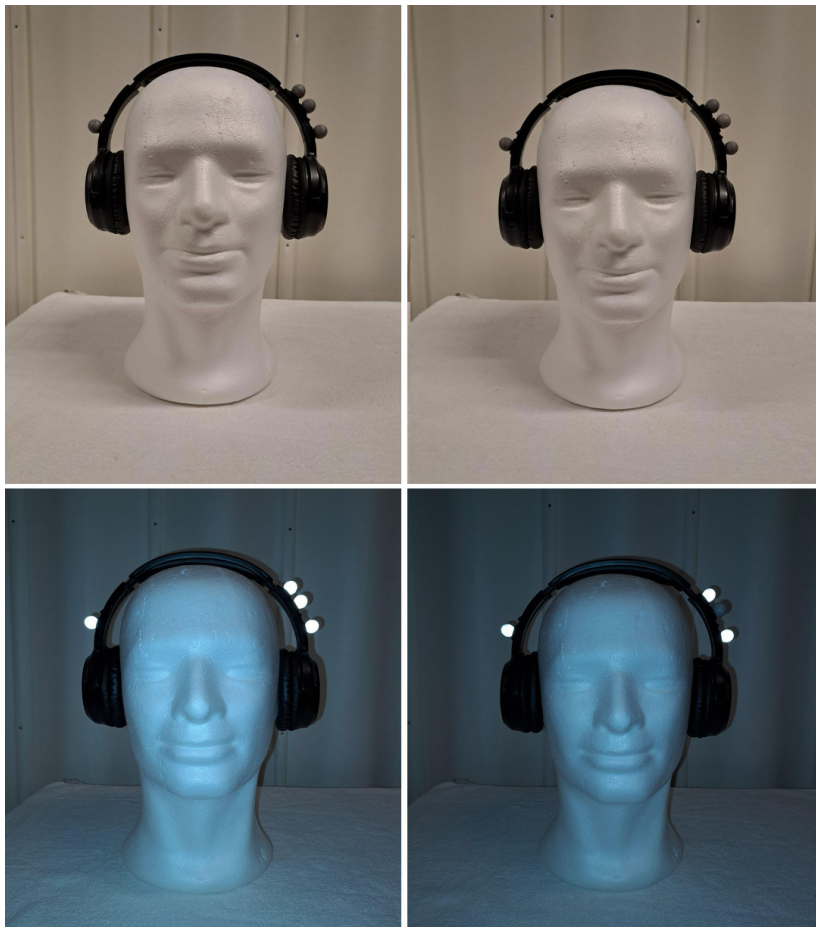


FIGURE 2
Headphones with reflective markers. Group 2 pictured on the right with the dummy marker. The top row shows the markers under normal lighting conditions, as they appeared to the participants.

the limited amount of empirical data available, we constrained our optimization efforts to only two parameters while maintaining fixed values for the rest.

Particularly, since the rotational dynamics represent a novel aspect of this model, we focused our optimization on parameters that directly influence this dynamic: gaze attraction strength and the constriction parameter, which affects the width of the modeled visual field. These parameters are crucial for accurately modeling how individual swarmalators adjust their gaze direction based on the positions and orientations of nearby peers, a key behavior observed in dance settings.

The fixed parameter values were adjusted to ensure that the mean distance between the swarmalators closely mirrored the trajectory observed in the empirical data from the silent disco experiment. This process involved iterative testing and refinement to achieve a dynamic alignment with real-world behavioral patterns. Consequently, we used the fixed values indicated in Table 1.

5.2.2 Optimization procedure

For the parameter optimization of our swarmalator model, we utilized simulated annealing (Kirkpatrick et al., 1983), a robust optimization technique particularly suited for handling complex

TABLE 1 Fixed parameter values used in the optimization.

Parameter name	Fixed value
Attraction strength	$A = 0.1 \text{ s}^{-1}$
Attraction range exponent	$a = 1$
Repulsion strength	$R = 1.5 \text{ s}^{-1}$
Repulsion decay exponent	$r = 2$
Phase-and-gaze-dependent attraction strength	$P = 0.5 \text{ s}^{-1}$
Spatial decay in phase-and-gaze coupling	$p = 1$
Spatial decay in rotational dynamics	$d = 1$
Auditory entrainment strength	$U = 0.8$
Visual entrainment strength	$V = 0.4$
Spatial decay in visual entrainment	$v = 1$
Attraction strength	$A = 0.1 \text{ s}^{-1}$

problems where the cost function may be non-continuous and non-differentiable. This characteristic arises in our model due to the inclusion of the grouping coefficient, which introduces discontinuities in the cost function. Simulated annealing is ideal for such scenarios as it effectively navigates the parameter landscape

to find global optima, avoiding local minima that are common with more traditional gradient-based optimization methods. The optimization was implemented using MATLAB's `simulannealbnd()` function.

Each of the four datasets from the silent disco experiment was used to set the initial configuration of the swarmalators, including both their positions and gaze directions. Following this initialization, we simulated the dynamics of the swarmalators for 1 min to observe the evolution of their configurations. In the simulations the phase of the external stimulus, φ_j , was set to be equal to the phase of the beat of the musical stimulus the respective participant was presented with. The differential equations were numerically simulated using the Euler method with a time step of 1/120 second.

To assess the alignment between our simulated swarmalator configurations and the empirical data from the silent disco settings, we developed a composite error measure that included:

1. The spatial variance of positions, reflecting the group size,
2. The grouping coefficient, gauging the extent to which swarmalators influenced by similar stimuli grouped together,
3. The centroidal alignment, measuring the orientation of swarmalators toward the group's centroid.

For each dataset, this error measure was calculated as the sum of the absolute differences between these three components in the empirical silent disco data and the simulated swarmalator configurations at the end of one minute. It is to be noted that for the sake of simplicity, we did not consider any measures of oscillatory self-organization in this simulation. However, with the parameter values used in the simulations, each swarmalator was accurately synchronized with its respective driving oscillation.

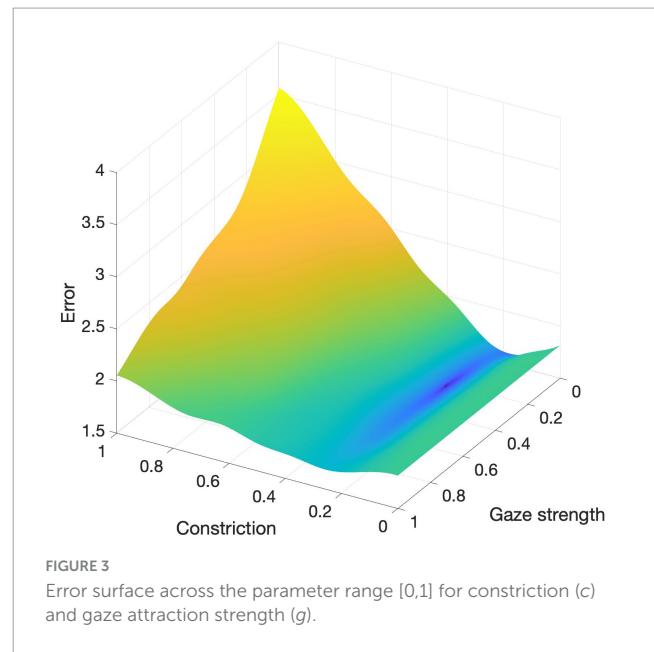
5.2.3 Results of optimization

The optimization process identified that the parameter values for constriction ($c = 0.252$) and gaze attraction strength ($g = 0.251$) resulted in the smallest error, effectively aligning the simulated behaviors of the swarmalators with the observed dynamics at the silent disco.

Figure 3 illustrates the error surface across the parameter range [0,1] for both c and g . The visualization highlights the model's sensitivity to changes in these parameters. Notably, the constriction parameter (c) has a more pronounced effect on the overall error compared to the gaze attraction strength (g), indicating that the width of the visual field modeled by constriction significantly impacts the accuracy of the model. Comparisons show that the model performs better with heading dynamics included ($c > 0$) than without ($c = 0$), with error values of 1.60 and 1.81, respectively.

Figure 4 displays the dynamic evolution of the three metrics used in the cost function—spatial variance, grouping coefficient, and centroidal alignment—over the first minute averaged across the four stimuli, using the optimal parameter values ($c = 0.25$ and $g = 0.25$). This visualization provides insights into how these metrics, integral to assessing the model's performance, change over time under the influence of the identified optimal settings.

The figure shows that group size decreases sharply at the outset before stabilizing, with the model closely mirroring the empirical data but slightly underestimating the change of group



size over time. The grouping coefficient begins low, indicating initial loose cohesion, and gradually increases; however, the model's response to this increase is smoother compared to the empirical data. Centroidal alignment exhibits considerable fluctuation with an overall downward trend, suggesting a gradual reduction in central alignment, with the empirical data displaying greater variability than the model's more uniform decline. These observations suggest that while the model captures the general trends in group behaviors effectively, its dynamics unfold slower than those observed in human interactions, highlighting a need for refining the model's responsiveness to more accurately simulate the quick adjustments seen in real human behavior.

Figure 5 shows the temporal evolution of the three metrics separately for each of the four stimuli. As can be seen, there are some differences in the model's accuracy between the stimuli. This is most notable for the second stimulus (Girls and Boys, phase shift 180°). In particular, for this stimulus the evolution of Grouping coefficient, while being of similar magnitude at the end of the 60-s interval, follows a more constant increase for the model than for the humans. Centroidal alignment for this stimulus, on the other hand, remains smoother and more stable in the model, while the human data shows greater fluctuation and a gradual decrease over time. This difference suggests that the model lacks the flexibility to capture the dynamic reorientations and variability seen in human behavior.

6 Discussion

The directional swarmalator model presented here may be useful in understanding how people coordinate on the social dance floor. By combining oscillatory, translational and rotational dynamics, it provides a model of group dynamics during dance. Crucially this enables the study of larger groups of dancers, going beyond dyadic interaction. In validating the model, we have

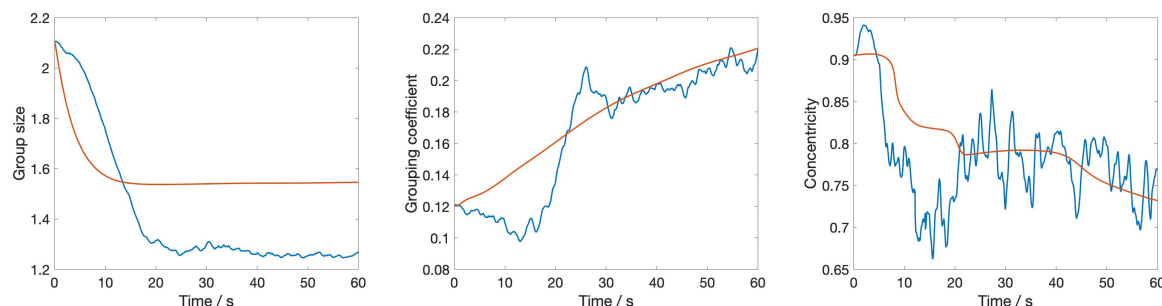


FIGURE 4

The temporal evolution of three key metrics—group size, grouping coefficient, and centroidal alignment—over a 1-min period averaged across the four stimuli. The blue lines represent empirical data from the silent disco experiment, while the red lines depict the corresponding metrics from the swarmalator model simulations.

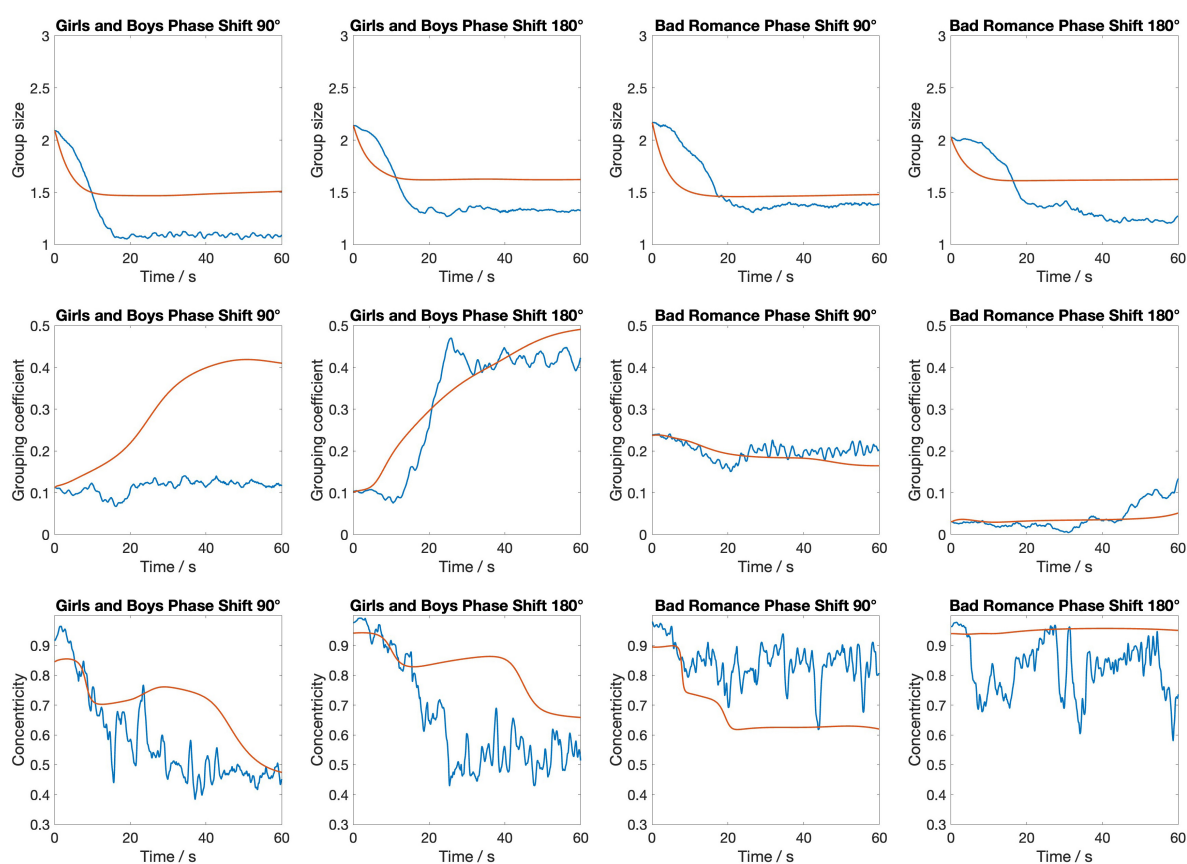


FIGURE 5

The temporal evolution of three key metrics—group size, grouping coefficient, and centroidal alignment—over a 1-min period for each of the four stimuli. The blue lines represent empirical data from the silent disco experiment, while the red lines depict the corresponding metrics from the swarmalator model simulations.

also developed metrics for measuring circularity and centroidal alignment that may be useful in future research.

Through the inclusion of directionality in the swarmalator model, circular shapes tended to form between agents. Circles are common in many dance cultures around the world (Chauvigné et al., 2019; Sachs, 1965), and this may be for anatomical reasons due to the frontal placement of the human eye. In our directional swarmalator model, optimizing the gaze constriction parameter was vital. In this instance, a fairly wide

gaze was found to be optimal. Previous studies have found that the horizontal field of view in humans is about 210 degrees (Strasburger, 2020), which approximates our findings within the model, although the gaze strength gradient may not perfectly reflect human data. Additionally, comparisons using our error measure indicate that the model performs slightly better when heading dynamics are included, further emphasizing the importance of gaze direction in accurately modeling collective behavior.

Although the current model approximates human behavior, there are some limitations. The most notable issue is that these directional swarmalators are too smooth in their movement. They tend to drift gradually toward an identified target, while the humans are more erratic in their motion and in their visual search behavior. This could be overcome by adding noise to the gaze direction dynamic, in order to simulate searching behavior. The directional swarmalator model is highly complex with many parameters, and the optimization of parameters was done with a very small dataset, which limits the generalizability of the model. Currently only two parameters were optimized, due to limited data availability. Collecting motion capture data with groups is time-intensive, but more data would be required for better optimization. The model could also be trained on a wider variety of data, as the silent disco task was quite limited by design. Participants were instructed to bounce, rather than dance, in order to reduce noise in the oscillatory dynamics. A more complex model may have been able to accommodate a wider variety of individual motion, beyond vertical oscillation, but that would be for future development.

The model could be further developed with a greater range of data. The silent disco task used here was restrictive in its instructions to bounce in time to the beat and to find a group. Future studies could investigate the effect of these instructions, for instance, whether participants behave differently if instructed to attend to other features of the other participants, other than their movement, or if they were instructed to sway rather than bounce, for example. The auditory stimuli could also be varied to investigate a wider variety of differences in timing or quality of movement.

In theory, the model could be extended to other behaviors beyond dance. Any situation where a group of agents form groups based upon visual features would be eligible for modeling using directional swarmalators. For instance, it could be used to study group formation dynamics for conversations at a cocktail party. Other features, other than phase matching, could be used as markers of similarity, such as types of gesture or matching clothing. Directional swarmalators may also be useful in modeling group formation in non-human animals, depending upon the importance of gaze direction. Existing swarmalator models do not account for visual fields (O’Keeffe et al., 2017). For species that move in three dimensions (e.g., schools of fish or flocks of birds) this would require adding elevation to the gaze parameter. In any case, further extensions could still be made for this model to better simulate dance movement as well. Currently swarmalators are reactive, rather than predictive, and anticipation of the beat is an important process in human sensorimotor synchronization (Keller, 2023; Van Der Steen and Keller, 2013). Adding an anticipation component to the model may increase complexity but may improve the dynamics. Overall, the directional swarmalator model presented here provides a step toward better understanding the role of visual attention on the dance floor, and potentially for other group dynamics.

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 requirement of ethical approval was waived by Human Sciences Ethics Committee, University of Jyväskylä for the studies involving humans because the study does not need to be reviewed according to the TENK guidelines. The studies were conducted in accordance with the local legislation and institutional requirements. The participants provided their written informed consent to participate in this study.

Author contributions

PT: Conceptualization, Formal analysis, Funding acquisition, Methodology, Writing – original draft, Writing – review & editing. JB: Conceptualization, Writing – original draft, Writing – review & editing. MT: Conceptualization, Data curation, Writing – original draft, Writing – review & editing.

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Conflict of interest

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Distinct and content-specific neural representations of self- and other-produced actions in joint piano performance

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During ensemble performance, musicians predict their own and their partners' action outcomes to smoothly coordinate in real time. The neural auditory-motor system is thought to contribute to these predictions by running internal forward models that simulate self- and other-produced actions slightly ahead of time. What remains elusive, however, is whether and how own and partner actions can be represented *simultaneously* and *distinctively* in the sensorimotor system, and whether these representations are *content-specific*. Here, we applied multivariate pattern analysis (MVPA) to functional magnetic resonance imaging (fMRI) data of duetting pianists to dissociate the neural representation of self- and other-produced actions during synchronous joint music performance. Expert pianists played familiar right-hand melodies in a 3 T MR-scanner, in duet with a partner who played the corresponding left-hand basslines in an adjacent room. In half of the pieces, pianists were motorically familiar (or unfamiliar) with their partner's left-hand part. MVPA was applied in primary motor and premotor cortices (M1, PMC), cerebellum, and planum temporale of both hemispheres to classify which piece was performed. Classification accuracies were higher in left than right M1, reflecting the content-specific neural representation of self-produced right-hand melodies. Notably, PMC showed the opposite lateralization, with higher accuracies in the right than left hemisphere, likely reflecting the content-specific neural representation of other-produced left-hand basslines. Direct physiological support for the representational alignment of partners' M1 and PMC should be gained in future studies using novel tools like interbrain representational similarity analyses. Surprisingly, motor representations in PMC were similarly precise irrespective of familiarity with the partner's part. This suggests that expert pianists may generalize contents of familiar actions to unfamiliar pieces with similar musical structure, based on the auditory perception of the partner's part. Overall, these findings support the notion of parallel, distinct, and content-specific self and other internal forward models that are integrated within cortico-cerebellar auditory-motor networks to support smooth coordination in musical ensemble performance and possibly other forms of social interaction.

KEYWORDS

joint action, fMRI, MVPA, music performance, pianists, motor simulation, internal models

1 Introduction

Coordinating own actions with the actions of a partner is necessary in many kinds of situations, such as holding a conversation, playing soccer or performing music in groups. One key component of successful interaction is the ability to predict the partner's action ahead of time to swiftly adapt one's own action if needed (Abalde et al., 2024; Knoblich et al., 2011; Vesper et al., 2017). It has been argued that these predictions can be formed via motor simulation of the partner action in one's own motor system (Kilner, 2011; Ridderinkhof, 2014; Sebanz et al., 2006; Wilson and Knoblich, 2005; Wolpert et al., 2003). However, if action coordination indeed involves the “motoric embodiment” of the partner, it remains elusive whether and how self- and other-produced actions are represented *simultaneously* and *distinctively* in the motor system during joint action. Moreover, many studies have focused primarily on global activity changes as proxy for predictive motor simulation (Bolt and Loehr, 2021; Calvo-Merino et al., 2006; Kohler et al., 2023), leaving unclear whether the motor system has distinct representation of the *specific content* of the partner's action. The present study capitalized on an existing functional magnetic resonance imaging (fMRI) dataset of duetting pianists (Kohler et al., 2023) to fill these gaps by seeking to dissociate neural representations of self- and other-produced actions during synchronous joint music performance using multivariate pattern analysis (MVPA).

1.1 The motor system in individual and joint action

Coordination of social interactions often benefits from knowing what others will do next. While there are numerous ways of predicting others' actions, e.g., based on abstract action schemas (Sartori et al., 2011, 2013; Wurm and Schubotz, 2017) or representations of action goals in space and time (Sebanz et al., 2006; Sebanz and Knoblich, 2009; Vesper et al., 2010), one mechanism that has been most central in theories of joint action is the simulation (sometimes called emulation or co-representation) of the partner action in one's own motor system (Hommel, 2009; Knoblich and Sebanz, 2006; Koch et al., 2010; Ridderinkhof, 2014; Sebanz et al., 2006; Vesper et al., 2010). Originally inspired by James (1890) ideomotor principle and based on the social “extrapolation” of motor control theories of self-produced actions (Miall and Wolpert, 1996; Wolpert et al., 2003), these (simulation) theories assume that we anticipate the outcome of partner actions very much in the same way as we anticipate the sensory consequences of our own actions: by running internal forward models in our sensorimotor system (Keller et al., 2007, 2016; Müller et al., 2021; Novembre and Keller, 2014; Patel and Iversen, 2014).

Internal forward models—originally studied in the context of self-produced actions—transform motor commands into a prediction of the sensory consequences of a movement (for review, see Ishikawa et al., 2016). These models are based on stored sensorimotor associations that are acquired during practice of the corresponding

action and increase in precision with training (Jeannerod, 2006; Wolpert et al., 2011). In terms of neural correlates, internal forward models have been associated with cortico-cerebellar loops. Accordingly, the cerebellum integrates the efference copy of the ongoing motor command issued in primary and premotor cortex (M1/PMC), and afferent sensory signals from the periphery. Based on learned sensorimotor links, the cerebellum estimates future sensory input, evaluates the accuracy of this estimation given the actual input, and links back to M1/PMC in case of a mismatch to adapt the movement (for reviews, see Bastian, 2006; Ishikawa et al., 2016; Ito, 2005; Johnson et al., 2019; Popa and Ebner, 2019; Tanaka et al., 2020; Wolpert et al., 1998). Importantly, this cortico-cerebellar “pre-play” or simulation of the action allows the sensorimotor system to preemptively detect (and potentially avert) impending execution errors in self-produced actions (Maidhof, 2013; Maidhof et al., 2009; Ruiz et al., 2009).

Evidence from action observation studies suggests that the outcome of *other*-produced actions is anticipated similarly in an agent's motor system, to seamlessly adapt to the behavior of interaction partners (Pacherie, 2008). For example, the cortical motor system, including PMC and inferior/superior parietal lobule (IPL/SPL), is robustly activated during action observation (for reviews, see Caspers et al., 2010; Hardwick et al., 2018; Papitto et al., 2020) taken to reflect motor simulation. Importantly, motor activity increases with the (motoric) familiarity of the observed actions (e.g., Calvo-Merino et al., 2005, 2006; Kohler et al., 2023; Ticini et al., 2019; Tomeo et al., 2013), often maps onto the somatotopy of the observed body kinematics, and—crucially—facilitates the anticipation of observed action outcomes (e.g., Aglioti et al., 2008; Candidi et al., 2014; Urgesi et al., 2012). This is in line with the idea that motor simulation of others' actions is predictive, and based on specific, practice-based sensorimotor associations, like internal forward models of self-produced actions.

Interestingly, motor activity associated with observed or real partner actions is stronger in interactive than non-interactive or solo contexts (e.g., Novembre et al., 2012; Sacheli et al., 2022; for review, see Bolt and Loehr, 2021). This activity increase in joint action may reflect a more detailed and exact simulation of a (potential) partner's action, leading to more accurate predictions that serve to smoothen coordination. If so, this would not only provide evidence that shared goals and task interactivity shape the use of motor simulation (see also Sacheli et al., 2019), but also highlight the need to investigate the neural processes underlying joint action in real social interactive settings (Redcay and Schilbach, 2019; Schilbach et al., 2013).

A number of studies have answered this call for interactive settings using musical joint action tasks. These studies typically asked pianists to perform duets with a (real or videotaped) partner, whereby one pianist played the right-hand melody and the other the left-hand bassline (c.f. Novembre et al., 2012). The critical manipulation was familiarity, that is, whether—prior to the experiment—pianists had or had not practiced the partner's part. If internal forward models depend on learned auditory-motor associations acquired during practice, predictive motor simulation should be stronger and more accurate during pieces with

familiar compared to unfamiliar partner actions, and should have measurable behavioral effects on interpersonal coordination. Indeed, the fMRI study of Kohler et al. (2023) found stronger cortico-cerebellar activity (including M1, PMC, and cerebellar lobule VIII), stronger auditory-motor connectivity, and greater cerebellar sensitivity to subtle temporal asynchronies when pianists were familiar than unfamiliar with the other's part. Correspondingly, inhibitory transcranial magnetic stimulation (TMS) of right M1/PMC (controlling the left hand, used by the partner) was found to perturb the temporal accuracy of pianists' own right-hand entries when taking turns in duets (Hadley et al., 2015) and to reduce pianists' precision in adapting to tempo changes induced by the duet partner (Novembre et al., 2014), but only when pianists were familiar with the partner's (left-hand) part. These combined results (see also Novembre et al., 2016; Ragert et al., 2013) support the assumption that internal forward models of familiar partner actions may be more accurate and boost the anticipation of an action's time course, with consequences for the temporal coordination of joint action.

However, what remains unclear is whether the motor system represents the *specific content* of the partner's action, and how it does so *simultaneously* with the execution of one's own action. So far, both TMS and fMRI evidence mainly builds on global activity changes, leaving unclear whether self and partner representations are really content-specific. How veridically do they reflect the kinematics of own and partner actions? Some TMS studies provide suggestive evidence for content-specificity by showing muscle-specific changes of cortico-spinal excitability that mirror complementary self- and other-produced actions observed in videos (Sartori et al., 2013, 2015). However, findings from other studies probing muscle-specific effects of partner actions in real synchronous musical interactions were not conclusive (Novembre et al., 2012; Novembre and Keller, 2014). More generally, it is rather difficult to test simultaneous self- and other-related representations in real interactive settings while measuring cortico-spinal excitability. An alternative approach to study action specificity of neural representations in joint action is to combine neuroimaging (fMRI) with multivariate pattern analysis (MVPA). In contrast to the coarseness of univariate measures that rely on global activity differences, MVPA capitalizes on information contained within fine-scale spatial activation patterns. If neural representations of partner actions are content-specific (e.g., reflecting a particular finger sequence), they should evoke specific patterns of activity across fMRI voxels, from which individual actions or action sequences may be decoded (Peelen and Downing, 2023). We applied MVPA to the fMRI dataset of Kohler et al. (2023) to investigate on this fine-grained level whether and how the motor system concurrently represents self- and other-produced actions during synchronous joint music performance.

1.2 Decoding own actions

Previous fMRI studies using MVPA have shown that the execution as well as motor imagery of self-produced hand actions is reflected in action-specific neural representations in the motor system. For example, simple actions like reaching vs. grasping (Gallivan et al., 2011, 2013; Gallivan and Culham, 2015), different types of grasps (Michalowski et al., 2022; Turella et al., 2013), and complex finger-movement sequences (Kornysheva and Diedrichsen, 2014; Wiestler et al., 2014; Wiestler and Diedrichsen, 2013) could be accurately classified based on patterns of brain

activity. Crucially, accurate classifications occurred in a broad range of sensorimotor regions, including M1, primary somatosensory cortices (S1), PMC, intraparietal sulcus (IPS), and the cerebellum. Neural activity patterns in similar sets of regions, including M1, S1, PMC and additional visual cortices, have also been found to represent *imagined* actions, such as simple reaching (Filimon et al., 2015), pointing and squeezing actions (Pilgramm et al., 2016; Zabicki et al., 2016, 2019) or different types of grasps (Monaco et al., 2020), as well as complex whole-body actions (Yang et al., 2023). Most importantly, the neural representations of own, unimanual actions are often strongly lateralized. For example, neural activity patterns representing (sequences of) right-hand finger movements were found to be more distinctive in left than right M1/PMC, i.e., contralateral to action execution (Wiestler et al., 2014; Yokoi et al., 2018), although lateralization is sometimes less clear-cut in PMC (Michalowski et al., 2022). Moreover, neural representations of finger sequences become more refined after practice, i.e., classification accuracy increases with motor familiarity (Wiestler and Diedrichsen, 2013), in line with the idea that content-specific motor representations are shaped by training.

Motor familiarity with an action has also been shown to strengthen expectations of the sensory consequences of that action, e.g., sounds during music production (Baumann et al., 2007; Jäncke, 2012; for review, see Zatorre et al., 2007), in line with the assumption that internal forward models are built on learned sensorimotor associations. For example, pianists exhibited stronger ERP responses when perceiving errors in auditory melodies that belonged to their motor repertoire compared to unrehearsed melodies (Mathias et al., 2015), and pianists' sensitivity to altered auditory feedback during own performance increased with the amount of musical training, in line with increasing precision of internal forward models with training (Pfordresher, 2012). More generally, previous MVPA studies showed content-specific neural activity patterns for perceived and/or imagined musical melodies (de Manzano et al., 2020; May et al., 2022; Regev et al., 2021; Schindler et al., 2013) in the superior temporal gyrus (STG), including Heschl's Gyrus (HG) and planum temporale (PT). Importantly, these auditory representations were more precise not only in highly trained listeners with more differentiated tonal knowledge (May et al., 2022), but also when listeners tapped along (Regev et al., 2021) or had previously practiced the heard melodies (de Manzano et al., 2020) in line with strengthened auditory representations through auditory-motor coupling (Kohler et al., 2023).

Taken together, execution and imagery of self-produced actions are reflected in action-specific neural activity patterns in the motor system. These activity patterns, especially in M1, are lateralized, increase in precision with motor familiarity, and are associated with auditory representations. Both the lateralization and the training-induced refinement of neural action representations may provide us with a means to dissociate representations of self- and other-performed actions in the present study, as explained below.

1.3 Decoding others' actions

Increasingly, MVPA studies focus on action observation (for review, see Oosterhof et al., 2013). These studies collectively demonstrate highly specific representations of others' actions in the

observer's brain, in terms of movement kinematics (Ridderinkhof et al., 2021; Ziccarelli et al., 2022), action goals (e.g., Molenberghs et al., 2012), or even abstract intentions (e.g., Koul et al., 2018). Typically, observing other-produced actions yields neural representations in similar motor regions as self-produced actions. For example, simple reaching actions (Filimon et al., 2015), different types of grasps (Errante et al., 2021; Sacheli et al., 2019), (non)social and (in)transitive hand actions (Lesourd et al., 2023), as well as complex finger sequences (Apšvalka et al., 2018) presented in videos have been reliably classified based on activity patterns in areas including left PMC, inferior/superior parietal lobule (IPL/SPL), and the right cerebellum (lobule VI and VIII), known to support own (right-hand) action execution (see above). Notably, classification of observed actions in PMC was more accurate in social interactive, compared to non-interactive, contexts (Sacheli et al., 2019) in line with the idea that sharing a goal with a co-actor shapes the accuracy of motor simulation and representations (Sacheli et al., 2022).

Overall, this research suggests that both self- and other-produced actions evoke action-specific patterns of brain activity in the motor system.

1.4 Current study and predictions

In the current study, we investigated how self- and other-produced actions are represented *simultaneously* in the sensorimotor system during synchronous joint action. To test this, we reanalyzed data of a previous study, in which pairs of pianists performed duets together (Kohler et al., 2023). One pianist played the right-hand part (melody) of the duets in an MR-scanner, while the co-performer played the corresponding left-hand part (bassline) on a piano outside the scanner room. To investigate whether and how pianists (in the scanner) neurally represent the left-hand actions of the co-performer, on top of their own right-hand actions, we manipulated their motor familiarity with the part played by the co-performer. That is, for half of the pieces performed in the MR-scanner ($N = 2$), pianists had practiced the co-performer's part (the bassline) prior to the experiment, while they had neither practiced, nor heard or seen the scores of their partner's basslines for the other half of the pieces ($N = 2$). Hence, they were motorically familiar or unfamiliar with their partner's actions, respectively.

We used multivariate pattern analysis (MVPA) in auditory-motor regions of interest (ROIs) and the whole brain (searchlight) to dissociate neural representations of self-produced right- and other-produced left-hand actions. ROIs were localized in left and right primary motor and premotor cortices (M1 and PMC), cerebellar lobule VIII (referred to as CER), and planum temporale (PT) based on the results of Kohler et al. (2023), that is, covering relevant areas of action execution, motor simulation and auditory perception/anticipation as introduced above. More precisely, these regions had shown stronger activity or functional connectivity when the partner played familiar (compared to unfamiliar) basslines, taken to indicate that these regions represent not only own actions, but also the actions produced by the partner (Kohler et al., 2023). In each ROI (and searchlight), we ran two separate MVPAs classifying which of two pieces was performed, separately for the two pieces with familiar and the two pieces with unfamiliar partner actions. Classification accuracies of these two analyses were compared within each ROI (and searchlight), and between the left and right hemisphere.

Following established knowledge of lateralized motor control (Chettouf et al., 2020; Goble and Brown, 2008; Welniarz et al., 2015), we reasoned that classification accuracies in left M1/PMC and right CER are primarily associated with self-produced right-hand actions, while classification accuracies in right PMC and left CER are rather associated with other-produced left-hand actions. Crucially, if motor simulation in internal forward models depends on specific, practice-based sensorimotor familiarity, neural representations in right PMC and left CER should be more precise, i.e., classification accuracies should be higher, for pieces with motorically familiar than unfamiliar partner actions. Finally, we explored the possibility of a similar effect of familiarity in (bilateral) PT, under the assumption that internal forward models of other-produced actions trigger more precise auditory sequence representations (de Manzano et al., 2020; Kohler et al., 2023; Regev et al., 2021). However, we also considered it possible that the (top-down) influence of motor familiarity on auditory representations might be cancelled out by the actually perceived (bottom-up) auditory input.

2 Methods

The current study reanalyzed the data of Kohler et al. (2023). Key details of the experimental methods are outlined below (for further information, see Kohler et al., 2023).

2.1 Participants

Forty expert pianists (age range: 18–39 years, $M = 25.25$ years, $SD = 5.30$, 4 left-handed, 20 identified as female, 20 identified as male) with an average of 17.18 years of piano training ($SD = 5.86$, range: 8–32 years; onset age $M = 7.70$, $SD = 3.07$, range: 4–16 years) and an average of 8.73 h of weekly practice at the time of testing ($SD = 9.69$, range: 2–50 h) were randomly allocated into 20 pairs (4 only-female, 4 only-male, 12 mixed-gender pairs, mean age difference between partners: 5.30 years, $SD = 4.43$). Pianists did not know each other before the experiment. Handedness of the pianists was assessed using the Edinburgh Handedness Inventory (Oldfield, 1971). All pianists had normal or corrected-to-normal vision, reported normal hearing, no neurological or psychiatric history, and no contraindication for MRI. They were naïve to the purpose of the study and received monetary compensation for their participation. The study was approved by the ethics committee of Leipzig University (016–15-26012015) and was conducted following the guidelines of the Declaration of Helsinki. All pianists provided written informed consent.

2.2 Materials

The musical material consisted of 8 excerpts of modified chorales by Johann Sebastian Bach, with a melody for the right hand played by the pianist in the scanner and a bassline for the left hand played by the duet partner outside (see Figure 1 for an example). Each chorale contained one musical phrase of 2 bars, a pause of 2 bars, followed by another musical phrase of 2 bars. Each musical phrase consisted of 7 quarter notes and a quarter-note pause. The 8 excerpts were split into 2 sets of 4 pieces, which were used when

player A or player B of a pair were in the MR-scanner, respectively (see below).

Approximately 2 weeks prior to the experiment, pianists received the scores of both sets of pieces for rehearsal at home. Crucially, to manipulate motor familiarity with the partner's part, pianists received full scores for only half of the pieces (2 in each set), for which they were asked to practice both their own and their partner's part (melody and bassline, respectively). These pieces were hence those with *familiar* (F) partner actions. For the remaining pieces, pianists received partial scores of only one part, i.e., they could practice either only the melody (2 pieces of the set they later performed inside the MR-scanner) or only the bassline (2 pieces of the other set). These pieces were hence those with *unfamiliar* (U) partner actions. The pieces for which both parts were practiced were counterbalanced across the group. Only pianists who were able to perform the practiced parts by heart in a pre-test were admitted to the experiment (for details, see Kohler et al., 2023).

An additional manipulation in the original study design of Kohler et al. (2023) required pianists to perform a tempo change in the second phrase (i.e., after the pause) which was executed without auditory feedback. The present analysis focused on the first phrase only (i.e., before the pause when pianists could hear each other) to study auditory-motor representations of self and other. A control analysis confirmed that the tempo manipulation in the second phrase had no effect on the present results in the first phrase (Supplementary Table S2).

2.3 Experimental procedure

The fMRI experiment consisted of 2 consecutive scanning sessions separated by a 30-min break. A short training (16 trials) at the

beginning of each session ensured that pianists had understood the instructions, were able to play the rehearsed pieces together, and heard each other's performance well via headphones. In the first session, pianist A played the piano in the MR-scanner in duet with co-performer B who played outside the scanner room. They swapped places in the second session. The pianist in the MR-scanner always played the melody of the pieces with the right hand, while the co-performer played the corresponding bassline with the left hand (Figure 1). During each session, the pianists played a set of 4 of the 8 practiced pieces, counterbalanced across pairs. They completed 128 trials in each session, 64 with familiar and 64 with unfamiliar partner actions, in pseudorandom order such that partner actions were familiar or unfamiliar in not more than three consecutive trials, and the same piece was never played twice in a row. Each piece was played 32 times over the course of the session.

The first phrase in each trial was played at a tempo of 120 bpm, while the second phrase had to be performed either at 150 bpm (faster) or 96 bpm (slower). Note that only the first phrase without tempo change was analyzed in the current study (for details on the tempo manipulation, see Kohler et al., 2023). Each trial started with a visual cue (1,000 ms) that indicated whether to speed up or slow down in the second phrase. After the cue, the musical scores of the pianist's respective part (but not the partner's part) appeared on screen and four metronome beats were presented at a tempo of 120 bpm (lasting 2,000 ms in total) after which pianists were supposed to start playing together at that same tempo. Trials lasted between 14.2 s and 16 s, depending on the tempo of the second phrase. The next trial started after a jittered inter-trial-interval between 3 and 9 s during which a fixation cross was shown. One fMRI scanning session lasted about 45 min. The whole experiment, including preparation time, two sessions and breaks, took about five hours per pair.

Pianist in the MR-scanner = Self



Duet partner outside = Other

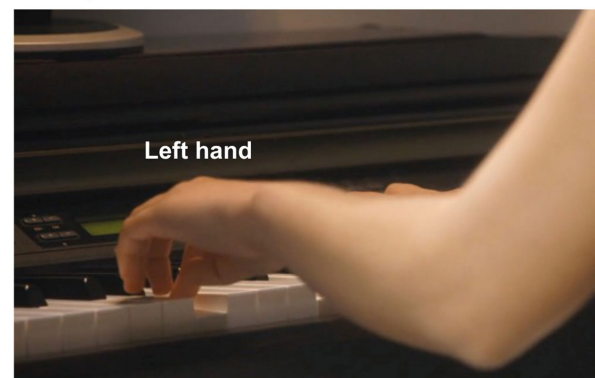


FIGURE 1

Experimental setup. Pianists in the MR-scanner (self, left upper panel) performed right-hand melodies in duet with a partner (other, right upper panel) who played the corresponding left-hand basslines outside the scanner room. Pianists saw the musical scores of their own, but not the partner's part, on a screen (see lower panel for an example).

2.4 Experimental setup and data acquisition

In the scanner, behavioral data were acquired via a custom-made 27-key MR-compatible MIDI-piano (Julius Blüthner Pianofortefabrik GmbH, Leipzig, Germany; see [Figure 1](#)), with auditory feedback received via MR-compatible in-ear headphones (Sensimetrics, MR confon GmbH, Magdeburg, Germany). The piano was placed on a slightly tilted wooden stand clipped into the scanner bed over the pianist's lap. An MR-compatible camera (12 M camera, MRC Systems, Heidelberg, Germany) was placed on top of the piano to record the pianist's finger movements. A double mirror system mounted on the head coil allowed the pianist to see both the piano and the visual stimuli projected onto a screen at the head-end of the MR-scanner. Pianist B was seated in a separate room at a Yamaha Clavinova CLP 150 on top of which a 16" Sony Trinitron Multiscan E220 monitor (100-Hz refresh rate) was placed for presentation of visual stimuli. Sound was delivered via DT 770 PRO, 250 Ohms headphones (beyerdynamic, Heilbronn, Germany). The audio-output of both pianos was fed into and mixed through an McCrypt SA-101 U USB DJ-mixer (Renkforce, Conrad Electronic SE, Hirschau, Germany) that was located in the control room where the experimenters were seated. The experiment was controlled with Presentation software (Version 16.5, Neurobehavioral Systems, Inc., Berkeley, CA, United States) and custom Python programs to record the MIDI output of the pianos.

MR-data were collected at the Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, in a 3-Tesla Siemens Skyra magnetic resonance scanner (Siemens AG, Erlangen, Germany) using a 32-channel head coil. Functional images were acquired with a whole-brain multi-band echo-planar imaging sequence (EPI; TR = 2,000 ms, TE = 22 ms, multi-band acceleration factor = 3, 60 axial slices in interleaved order, voxel size = 2.5 mm³, 10% inter-slice gap, flip angle = 80°, field of view = 204 mm; [Feinberg, 2010](#); [Moeller et al., 2010](#)). Anatomical T1-weighted images were acquired with a whole-brain magnetization-prepared rapid acquisition gradient echo sequence (MPRAGE; TR = 2,300 ms, TE = 5.52 ms, 176 sagittal slices, voxel size = 1 mm³, flip angle = 9°, field of view = 256 mm; [Mugler and Brookeman, 1991](#)).

2.5 FMRI data analysis

To evaluate how self- and other-produced actions are neurally represented during joint music performance, we used MVPA to decode, in predefined ROIs, which piece pianists performed. Decoding was done separately for the two pieces with familiar and with unfamiliar partner actions, in bilateral M1, PMC, CER, and PT. Classification accuracies were then statistically compared between (un)familiar pieces and homologous left and right hemispheric ROIs using repeated measures ANOVAs. An analogous whole-brain searchlight MVPA was applied to explore potential representations of self- and other-produced actions outside the predefined auditory-motor ROIs.

2.5.1 Preprocessing

FMRI data were pre-processed using SPM12 (Wellcome Trust Centre for Neuroimaging, London, UK) in Matlab version 9.3 (R2017b). Preprocessing included slice-time correction, realignment,

unwarping, and co-registration of functional and anatomical scans, as well as segmentation.

2.5.2 First-level design matrix

To build individual level design matrices, trials were first grouped into four predictors, i.e., one predictor for each piece depending on whether pianists were (un)familiar with their partner's part. Predictors were labelled familiar piece 1 (F1), familiar piece 2 (F2), unfamiliar piece 1 (U1), and unfamiliar piece 2 (U2). Each predictor was then split into 8 folds across time to simulate separate runs and allow training and testing of the classifier including cross-validation. Each fold contained 4 trials of the respective piece, except for two participants for whom we included only 2–3 or 3–4 trials in each fold due to early termination of the session. The resulting 32 predictors were labelled by piece (F1, F2, U1, U2) and numbered 1–8, respectively. Furthermore, 6 motion parameters were entered as covariates of no interest to control for subtle head movements.

We modelled brain activity using a General Linear Model with finite impulse response (FIR) functions at a lag of +4 s relative to trial onset to account for the lag of the hemodynamic response. We used a FIR model rather than a canonical hemodynamic response model (HRF) to isolate brain activity specifically during pianists' joint performance during the first phrase, and to avoid blurring this stage with activity of the adjacent stages of the trial. The FIR model was composed of 4 separate impulse functions with a length of 4 s each, modelling the 4 consecutive stages within trials, resulting in 4 beta images for each piece and fold. The first beta image reflected brain activity associated with the presentation of the visual cue and scores and hearing the metronome. Beta image 2 reflected activity evoked by the joint performance during the first phrase and was relevant for the present analysis. Beta images 3 and 4 reflected the pause and the subsequent second phrase, respectively. Only beta image 2 data were used in the MVPA. The final design matrix of each participant consisted of 134 columns, comprising 4 pieces (F1, F2, U1, U2) × 8 folds (with ~4 trials of each piece) × 4 functions of the FIR model + 6 motion parameters.

2.5.3 Definition of grey matter masks

All analyses were confined to grey matter voxels. Therefore, a structural grey matter mask was created in native-space for each participant, following the pipeline of [de Manzano et al. \(2020\)](#). First, individual grey matter tissue probability maps obtained during segmentation were thresholded at 0.5, then smoothed by 6 mm FWHM, and thresholded again at 0.2. The resulting images were then re-sliced to match the functional masks generated by SPM during the first-level analysis. Only voxels contained in both the functional masks and the grey matter maps were retained in the final native-space grey matter masks for individual-level analyses. For the group-level searchlight analysis, a group-level grey matter mask was created by normalizing all native-space grey matter masks into MNI space and retaining only voxels common to all individual masks.

2.5.4 Definition of regions of interest (ROIs)

MVPA was first conducted in predefined ROIs in bilateral M1, PMC, CER, and PT, i.e., auditory-motor regions involved in joint action. More specifically, in [Kohler et al. \(2023\)](#), these regions had shown stronger activity or functional connectivity when pianists performed duets with a partner who played familiar (compared to unfamiliar) basslines. Given that motor simulation in internal forward

models depends on motor familiarity (e.g., Calvo-Merino et al., 2005, 2006; Ticini et al., 2019; Tomeo et al., 2013; Jeannerod, 2006; Wolpert et al., 2011), we considered these areas as most promising candidates for representing partner actions, on top of own actions. ROIs were created using the MarsBaR toolbox for SPM12 (Brett et al., 2002) by centering spheres on MNI group coordinates obtained in Kohler et al. (2023). Right PMC [26–12 60], left PMC [−32–10 68], and left M1 [−44–22 62] corresponded to peak coordinates of clusters showing stronger activity when performing pieces with familiar compared to unfamiliar partner actions (see the univariate contrast in Kohler et al., 2023). To obtain coordinates for right M1 [44–22 62], the sign of the left M1 x-coordinate was flipped. Both M1 coordinates were located in the primary hand motor area reported in a meta-analysis by Mayka et al. (2006). The ROI in left cerebellar lobule VIII (CER) [−26–56 −50] was centered on the peak coordinates of a cluster that had shown sensitivity to subtle temporal asynchronies between pianists' keystrokes when they were familiar (compared to unfamiliar) with their partner's actions (see Kohler et al., 2023). The homologous right CER coordinates [26–56 −50] were again obtained by flipping the sign of the x-coordinate. According to the Cerebellar atlas (Diedrichsen et al., 2009) of the SPM Anatomy Toolbox (Eickhoff et al., 2005, 2006, 2007), these coordinates lay in lobule VIII with a probability of 76%. Finally, the center coordinates for left and right PT [±60–30 15] were selected based on their stronger functional connectivity with motor areas when pianists were familiar (compared to unfamiliar) with their partner's part (see Kohler et al., 2023). Note that these coordinates were slightly shifted compared to Kohler et al. (2023), to increase the

probability of assessing representations in PT. According to the Harvard-Oxford Cortical Structural Atlas (Desikan et al., 2006; Mazziotta et al., 2001), both coordinates lay in PT with probabilities of 49% for the right, and 52% for the left hemisphere. ROI locations are visualized in Figure 2.

We built spheres with 4 mm (9 voxels), 6 mm (33 voxels) and 8 mm radius (79 voxels) around each of these 8 coordinates. Three sphere sizes were used following the procedure of de Manzano et al. (2020) in order to control for ROI size (see recommendation by Shashidhara et al., 2020). The resulting 24 spheres (4 regions × 2 hemispheres × 3 sizes) were then transformed into native space by using the individual deformation fields obtained when normalizing individual brains to MNI standard space. Finally, the individual native space ROIs were reduced to grey matter voxels by performing a conjunction between the ROIs and the individual grey matter masks described above.

2.5.5 Multivariate pattern analysis in regions of interest (ROI)

Multivariate pattern analyses were carried out in each ROI using the CoSMoMVPA toolbox (Oosterhof et al., 2016) in Matlab. First, the beta images corresponding to brain activity during the joint performance of the first phrase (see above) were demeaned to ensure that the results would not be merely driven by differences in activity strength. Then, a linear support vector machine (SVM) (Chang and Lin, 2011) was used to classify which of two pieces was performed, separately for the pieces with familiar (F1, F2) and for the pieces with

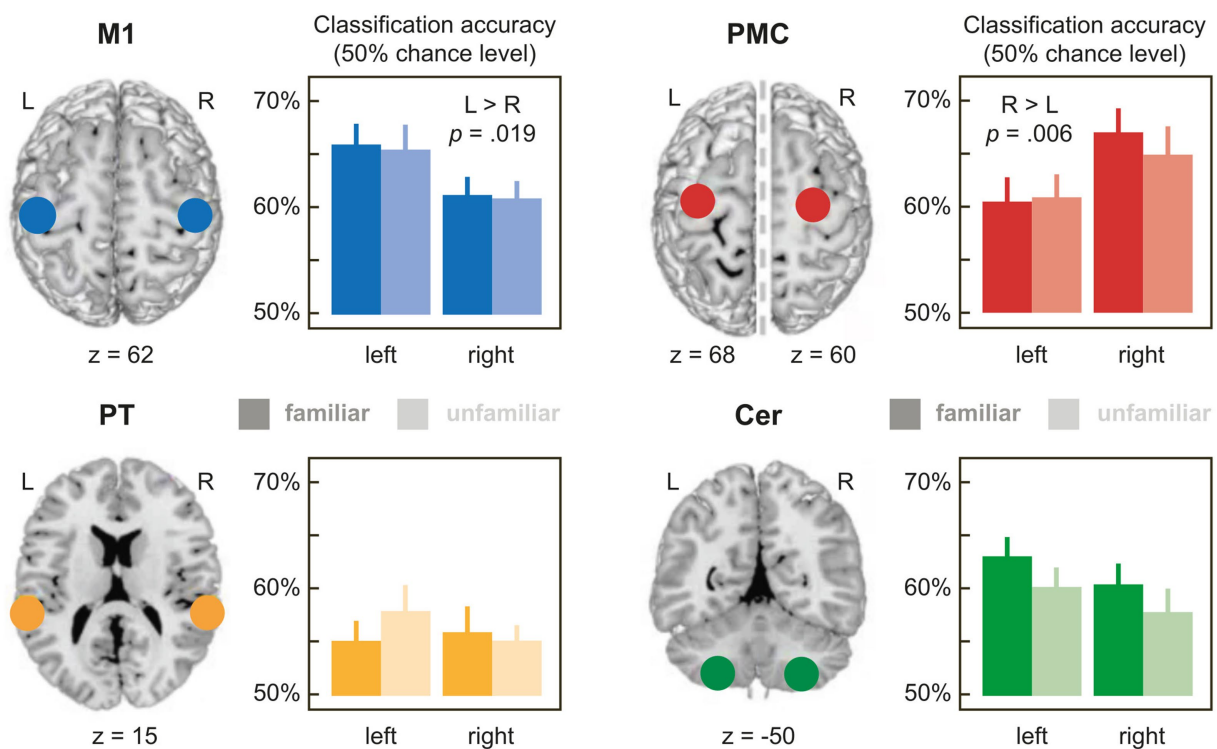


FIGURE 2

Mean accuracies for the classification of pieces with familiar (dark bars) and unfamiliar partner actions (light bars) in the 4 bilateral ROIs with 6 mm radius (for a full list of accuracies in the ROIs with 4 mm, 6 mm or 8 mm radius, see Supplementary Table S1). 50% on the y-axis corresponds to empirical chance level. M1: primary hand motor cortex; PMC: premotor cortex; PT, planum temporale; CER, lobule VIII of the cerebellum. Error bars denote ± 1 SEM.

unfamiliar (U1, U2) partner actions. We used a leave-2-out cross-validation scheme, i.e., trained the classifier on 6 folds and tested on the 2 remaining folds. Training and testing were done exhaustively on all 28 possible combinations of folds per subject. Classification accuracies of all 28 iterations were averaged, per participant and region. To estimate the individual chance level, the same procedure was repeated 10,000 times with randomly labelled trials for each participant and ROI. Chance level was found to be 50% in all cases (Supplementary Table S1). Paired *t*-tests with FDR-correction were used to ensure that classification accuracies were significantly higher than this empirical chance level.

Further statistical analyses were restricted to accuracies above chance, and were performed on the differences between accuracies and empirical chance-level, referred to as relative accuracies. Relative accuracies were compared in 3-way repeated measures ANOVAs with the factors FAMILIARITY (familiar, unfamiliar partner actions), HEMISPHERE (left, right), and SIZE of sphere radius (4 mm [only for M1, PMC], 6 mm, 8 mm), separately for each ROI (M1, PMC, CER, PT). All ANOVAs were performed using the *ez* package (Lawrence, 2016) in R.

2.5.6 Multivariate pattern analysis with whole-brain searchlight approach

To explore whether any regions outside the predefined auditory-motor ROIs represent self- and other-produced action, we conducted a whole-brain searchlight MVPA analogous to the ROI-based analyses. The same SVM classifier and leave-2-out cross-validation scheme was used to classify pieces with familiar (F1, F2) and unfamiliar (U1, U2) partner actions in a searchlight moving through each participant's grey matter mask (see above). The searchlight sphere

had a 7.5 mm (3 voxel) diameter as suggested in previous studies (de Manzano et al., 2020; Kriegeskorte et al., 2006). For each participant, unfamiliar classification accuracy maps were subtracted from familiar maps, assuming similar chance-levels for both conditions (Supplementary Table S1).

The resulting difference maps were then normalized to MNI space and combined into a 4D volume, containing one 3D volume per participant. A one-sided one-sample *t*-test against zero was performed on this 4D MNI accuracy map using SPM 12, to identify regions in which classification accuracy was higher when partner actions were familiar compared to unfamiliar. To correct for multiple comparisons, threshold-free cluster-enhancement (Smith and Nichols, 2009) was applied through Monte Carlo simulation (Oosterhof et al., 2016) with a threshold of $\alpha = 0.05$.

3 Results

3.1 Multivariate pattern analysis in regions of interest (ROI)

Familiar and unfamiliar pieces were classified significantly above empirical chance level in all M1 and PMC ROIs. Statistical values are reported in Supplementary Table S1. In the CER and PT, 1 and 3 out of respective 12 classification accuracies missed the level of significance at 4 mm sphere size. Hence, the 4 mm sphere size was excluded from further analyses in CER and PT.

Table 1 shows the results of the 3-way rmANOVAs with the factors FAMILIARITY (familiar, unfamiliar partner actions), HEMISPHERE (left, right), and SIZE (4 mm [only for M1 and PMC],

TABLE 1 ANOVA results in the 4 ROIs.

	<i>df</i>	M1			PMC		
		<i>F</i>	<i>p</i>	η_p^2	<i>F</i>	<i>p</i>	η_p^2
Familiarity	1.38	0.02	0.903	< 0.01	0.13	0.724	< 0.01
Hemisphere	1.38	6.02	0.019	0.14	8.39	0.006	0.18
Size	2.76	36.82	< 0.001	0.49	39.03	< 0.001	0.51
Fam. × Hem.	1.38	0.04	0.838	< 0.01	0.74	0.396	0.02
Fam. × Size	2.76	0.58	0.520	0.02	0.38	0.612	0.01
Hem. × Size	2.76	1.49	0.234	0.04	1.00	0.374	0.03
Fam. × Hem. × Size	2.76	0.70	0.457	0.02	0.11	0.893	< 0.01

	<i>df</i>	CER			PT		
		<i>F</i>	<i>p</i>	η_p^2	<i>F</i>	<i>p</i>	η_p^2
Familiarity	1.38	2.66	0.111	0.07	0.74	0.396	0.02
Hemisphere	1.38	0.47	0.496	0.01	0.20	0.654	0.01
Size	1.38	1.93	0.172	0.05	11.22	0.002	0.23
Fam. × Hem.	1.38	0.00	0.982	0.01	0.47	0.499	0.01
Fam. × Size	1.38	0.01	0.937	0.01	3.47	0.070	0.08
Hem. × Size	1.38	4.42	0.042	0.10	0.31	0.579	0.01
Fam. × Hem. × Size	1.38	0.00	0.994	0.01	0.74	0.396	0.02

Significant results are printed in bold font. M1, primary motor cortex; PMC, premotor cortex; CER, cerebellar lobule VIII; PT, planum temporale.

6 mm, 8 mm sphere radius), performed on relative accuracies, separately for each ROI. **Figure 2** illustrates the results for the ROIs with 6 mm radius. Mean accuracy values for all ROIs can be found in **Supplementary Table S1**.

M1, PMC, and PT showed a main effect of sphere SIZE (all $ps < 0.003$), replicating generally increasing relative accuracies with growing ROI size reported in the literature (e.g., de Manzano et al., 2020). More interestingly, relative classification accuracies in M1 and PMC differed significantly between hemispheres irrespective of sphere size as indicated by main effects of HEMISPHERE in both regions (M1: $p = 0.019$; PMC: $p = 0.006$), in the absence of interactions involving HEMISPHERE and sphere SIZE ($ps > 0.234$). Most importantly, both ROIs showed effects with *opposite* lateralization: While mean accuracies in M1 were higher in the left than in the right hemisphere, the opposite was true in PMC, showing higher relative accuracies in the right than in the left hemisphere (see **Figure 2** and **Supplementary Table S1**). These results are compatible with dissociated representations of self- (M1) and other-produced actions (PMC) related to the right and left hand, respectively.

As expected, accuracies in M1 did not differ depending on FAMILIARITY with the partner's action (main effect of FAMILIARITY or interactions: $ps > 0.457$), in line with the idea that M1 represents self-produced actions (which were familiar for all pieces). However, unexpectedly, no effects of FAMILIARITY with the partner's action were found in PMC either ($ps > 0.396$).

In CER and PT, relative accuracies did not differ, neither as a function of HEMISPHERE nor of FAMILIARITY. A significant two-way interaction of HEMISPHERE $\times$ sphere SIZE in CER ($p = 0.042$) proved inconclusive when resolved with 2 paired t -tests comparing accuracies between the left and right hemisphere for each sphere SIZE [6 mm: $t(77) = -1.460$, $p = 0.297$; 8 mm: $t(77) = 0.323$, $p = 0.748$; FDR-corrected p -values].

3.2 Multivariate pattern analysis with whole-brain searchlight approach

The whole-brain searchlight analysis yielded no significant differences between classification accuracies for pieces with familiar and unfamiliar partner actions, mirroring the findings of the ROI analysis.

3.3 Control analysis

The present analysis focuses on the first phrase of the musical pieces during which pianists performed together at 120 bpm (**Figure 1**). The original paradigm of Kohler et al. (2023) contained an additional second phrase during which pianists had to either speed up or slow down to a tempo indicated at the beginning of each trial (see *Methods*). It has been shown that these impending tempo changes in the second phrase have subtle effects on performance timing already in the first phrase, indicative of pianists' long-range planning (Kohler et al., 2023; see also Gugnowska et al., 2022; Novembre et al., 2016). To account for spurious effects of these anticipated tempo changes on the reported classification accuracies, we re-ran all ROI and searchlight analyses by adding the mean absolute asynchronies between partners' keystrokes of the first phrase as a parametric modulator of no interest

to the design matrix. The results of this control analysis (**Supplementary Table S2**) were highly similar to those described above, excluding that the present results were driven by the tempo change manipulation.

4 Discussion

The present study investigated neural processes underlying synchronous joint action in music performance by using multivariate pattern analysis (MVPA) to dissociate neural representations of self- and other-produced actions in auditory-motor regions of duetting pianists. We re-analyzed fMRI-scans from pianists performing melody-bassline duets with a partner, where we manipulated whether, prior to the experiment, pianists had previously rehearsed their own right-hand melody part only (unfamiliar bassline), or if they previously rehearsed both their right-hand part in addition to their partner's left-hand part (familiar bassline) (Kohler et al., 2023). The data show higher accuracies in left M1 and right PMC. Based on previous studies, the most plausible interpretation of these findings is that pianists represented contents of their own right-hand action in left M1 concurrently with contents of their partner's left-hand action in right PMC, as will be explained below. These simultaneous representations at different levels of the cortical motor hierarchy (reflecting execution of own and simulation of the partner's action in M1 and PMC, respectively) lend initial evidence for parallel self and other internal forward models proposed by theories of joint action (Keller et al., 2016; Müller et al., 2021; Novembre and Keller, 2014; Pacherie, 2008; Wolpert et al., 2003). Future studies using novel tools like interbrain representational similarity analyses (Varlet and Grootswagers, 2024) may further substantiate this notion by demonstrating the representational alignment between partners' M1 and PMC more directly. Interestingly, contents of familiar and unfamiliar partner actions were represented with similar precision. This seems to contrast previous findings showing global activity increases in motor regions when performing duets with familiar accompaniments (Kohler et al., 2023) or when observing familiar actions (Aglioti et al., 2008; Calvo-Merino et al., 2005, 2006; Candidi et al., 2014; Ticini et al., 2019). However, motor representations of unfamiliar accompaniments were likely generalized from the familiar accompaniments, based on the similarity of musical structures, potentially triggered by the external auditory perception of the partner's part (Apšvalka et al., 2018; Pfondresher, 2012; see also de Manzano et al., 2020). Indeed, such a transfer is highly possible especially as our participants were highly trained pianists. Overall, findings across studies suggest that fine-grained activity patterns and global activity changes complement each other and elucidate how action contents are *represented* and *used* for simulating, anticipating, and coordinating one's own and other's actions during social interaction.

4.1 Lateralization suggests distinct representations of self- and other-produced actions

Classification accuracies were overall higher in left than right M1, i.e., in primary motor areas controlling the right hand used by the

pianist to play the melodies. It is well established that M1 involvement is strongly lateralized towards the hemisphere contralateral to movement execution, reflected both in stronger activity (see, e.g., Chettouf et al., 2020; Horenstein et al., 2009) as well as higher classification accuracy (Kornysheva and Diedrichsen, 2014; Nambu et al., 2015; Wiestler and Diedrichsen, 2013). Accordingly, our results can be interpreted as suggesting that left M1 represented self-related information about the ongoing right-hand execution of the melody. Future studies could investigate in more detail how exactly pianists represent their own actions during joint music performance, as individual keypresses or chunked finger sequences, in terms of key-to-finger mappings, force profiles or rhythm and timing of keypresses (for studies starting to tackle these questions in individuals performing non-musical motor sequences; see Kornysheva and Diedrichsen, 2014; Yokoi et al., 2018; Yokoi and Diedrichsen 2019).

Lateralization was reversed in PMC, that is, classification accuracies were higher in the right than left hemisphere. This lateralization is interesting, not only because activity in PMC is typically less strongly lateralized than in M1, especially in complex sequential motor tasks and univariate analyses (for review, see Chettouf et al., 2020). Notably, multivariate studies that have reported (weakly) lateralized motor representations in PMC, clearly linked these representations to movements of the contralateral hand (e.g., Diedrichsen et al., 2013; Kornysheva and Diedrichsen, 2014; Wiestler and Diedrichsen, 2013). In the present study, this corresponds to the left hand, used by the partner. Additionally, MVPA studies on action observation have shown that PMC carries information related to contralateral hand actions performed by others (Errante et al., 2021; Filimon et al., 2015). For example, Errante et al. (2021) were able to decode from left PMC which type of grip participants observed in videos of a right hand opening or closing a box lid. Although these studies rarely compared classification accuracies between ipsi- and contralateral PMC, or sometimes reported bilateral representations (Apšvalka et al., 2018), these combined findings are compatible with the idea that the neural patterns we found in right PMC reflect representations of the contralateral left-hand actions performed by the partner.

However, before drawing any definite conclusions, several alternatives should be considered: For example, it might be argued that right PMC represents (i) *ipsilateral* hand actions, potentially merely mirroring the left-hemispheric patterns of self-produced movements, (ii) the *integration* of left- and right-hand actions in a bimanual task, rather than left-hand representations, or (iii) just trivially hand dominance. Yet, none of these alternatives can fully explain the stronger representations in right than left PMC: Interpretation (i) does not seem plausible as ipsilateral representations are usually weaker than their contralateral counterparts (for reviews, see Bundy and Leuthardt, 2019; Chettouf et al., 2020), while for interpretation (ii), bimanual integration has been shown bilaterally (e.g., Diedrichsen et al., 2013). Finally, interpretation (iii) is unlikely as right-hand dominance has been consistently shown to lateralize to left PMC (for review, see Goble and Brown, 2008). Hence, the most plausible interpretation for now remains that the information in right PMC reflects the representation of the contralateral left-hand basslines performed by the partner.

Furthermore, it might be argued that the literature underlying the present interpretation often concerns unimanual solo actions. However, the field is steadily scaling up to more complex

(complementary) bimanual (e.g., Diedrichsen et al., 2013) or joint actions (Cirillo et al., 2018; Sacheli et al., 2022) and is beginning to reveal which mechanisms generalize to more ecologically valid motor behavior as tested here. Our approach may further contribute to that discussion by adding a solo and truly bimanual condition to the paradigm. Ultimately, strongest support for our conclusions may be gained by means of novel tools like interbrain representational similarity analyses (Varlet and Grootswagers, 2024) which provide a more direct way of measuring aligned representations between partners' M1 (self) and PMC (other).

Another question is whether these representations pertain to the motor *simulation* of the partner's part, or the *inhibition* of the corresponding left-hand movements. Arguments for the former interpretation can be derived from previous TMS studies using a similar duetting paradigm (e.g., Novembre et al., 2012). In these studies, pianists performing melodies with a partner who played the basslines showed increased (rather than decreased) excitability of right hand motor cortex, i.e., larger (rather than smaller) motor-evoked potentials related to the partner's left-hand part. This pattern is incompatible with inhibition and supports the notion of simulation. It should be noted that activity patterns reminiscent of inhibition were also found, but only during solo performance of the melodies, not when pianists performed in duet with a partner (Novembre et al., 2012), as in the present study. Such inhibitory patterns may reflect the suppression of mirror movements in the contra-lateral hand (Bundy and Leuthardt, 2019; Chettouf et al., 2020; Welniarz et al., 2015). Overall, these combined results suggest that social interactive settings facilitate motor simulation rather than inhibition of partner actions, consistent with previous work (e.g., Sacheli et al., 2019) and reflected in the present right-lateralized PMC patterns.

Overall, the opposite lateralization in M1 and PMC suggests distinct representations of self and other at different levels of the cortical motor hierarchy: while the findings in M1 likely reflect the *execution* of self-produced right-hand melodies, the findings in right PMC likely reflect the *simulation* of partner-produced left-hand basslines, aligning with its role in motor simulation (Sacheli et al., 2019, 2022). This M1-PMC integration reveals an initial glimpse into how bimanual actions are coordinated simultaneously within a dyadic motor plan, where agents would apply sensorimotor control processes for both self and partner actions (Sacheli et al., 2021). It underscores the simultaneity and content-specificity of internal forward models for self- and other-produced actions, predicted by theories of joint performance coordination (Keller et al., 2016; Müller et al., 2021; Sebanz and Knoblich, 2009).

4.2 Auditory-motor transfer of other-produced actions

Another strategy that we employed to identify neural representations of other-produced actions was by manipulating motor familiarity. We hypothesized that compared to being unfamiliar with a co-performer's accompanying part in a duet (i.e., the bassline), familiarity with the other's part would evoke stronger internal modelling, that is, stronger motor (in PMC and CER) and possibly also auditory (in PT) representations (Jeannerod, 2006; Keller et al., 2016; Kohler et al., 2023; Müller et al., 2021; Novembre and Keller, 2014; Patel and Iversen, 2014), reflected by increased classification

accuracy. However, there was no significant difference in classification accuracy between familiar and unfamiliar conditions in any brain area. While the absence of effects in CER and PT may be explained, e.g., by overall higher noise levels in cerebellar than cerebral cortical fMRI signals (Kornysheva and Diedrichsen, 2014; Wiestler et al., 2014), and a saturation of PT activity due to the ongoing perception of the jointly performed pieces (de Manzano et al., 2020; May et al., 2022; Regev et al., 2021; Schindler et al., 2013), the PMC findings deserve more in depth discussion.

One possible explanation for the non-significant effect of familiarity in (right) PMC is auditory-motor transfer, that is, the emergence of motor patterns from the auditory perception of the basslines. In expert pianists, such as our participants, auditory and motor systems are strongly coupled (Bangert et al., 2006; Baumann et al., 2007; Jäncke, 2012; Novembre and Keller, 2014; Zatorre et al., 2007). Therefore, simply hearing the bassline (performed by the partner) may have indeed evoked bottom-up auditory-informed motor patterns in PMC, even when the basslines were unfamiliar. This effect may have been reinforced by the ability of pianists to generalize motor patterns across similar sequences, based on their long-term musical training (Meyer and Palmer, 2003; Palmer and Meyer, 2000; Pfordresher, 2012). In the current study, all stimuli were simple Bach chorale sequences that were repeated several times during a session, making it possible that the expert pianists in our study generalized across familiar and unfamiliar accompaniments, based on common abstract structural characteristics. This idea finds general support in two recent MVPA studies in non-pianists who exhibited comparable classification accuracies in motor areas for trained and untrained finger sequences with similar structure, after 4 sessions of observational training (Apšvalka et al., 2018), or even just only 20 min of piano training, compared to novices (de Manzano et al., 2020). This demonstrates that content-specific neural motor representations can generalize across similar pieces when passively watching or listening to another piece, an effect that may have been particularly strong in our highly trained participants (see *Methods*). Together, the high classification accuracy irrespective of familiarity may derive from the bottom-up/top-down interplay in auditory-motor systems. In pianists with long-term musical knowledge, hearing the basslines may have evoked bottom-up audio-informed representations in PMC (de Manzano et al., 2020), which might be indistinguishable from top-down motor-informed representations that generalize across structurally similar sequences.

A final, broader conceptual consideration that should be highlighted here is the complementarity of insights that can be gained from univariate and multivariate analyses. Contrary to the present findings, univariate analyses yielded significant effects of familiarity, that is, increased activity and connectivity in familiar conditions (Kohler et al., 2023), revealing the potential use of motor knowledge for simulating partner actions. In contrast, MVPA (the current study) reveals the *representation* of motor patterns, irrespective of whether they are more motor- or audio-informed. In other words, these findings based on either global activity changes (univariate analyses) or fine-grained activity patterns (multivariate analyses) may capture different aspects of neural processing: the use versus the representation of action content. Together, both approaches draw a more complete picture of the mechanisms of joint action, emphasizing the integration of self- and other-produced movements within cortico-cerebellar auditory-motor networks. This

integration ultimately contributes to the dynamic embodiment required for smooth coordination in musical ensemble performance and, possibly, other forms of social interaction.

5 Conclusion

The current study provides initial evidence for parallel, distinct and content-specific auditory-motor representations of complementary self- and other-produced actions in musical duets. This was reflected in the opposite hemispheric lateralization of neural information concurrently represented in M1 (own-action execution) and PMC (simulation of partner actions), which cannot be explained by lateralization properties currently known from the motor literature. These results are in line with theories proposing distinct yet integrated self and other internal forward models contributing to smooth coordination in social interactions (e.g., Keller et al., 2016; Knoblich and Sebanz, 2006; Müller et al., 2021; Novembre and Keller, 2014). Notably, the precision of these representations was less dependent on motor familiarity than previously believed, suggesting that general auditory-motor piano practice, even without in-depth motor knowledge of a partner's part, may lead to informed (forward) models that can support joint music performance. This extends the role of internal models beyond highly specific instances of motor familiarity. Future studies testing the representational alignment between partners' motor systems more directly (Varlet and Grootswagers, 2024) should substantiate our conclusions and clarify to what extent our findings generalize to less experienced musicians and other forms of social interaction. More generally, this research highlights new ways of how to combine the complementary strengths of uni- and multivariate approaches to gain novel insights into the neural mechanisms underpinning human social actions.

Data availability statement

The datasets presented in this article are not readily available because of the lack of explicit consent from participants. Requests to access the datasets should be directed to daniela.sammler@ae.mpg.de.

Ethics statement

The study was approved by the ethics committee of Leipzig University, Germany (016-15-26012015). The study was conducted in accordance with the local legislation and institutional requirements. The participants provided their written informed consent to participate in this study.

Author contributions

NK: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. AC: Data curation, Writing – original draft, Writing – review & editing. ÖM: Formal analysis, Software, Writing – review & editing. GN: Conceptualization, Methodology, Supervision,

Writing – review & editing. PK: Conceptualization, Methodology, Writing – review & editing. AV: Funding acquisition, Resources, Supervision, Writing – review & editing. DS: Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

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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.2025.1543131/full#supplementary-material>

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In sync with oneself: spontaneous intrapersonal coordination and the effect of cognitive load

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Spontaneous intrapersonal coordination is the unintentional coordination of periodic behaviors within an individual. Spontaneous interlimb coordination involving finger-, arm-, foot-, leg- and orofacial muscle movements may be weaker between finger-tapping and walking than between finger-tapping and vocalizing. This could be due to the additional attentional cost of walking, which may be more complex than other periodic movements. Here we compared the coordination stability of simultaneous finger-tapping and walking against simultaneous finger-tapping and repetitive vocalization. We also tested the coordination stability of tapping-walking and tapping-vocalizing under additional cognitive load imposed through concurrent cognitive tasks. Two experiments conceptually replicated spontaneous intrapersonal coordination between the pairs of periodic tasks as well as the effect of concurrent cognitive tasks on coordination stability. To assess coordination, we compared the phase coherence of two periodic tasks, tapping with walking (Experiment 1) or tapping with vocalization (Experiment 2), when produced separately (single task) versus simultaneously (dual task). In the first experiment, participants regularly tapped a microphone while walking, either with no concurrent cognitive task or with concurrent backward counting. In the second experiment, participants tapped while repeating the word “tick,” again either with no concurrent cognitive task, or with concurrent visual pattern-matching. Higher spontaneous intrapersonal coordination was evident between periodic tasks when performed simultaneously compared to separately, and lower task coordination stability was evident with a concurrent cognitive task compared to without. These results were in line with past findings. Coordination stability between tapping and walking was lower than that between tapping and ticking overall. This finding supports the categorization of walking as a more complex cognitive task compared to other periodic tasks, as the additional attentional load involved in walking could have resulted in lower coordination stability between tapping and walking. Spontaneous intrapersonal coordination appears sensitive to the attentional costs of performing periodic activities and achieving / maintaining coordination between them.

KEYWORDS

coordination, synchronization, intrapersonal, spontaneous, coupling, attention, cognitive load, interpersonal

1 Introduction

Coordinated movement is such an integral component of human nature that it often goes unnoticed. For example, imagine an audience, watching musicians and dancers perform, and grooving along with the artists by tapping their feet, snapping their fingers, clapping their hands, and bobbing their heads. These periodic behaviors often interact and influence each other unintentionally. The unintentional temporal coordination that emerges spontaneously between periodic movements may occur intrapersonally, as in the case of interlimb coordination during bimanual finger-tapping (Kelso, 1984; Lorås et al., 2019). Coordination may also occur interpersonally, as in the case of spontaneous synchronization of footsteps (while walking together) observed in dyads (Zivotofsky and Hausdorff, 2007) and pedestrian crowds (Fujino et al., 1993; Ma et al., 2021).

Although “coordination,” especially interpersonal, is often referred to as “synchronization” in the literature, coordinated periodic behaviors seldom happen strictly at the “same time or rate” as per the lexical definition of synchronization. This is because synchronization between individuals is not perfect, because there is variability. For example, although stride time variability in healthy young adults is under 3% in general (Beauchet et al., 2009), it is not zero. Synchronization therefore requires individuals to coordinate their individual rates to adopt either the same rate or a related rate (harmonic or subharmonic) such that the relative asynchronies between corresponding repetitions of the behavior (e.g., step times) tend toward a constant value. This applies not only to synchronization involving walking, but also to other periodic tasks such as finger-tapping, where inter-tap interval varies with every tap (Yamada, 1995). So, two partners performing a periodic behavior together will likely have slightly different rates, say, f_1 and f_2 , respectively instead of a common rate (F), and also, the exact times of their corresponding repetitions, say, t_1 and t_2 , respectively, will likely be slightly different as well, such that $t_1 - t_2 \neq 0$. Under synchronization, $t_1 - t_2$ will tend toward a constant value. Fraise, in the context of sensorimotor synchronization of finger taps to periodic auditory stimuli, made this observation as early as 1966; he termed it as quasi-simultaneity and categorized this form of coordination as a viable mode of synchronization (Fraise, 1966; Fraise and Repp, 2012). Definitions of interpersonal synchronization over the years echo Fraise’s categorization: “Rhythmic coordination of perception and action” (Repp, 2005, p. 969), “coordination of rhythmic movement with an external rhythm” (Repp and Su, 2013, p. 403), and “temporal coordination between humans” (Tranchant et al., 2022), are some of the definitions of synchronization found in the literature as on date. We make this point about synchronization and coordination at the outset to clarify that, contrary to Fraise’s categorization of coordination as a viable mode of synchronization, coordination subsumes synchronization: Synchronization, as predicted by the coordination pattern dynamics model, is the most stable pattern of coordination (Haken et al., 1985). This clarification is to avoid confusion due to interchangeable usage of the terms “synchronization” and “coordination” going forward.

The stability of coordination between interacting periodicities depends upon their coupling strength, which refers to the intensity of the influence between two systems. This influence can be either

unidirectional or bidirectional (Haken et al., 1985; Boccaletti et al., 2002). Stronger coupling increases the likelihood of coordination between behaviors. Interpersonal coupling is typically achieved through exchange of sensory feedback – visual, auditory, or tactile. Exchange of tactile feedback by holding hands has proved to be the most effective in eliciting spontaneous synchronization of gait (Zivotofsky and Hausdorff, 2007; Zivotofsky et al., 2012, 2018; Sylos-Labini et al., 2018). Although not as consistent as their tactile counterpart, visual and auditory feedback have, in some cases, been effective in triggering an increase in spontaneous interpersonal synchronization of various activities, including swinging a handheld pendulum, swaying in a rocking chair, walking, and running (Schmidt and O’Brien, 1997; Richardson et al., 2007; Oullier et al., 2008; Lopresti-Goodman et al., 2008; Harrison and Richardson, 2009; Zivotofsky et al., 2012). Even in naturalistic settings, spontaneous synchronization seems to follow the natural exchange of sensory feedback between interacting entities. Audiences spontaneously synchronize their applause – what begins as random, incoherent clapping becomes synchronized (Néda et al., 2000a, 2000b, 2003). Also, humans synchronize their footsteps spontaneously when walking with others; such observations have been reported in dyads (Zivotofsky and Hausdorff, 2007), as well as in crowds of pedestrians (Fujino et al., 1993; Ma et al., 2021). As strong as spontaneous interpersonal coupling is, enough to trigger synchronization, it is not as strong as spontaneous intrapersonal coupling and the resultant coordination (Schmidt et al., 1998). Intrapersonal coordination occurs spontaneously in bimanual tapping (Kelso, 1984; Loras et al., 2019), between arm and leg movements (Sakamoto et al., 2007), as well as between limb movements and orofacial muscle movements, such as walking and chewing gum (Samulski et al., 2019). When performed concurrently, finger-tapping and speaking influence each other in terms of rates, variabilities as well as stress patterns (Hiscock et al., 1985; Smith et al., 1986; Parrell et al., 2011).

In a study by Qi et al. (2019) participants aged 20–30 years performed finger-tapping at a given inter-tap interval of 375 ms with concurrent foot movements at a given inter-(heel)-strike interval of 600 ms; the foot movements were alternative bilateral heel tapping from a sitting position, and unilateral heel tapping with the leg ipsilateral to the tapping finger from a sitting position. Each participant also performed the finger-tapping task (at 375 ms inter-tap interval) with concurrent walking, both at given pace (at 400, 600, and 800 ms inter-step intervals) as well as at preferred pace (self-paced). Despite the given inter-repetition intervals for finger-tapping and heel-striking being unrelated (by design), spontaneous interlimb coordination of finger-tapping was significant with all the concurrent foot movements except, however, with given-paced walking and self-paced walking. Researchers concluded that tapping and walking could be done with “independent rhythms”. In general, weaker coordination could be indicative of higher attentional cost of intentionally maintaining the coordination (Zanone et al., 2001; Temprado et al., 1999; Pellicchia et al., 2005). In this study, the weaker coordination between finger-tapping and walking (compared to heel tapping) could have been due to higher attentional cost involved in walking. Evidence suggests that walking, compared to other periodic tasks like finger-tapping, could be a more complex cognitive activity (Sheridan and Hausdorff, 2007; Hausdorff et al., 2005). Given that, the attentional cost

required to intentionally maintain the coordination of finger-tapping with walking would be more compared to that of finger-tapping with other periodic tasks, explaining the finding by Qi et al. (2019).

The above explanation could be further tested by comparing the stability of coordination of finger-tapping and walking against that of finger-tapping and other periodic tasks. For such a comparison, repetitive vocalization could be a suitable periodic task to be paired with finger-tapping as concurrent finger-tapping and speaking influence each other in terms of rates, variabilities as well as stress patterns (Hiscock et al., 1985, Smith et al., 1986; Parrell et al., 2011). Furthermore, stability of bimanual coordination decreases with concurrent cognitive tasks such as reaction time task (Temprado et al., 1999) and backward counting task (Pellecchia et al., 2005). This is understandable given how the variability of finger-tapping (as a single task) increases with concurrent n-back task (Kirchner, 1958) or mental arithmetic tasks (Irie et al., 2022; Bååth et al., 2016). In that vein, given how concurrent backward counting affects gait speed and variability (Li et al., 2014; Beauchet et al., 2005), it would be understandable if the stability of coordination involving walking decreased with concurrent backward counting. Therefore, put together, we could expect the stability of coordination between tapping and walking to decrease with concurrent backward counting. Also, finger-tapping and vocalizing simple repeated sequences interfered with performance in the concurrent Multiple Object Tracking (MOT) task (Trick et al., 2006), suggesting that all three tasks shared attentional resources. Therefore, we could expect the stability of coordination between tapping and repetitive vocalization to decrease with a concurrent visuospatial task. Further, findings to date are unclear as to whether the concurrent attentional load could be altered by varying task difficulty. For example, backward counting in 3's versus 7's has been found to alter concurrent attentional load in some cases (Kroll and Kellicutt, 1972) while not in others (Houghton et al., 2003). Given that, it is worth testing if varying task difficulty varies the effect of the concurrent cognitive task on coordination stability.

In the current study, we compared the stability of spontaneous (unintentional) coordination of repetitive finger-tapping with walking as well as with repetitive vocalization, where all the periodic behaviors were at preferred rates. Here, any difference between tapping-walking and tapping-vocalization in terms of coordination stability could partially be due to the difference in attentional costs of walking and repetitive vocalization. To isolate that part, the attentional costs incurred through other factors had to be minimized. To that effect, first, unintentional coordination was compared instead of intentional coordination for the dual tasks as the former has been found to incur less attentional cost (Aubin et al., 2021); second, coordination at preferred rates was compared instead of the same at given rates as the attentional cost is at its minimum when coordination pattern is at preferred frequency (Zanone et al., 2001). In the current study, we also compared the effect of backward counting across difficulty levels on spontaneous tapping-walking coordination, as well as the effect of matching visual-patterns across difficulty levels on spontaneous tapping-vocalization coordination.

We conducted two conceptual replication experiments. In each experiment, we tested the stability of spontaneous (unintentional) intrapersonal coordination between the periodic behaviors at

preferred rates, with and without concurrent cognitive task. The research question was, with no concurrent cognitive task, would the stability of coordination of finger-tapping be lower with walking than with repetitive vocalization? The evidence showing walking as a more complex cognitive task compared to other periodic tasks was not enough to assume that repetitive vocalization was one of the other periodic tasks, rendering any hypotheses in response to the research question not justified enough. We therefore made *post hoc* comparisons of the two periodic task pairs (tapping-walking and tapping-vocalization) in terms of their coordination stability when no concurrent cognitive task was performed. As the cognitive tasks were different across the two experiments for reasons discussed above, such a comparison was not meaningful when the concurrent cognitive task was performed.

2 Materials and methods

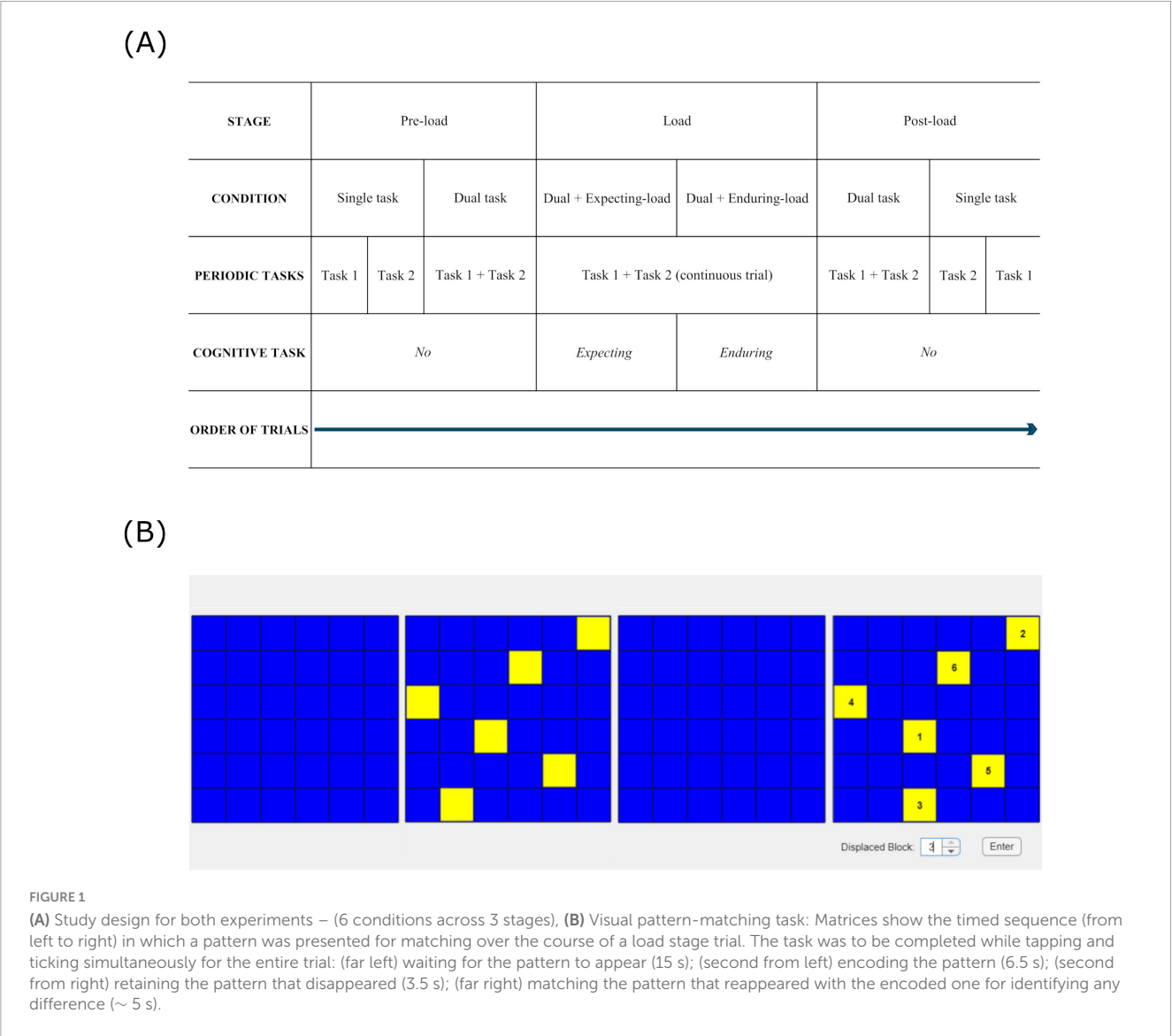
2.1 Participants

Twenty-four participants (mean age = 22.58 years; range = 18–33; SD = 5.5; 10 males and 14 females; all right-handed) were recruited for the study comprising 2 experiments. Each participant completed both experiments. Age, gender and dominant hand were self-reported. Fourteen participants were recruited from the Psychology research participation pool at Western University and received 1 course credit compensation. The remaining 10 participants were recruited from students and the general public and compensated \$10 for the 1-h study. The study was approved by the Non-Medical Research Ethics Board at Western University.

2.2 Design

The study comprised two experiments, completed in a single session lasting 1 h. The order of completion of the experiments was counterbalanced across participants. The study design (see Figure 1A) was common to both experiments.

Each experiment had a different pair of periodic tasks (performed separately as single tasks, and simultaneously as dual task), and a different cognitive task with multiple difficulty levels (performed concurrently with dual task). Experiment 1 had repetitive finger-tapping and walking as periodic tasks, and backward counting as the concurrent cognitive task with two difficulty levels (counting backward in 3's and 7's). Experiment 2 had repetitive finger-tapping and repetitive vocalization of the word “tick” (ticking) as periodic tasks, and visual pattern-matching as the concurrent cognitive task with six difficulty levels (matching patterns comprised of 4–9 blocks). The word “tick” was selected for repetitive vocalization as piloting showed it was easy to extract durations between successive peak intensities in the audio waveform if a short vowel with a glottal stop was used to reduce vowel duration variability. Backward counting was not used in Experiment 2 as it was incompatible with vocalizing “tick”. As matrix patterns are not easily verbalizable (Della Sala et al., 1999), visual pattern-matching task was used instead. The task involved determining whether sequentially presented patterns on two adjacent 6x6 matrices were the same or different. Six levels of



cognitive load were induced by manipulating the number of blocks in the patterns, from 4 to 9. The task was designed based on a 2005 study where simultaneous presentation of patterns were used in a matching task, where subjects were allowed 1 s to encode each block in the pattern: for example, 5 s would be allowed to encode a 5-block pattern (Lecerf and de Ribaupierre, 2005). This was in line with the common block-tapping rate of 1 s per block, used widely in the administration of the Corsi Block Test (Arce and McMullen, 2021; Corsi, 1972). Therefore, we allotted 6.5 s on average to encode each pattern with 4 to 9 blocks.

Each experiment had 3 cognitive load stages: pre-load, load, and post-load. During the pre-load stage, the two periodic tasks were performed separately (single task) as well as simultaneously (dual task), always in that order. During the load stage, we assessed whether dual task performance was affected by the anticipation of the concurrent cognitive task (“expecting-load” condition); we also assessed dual task performance with concurrent cognitive task (“enduring-load” condition). Load stage trials ran the expecting-load condition for the first half, and the enduring-load condition for the second half. Expecting-load was treated as a separate condition

as the anticipation of dealing with the imminent demands of cognitive functioning could worsen working memory performance (Hyun et al., 2019). During the post-load stage, we tested for any persisting effects of the load stage (e.g., any change in coordination stability that may have occurred then). Here the order of dual task and single task conditions was reversed compared to the pre-load stage. Also, the order of completion of the periodic tasks in the single task condition was reversed across pre-load and post-load stages. The specific periodic task (e.g., tapping or walking) that was assigned to be “Task 1” and “Task 2” was counterbalanced across participants.

2.3 Materials

For Experiment 1, walking data was captured using the Zeno Walkway gait mat and ProtoKinetics Movement Analysis Software (PKMAS); tapping was audio recorded in version 3.3.3 of Audacity®, a free software distributed under the terms of

the GNU General Public License.¹ For all audio recordings, Fifine Technology Bluetooth receivers and wireless microphones, Focusrite Scarlett 2i2 audio interface, and Windows laptop were used. Sound intensity data were extracted from audio recordings using version 6.2.14 of Praat, a speech analysis software in phonetics (Boersma and Weenink, 1992–2022). Data were sorted in Microsoft Excel (2016). Metrics were calculated using code written for the study in MATLAB (R2022a). Data analyses were done in Jamovi (2.3.21). Graphing was done in JASP (0.18.3).

2.4 Procedure

The participants were seated at a table on which the laptop running Audacity was placed. The Bluetooth receivers were plugged into the Focusrite audio interface, one on each channel. There were two wireless microphones; one of them was used as a hand mic for tapping (Experiments 1 and 2), and the other one was used on the stand for ticking (Experiment 2). Participants were instructed to use their non-dominant hand for holding the hand mic, and the index finger of their dominant hand for tapping on the mic. The dominant and non-dominant hands were self-reported. The hand mic was paired to the receiver on line 1 of the audio interface, and the stand mic was paired to the receiver on line 2; this was to make sure the signal from the hand mic was always recorded onto the left stereo channel, and that from the stand mic was always recorded onto the right. Audio input levels were checked and optimized for each participant before the start of the trials, so that the signals were neither too low nor too high. In Experiment 1, at the start of each trial involving the simultaneous performance of the periodic tasks, the hand mic was tapped gently on the gait mat by the experimenter to create two events of reference at the same timepoint, one on the gait mat recording of the walking task, and the other on the audio recording of the tapping; this was done to create a synchronization trigger between the audio and gait data, for temporally aligning tapping and walking responses. Signed informed consent was obtained from each participant.

2.4.1 Experiment 1—walking and tapping

Participants practiced counting backward before completing the tasks in the following order.

Pre-load stage

Single task condition

Tapping: Participants were instructed to tap on the hand mic repetitively at whatever rate felt natural. For each trial, they were to start and stop tapping as prompted by the experimenter. They completed 2 trials, lasting 20 s each, with a 20 s break.

Walking: The participants were instructed to start walking at whatever rate felt natural from just behind a tape line on the floor, marking 1.78 m from the edge of a 4.88-m Zeno pressure-sensor gait mat, and continue walking across the mat to its other side; they were instructed to maintain their stride as they walked off the mat a further 1.78 m on the other side, marked by another tape on the floor, before making a wide U-turn to walk back onto the mat for the next lap. For each trial, they were to start and stop walking as

prompted by the experimenter. They completed 2 trials of 4 laps each, with a 20 s break.

In this stage, all participants completed tapping first, followed by walking.

Dual task condition

The participants were instructed to tap and walk simultaneously at whatever rates felt natural. For each trial, they were instructed to start and stop both tasks at the same time, as prompted by the experimenter. They completed 2 trials of 4 laps each, with a 20 s break.

Load stage

During the first half of each trial, from lap 1 to 3 (expecting-load condition), participants were instructed to tap and walk simultaneously at whatever rates felt natural, while waiting to begin counting backward from lap 4 when the enduring-load condition would commence (without a break). During the second half, from lap 4 to 6 (enduring-load condition), they were instructed to continue tapping and walking simultaneously at whatever rates felt natural, while counting backward from a 3-digit number (between 600 and 999) using a negative counter (3 or 7, representing cognitive load levels 1 and 2, respectively); the number and the counter were given at the start of the trial. They completed 4 trials, 2 at load level 1 followed by 2 at level 2.

Each load stage trial lasted 6 laps instead of 8 for the following reason: During piloting, some participants indicated it was taxing to keep track of which lap they were in during the expecting-load condition, which they needed to do to know when to begin counting backward for the enduring-load condition. To avoid such taxation, if needed, the experimenter visually cued the participants to count backward as they were about to start the enduring-load condition. Such cueing was more seamless at the start of the even-numbered laps, when the participants faced the experimenter, than the odd-numbered ones, when they faced away. This made lap 4 more preferable, instead of lap 5, to begin counting backward; such a preference was therefore accommodated in the trials.

Post-load stage

The dual task condition was performed first with no additional cognitive load, followed by the single task condition. The order of completion of the periodic tasks in the single task condition was reversed compared to the pre-load stage: walking followed by tapping.

2.4.2 Experiment 2—tapping and ticking

A customized application developed using the MATLAB App Designer was used to administer the tasks and record task performance. The primary purpose of using the application was to administer the trials in the load stage conditions, where simultaneous presentation of the visual pattern-matching task and recording audio of taps and ticks was needed. Subsequently, for consistency of task administration interface across stages, we used the application for administering the pre-load and post-load stage trials as well. Before the trials, the participants were briefed about the visual pattern-matching task, after which they practiced the task through the “demo” version on the application. Participants completed the tasks in the following order.

Pre-load stage

Single task condition

In this stage, participants completed tapping first, followed by ticking.

¹ <https://audacityteam.org>

Tapping: Participants were instructed to tap on the hand mic repetitively at whatever rate felt natural. For each trial, they were to start and stop tapping as prompted by the MATLAB application. They completed 2 trials, lasting 15 s each, with a 15-s break.

Ticking: The participants were instructed to repeat the word “tick” into the stand mic at whatever rate felt natural. For each trial, they were to start and stop ticking as prompted by the MATLAB application. They completed 2 trials, lasting 15 s each, with a 15-s break.

Dual task condition – The participants were instructed to tap and repeat the word “tick” simultaneously at whatever rates felt natural. For each trial, they were instructed to start and stop both tasks at the same time, as prompted by the MATLAB application. They completed 2 trials of 15 s each, with a 15-s break.

Load stage

During the first half of each trial (expecting-load condition lasting 15 s), the participants waited for a pattern to appear on the computer screen. While waiting, they tapped and ticked simultaneously at whatever rates felt natural. Enduring-load condition commenced after 15 s when a pattern comprised of yellow blocks appeared on a blue 6x6 matrix on the left side of the screen. In this condition, participants continued tapping and ticking simultaneously at whatever rates felt natural. Additionally, they encoded the pattern for 6.5 s, at which point the pattern disappeared. They retained the pattern in memory for the next 3.5 s, at which point the pattern reappeared on a similar matrix on the right side of the screen. The yellow blocks on the pattern that reappeared would be numbered, with one of them possibly displaced. Participants identified the displaced block, if any, by matching the pattern on the screen against the one encoded in memory. They entered the number on the displaced block as the answer, or entered “0” if none was displaced. Matching lasted for ~5 s (see Figure 1B). Total trial duration was ~30 s. They completed 12 trials, 2 at each cognitive load level, from 1 to 6 based on the number of blocks in the pattern (4–9, respectively).

Post-load stage

The dual task condition was performed first without additional cognitive load, followed by the single task condition. In the single task condition, ticking was performed first, followed by tapping.

2.4.3 Data extraction

Walking: First contact times of footsteps were extracted for each trial with gait mat movement analysis software (PKMAS), and exported to Excel.

Tapping and Ticking: For Experiment 1, the recorded stereo track of the tapping audio on Audacity was split into left and right mono tracks, and the left mono track (tapping) was exported as a wave file. For Experiment 2, the split gave two mono tracks: left (tapping) and right (ticking). Tracks were imported into Praat. In Praat, sound intensity data were extracted from the intensity listings. For each trial, start and end times, as well as the number of sound events (taps or ticks), were extracted manually from the intensity waveform. The extracted data were imported into Excel, sorted, and imported into the MATLAB program that extracted the timing of each sound intensity peak for each tap or tick in each trial.

(MATLAB function for finding peaks in audio was not reliably accurate in extracting event times, especially for ticking. The customized MATLAB code generated for extracting “tick” times worked best with sound intensity data from audio files readily

exportable from Praat. Although this meant more extraction steps, we opted for them for reliable extraction accuracy. For consistency, we followed these steps to extract tap times as well).

2.4.4 Phase coherence

We used phase coherence to measure coordination stability. Phase coherence refers to how aligned two periodic inputs are with each other over time. If the phases are in a fixed relationship with each other, they are said to be fully phase-coherent. When phase-coherent, the oscillators may not necessarily be perfectly synchronized in terms of having the exact same phase (i.e., they could still be offset by a constant phase difference), but their phases exhibit a stable relationship. Phase coherence ranges from 0 to 1, where 0 means no coordination at all and 1 means absolute coordination (synchrony). Standard deviation (SD) of relative phase is the standard measure of coordination stability in the literature. However, phase coherence was chosen as its scaling from 0 to 1 offers a more intuitive interpretation of coordination stability, and it is equally sensitive to the variability of relative phase.

For each trial, phase coherence was calculated for each periodic task from its relative phase angles (θ_j) by applying the global order parameter of the Kuramoto model (Acebrón et al., 2005; Kuramoto, 1975). This parameter is a measure of synchronization, quantifying how well the phases of the two task inputs (e.g., taps and ticks) are aligned. As illustrated in Figure 2, each periodic task is a phase vector, and each individual repetition of a periodic task is a cycle. Imagine tapping is task 1 and ticking is task 2. The instant a tap occurs, the task 1 vector is at 0° to the X-axis; also, at that instant, the phase vector representing the ticking task, the task 2 vector, would make a relative phase angle with the task 1 vector. As task 1 is the reference in this illustration (Figure 2), the task 1 vector is fixed at 0° ; a, b, c are relative phase angles made by the task 2

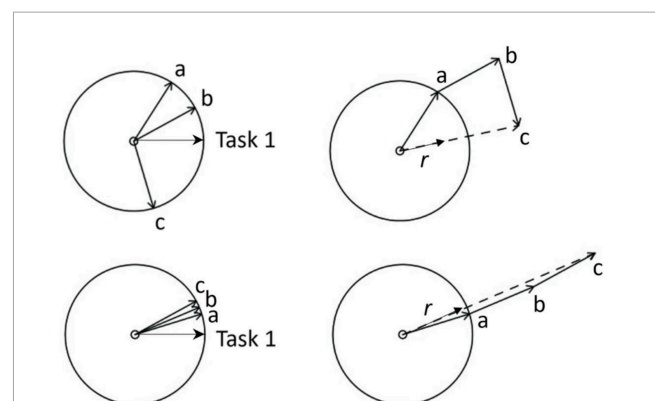


FIGURE 2

Phase angles [a, b, c] of Task 2 vector relative to Task 1 vector, indicating the positions of one periodic task in the event cycle (Task 2 event in this case – e.g., a footstep) when the other periodic task event occurs (Task 1 event in this case – e.g., a finger tap). Higher phase angle clustering (bottom left compared to top left) of Task 2 relative to Task 1 resulting in greater length (r) of the average Task 2 vector (bottom right compared to top right), reflecting higher phase coherence as a measure of higher coordination stability. For example, lower variability of time difference between corresponding events of periodic tasks (e.g., between corresponding footsteps and finger-taps) means lower variability (higher clustering) of relative phase angles, and therefore, higher phase coherence between the tasks.

vector relative to the task 1 vector, such that, $\theta_j = [a, b, c]$. We then applied the global order parameter (to “apply” means to calculate over time) of the Kuramoto model to θ_j using Equation 1 below: In this general model of coupled oscillators, θ_j is represented as an array of N complex numbers $e^{i\theta_j}$, the average of which represents the average value of the task 2 vector both in terms of length as well as phase angle.

$$re^{i\psi} = \frac{1}{N} \sum_{j=1}^N e^{i\theta_j} \quad (1)$$

Here, “ r ” is the length of the average vector, ψ is the phase angle of the average vector, and “ i ” is the imaginary unit $\sqrt{-1}$. The value of “ r ” represents phase coherence ($0 \leq r \leq 1$ for an array of unit vectors), indicating the degree to which the relative phase angles (θ_j) are clustered. As clustering increases, the length of the average vector increases, indicating an increase in phase coherence, and thereby, coordination stability. Phase coherence r was determined according to Equation 2 below (Acebrón et al., 2005; Kuramoto, 1975).

$$r = \left| \frac{1}{N} \sum_{j=1}^N e^{i\theta_j} \right| \quad (2)$$

For each trial, for each task, based on periodic task timings (t) in seconds, momentary rates (f) in cycles per second were calculated: $f_n = 1/(t_n - t_{n-1})$, where t_n is the timing of an individual repetition, t_{n-1} is the timing of the previous repetition, and f_n is the momentary rate at t_n . An array of momentary rates (F_j) was thus calculated for each periodic task. Also, every repetition of one periodic task was paired exclusively with a repetition from the other task, such that each one in a pair of corresponding

repetitions was temporally the most proximal counterpart to the other. For example, in a 15-s dual task trial of tapping and ticking by a subject in the study (see Figure 3), the subject produced the taps and the ‘ticks’ in approximately a 2:1 ratio. There were 17 ticks against 33 taps in the trial. Each of the ticks, from 1 to 17 in ascending order, was paired exclusively with the corresponding tap from the array comprised of the 17 odd-numbered taps, from 1 to 33 in ascending order. For each trial, after such pairings, a two-way difference in timing between the counterparts in each pair was calculated, yielding two arrays of relative asynchronies, one for each periodic task (td_j); the corresponding values of the two arrays were identical in magnitude but opposite in sign. Arrays of relative phase angles (θ_j), one for each periodic task, were then calculated: $\theta_j = td_j \times F_j \times 2\pi$. Applying the model as explained above, phase coherence (r) for each periodic task, relative to the other, was then calculated.

2.4.5 Statistical analyses

For both experiments, phase coherence of each periodic task, relative to the other, was analyzed with a 2×2 repeated measures ANOVA: (*task*: single, dual) $\times$ (*stage*: pre-load, post-load). Then, phase coherence of tapping, relative to walking and ticking, was analyzed across pre-load and post-load stages with 2×2 repeated measures ANOVAs: (*task*: single, dual) $\times$ (*co-task*: walking, ticking).

For Experiment 1, phase coherences of tapping and walking, relative to each other, were analyzed with a 2×2 repeated measures ANOVA: (*load condition*: expecting-load, enduring-load) $\times$ (*load level*: 1, 2), and two one-way repeated measures ANOVAs with four within-subject levels each: (*load condition*: pre-load dual task, expecting-load (level 1 and 2), post-load dual task), and (*load*

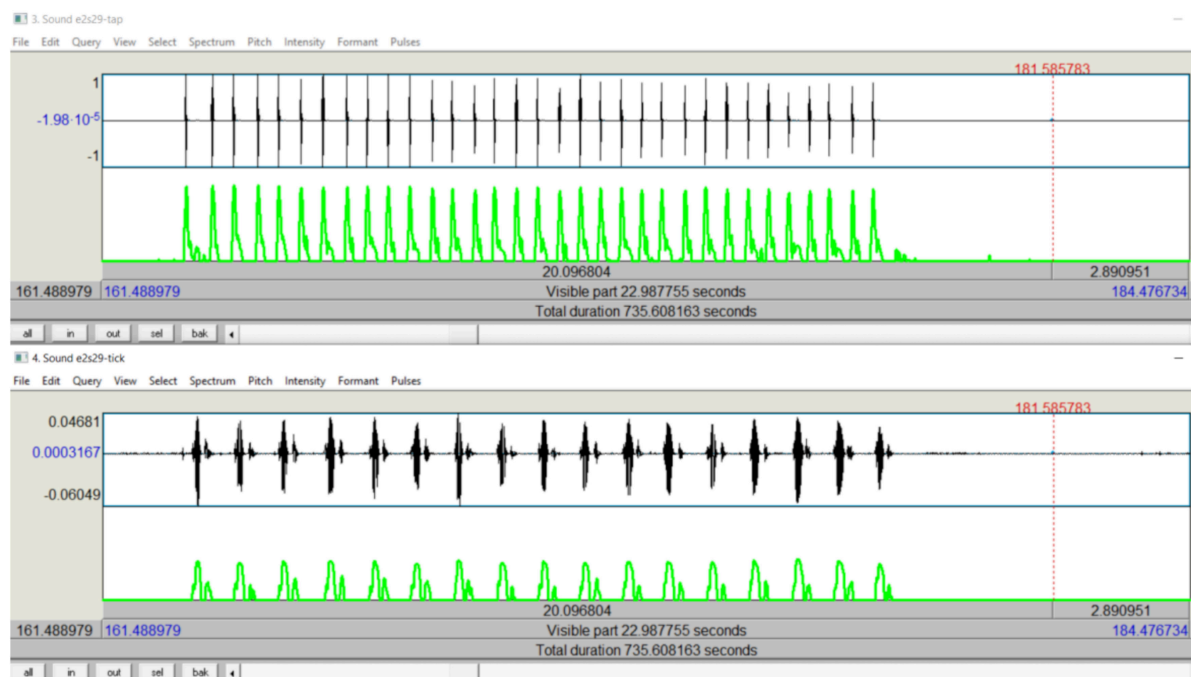


FIGURE 3

Sound intensity representations of a dual-task trial: screenshot showing temporal alignment between tapping and ticking performed simultaneously.

condition: pre-load dual task, enduring-load (level 1 and 2), post-load dual task).

For Experiment 2, phase coherences of tapping and ticking, relative to each other, were analyzed with a 2×6 repeated measures ANOVA: (*load condition*: expecting-load, enduring-load) $\times$ (*load level*: 1 to 6), and two one-way repeated measures ANOVAs with eight within-subject levels each: (*load condition*: pre-load dual task, expecting-load (level 1 to 6), post-load dual task), and (*load condition*: pre-load dual task, enduring-load (level 1 to 6), post-load dual task).

Post hoc tests with Bonferroni correction as well as with no correction were conducted as required. All hypothesis tests used $\alpha = 0.05$ for significance.

3 Results

3.1 Experiment 1—tapping and walking

3.1.1 Phase coherence during single task vs. dual task - 2×2 repeated measures ANOVA

Phase coherence was significantly higher during dual task than during single task, $F(1, 23) = 11.331$, $p = 0.003$, $\eta^2_p = 0.330$

for tapping, and $F(1, 23) = 19.690$, $p < 0.001$, $\eta^2_p = 0.461$ for walking (see **Figure 4A**). This indicates that tapping and walking were more coordinated when performed simultaneously than separately. Phase coherence did not significantly differ between pre-load and post-load stages, $F(1, 23) = 0.712$, $p = 0.407$, $\eta^2_p = 0.030$ for tapping, and $F(1, 23) = 1.514$, $p = 0.231$, $\eta^2_p = 0.062$ for walking. No significant interaction was found between task and stage, $F(1, 23) = 0.246$, $p = 0.624$, $\eta^2_p = 0.011$ for tapping, and $F(1, 23) = 0.305$, $p = 0.586$, $\eta^2_p = 0.013$ for walking.

3.1.2 Phase coherence during expecting-load vs. enduring-load - 2×2 repeated measures ANOVA

Phase coherence was significantly lower while enduring load than while expecting load, $F(1, 23) = 18.587$, $p < 0.001$, $\eta^2_p = 0.447$ for tapping, and $F(1, 23) = 9.399$, $p = 0.005$, $\eta^2_p = 0.290$ for walking (see **Figure 4B**). This indicates that, coordination stability between tapping and walking during dual task decreased when participants concurrently counted backward compared to when they were only expecting to count backward. Phase coherence was not significantly different across load levels 1 and 2, $F(1, 23) = 0.407$, $p = 0.530$, $\eta^2_p = 0.017$ for tapping, and $F(1, 23) = 0.062$, $p = 0.805$, $\eta^2_p = 0.003$ for walking, indicating that counting backward by 3's versus 7's did not significantly differ in terms of how much they

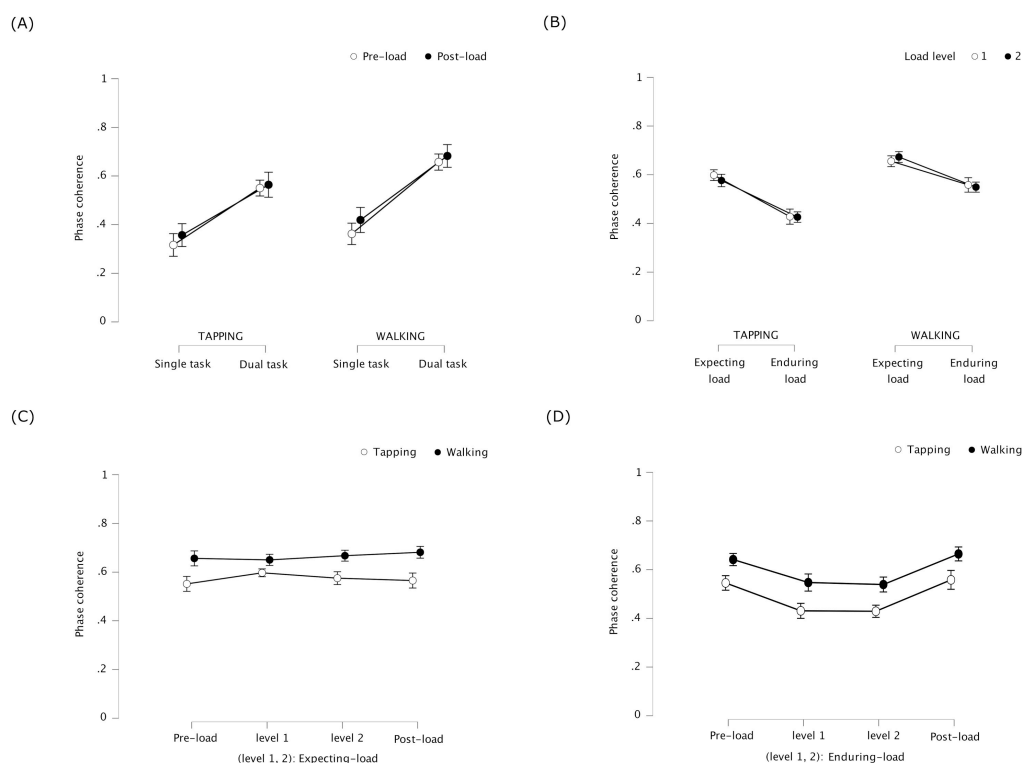


FIGURE 4

Experiment 1: phase coherence of tapping and walking representing coordination stability between the periodic tasks – (error bars indicate standard error) **(A)** Single task / dual task $\times$ pre-load stage / post-load stage – coordination stability increased between simultaneous tapping and walking (dual task) compared to separate (single task); the increase did not significantly differ between pre-load or post-load. **(B)** Expecting-load / enduring-load $\times$ load level (1 and 2) – coordination stability decreased in the tapping-walking dual task under cognitive load (enduring load) compared to Expecting load; the decrease was not significantly different across load levels 1 and 2 (counting backward in 3's and 7's, respectively). **(C)** Pre-load dual task / expecting-load (level 1 and 2) / post-load dual task – coordination stability was similar in the tapping-walking dual task between expecting cognitive load versus not (pre-load and post-load). **(D)** Pre-load dual task / enduring-load (level 1 and 2) / post-load dual task – coordination stability decreased in the tapping-walking dual task while enduring cognitive load versus not (pre-load and post-load).

affected coordination stability. There was no significant interaction between load condition and load level, $F(1, 23) = 0.558$, $p = 0.463$, $\eta^2_p = 0.024$ for tapping, and $F(1, 23) = 1.228$, $p = 0.279$, $\eta^2_p = 0.051$ for walking.

3.1.3 Phase coherence during pre-load, expecting-load and post-load: one-way repeated measures ANOVA with four within-subject levels

Phase coherence did not significantly differ between pre-load dual task, expecting load (level 1 and 2), and post-load dual task, $F(3, 69) = 1.050$, $p = 0.377$, $\eta^2_p = 0.044$ for tapping, and $F(3, 69) = 0.709$, $p = 0.550$, $\eta^2_p = 0.030$ for walking (see Figure 4C). This indicates that the effect of expecting load on coordination stability between tapping and walking was similar to that of no such expectation.

3.1.4 Phase coherence during pre-load, enduring-load and post-load: one-way repeated measures ANOVA with four within-subject levels

Phase coherence was significantly different between pre-load dual task, enduring load (level 1 and 2), and post-load dual task, $F(3, 69) = 7.465$, $p < 0.001$, $\eta^2_p = 0.245$ for tapping, and $F(3, 69) = 7.36$, $p = 0.001$, $\eta^2_p = 0.242$ for walking (see Figure 4D). Post hoc tests with Bonferroni correction revealed that, (1) compared to pre-load dual task, phase coherence was significantly lower for tapping while enduring load level 1, $t(23) = 3.084$, $p = 0.031$, as well as level 2, $t(23) = 3.870$, $p = 0.005$; it was significantly lower for walking while enduring load level 2, $t(23) = 3.416$, $p = 0.014$, but not level 1, and (2) compared to post-load dual task, phase coherence was significantly lower for tapping while enduring load level 2, $t(23) = 3.206$, $p = 0.024$, but not level 1; it was significantly lower for walking while enduring load level 2, $t(23) = 3.684$, $p = 0.007$, but not level 1. Overall, except for tapping during pre-load dual task, concurrent counting backward in 3's did not affect coordination stability between tapping and walking. On the other hand, counting backward in 7's effected a significant decrease in coordination stability between tapping and walking across all conditions the cognitive task was performed concurrently.

3.2 Experiment 2—tapping and ticking

3.2.1 Phase coherence during single task vs. dual task - 2 x 2 repeated measures ANOVA

Phase coherence was significantly higher during dual task than during single task, $F(1, 23) = 129.13$, $p < 0.001$, $\eta^2_p = 0.849$ for tapping, and $F(1, 23) = 104.363$, $p < 0.001$, $\eta^2_p = 0.819$ for ticking (see Figure 5A). This indicates that tapping and ticking were more synchronous when performed simultaneously than separately. Phase coherence did not significantly differ between pre-load and post-load stages, $F(1, 23) = 0.902$, $p = 0.352$, $\eta^2_p = 0.038$ for tapping, and $F(1, 23) = 0.048$, $p = 0.829$, $\eta^2_p = 0.002$ for ticking. No significant interactions were found between task and stage, $F(1, 23) = 1.782$, $p = 0.195$, $\eta^2_p = 0.072$ for tapping, and $F(1, 23) = 0.255$, $p = 0.618$, $\eta^2_p = 0.011$ for ticking.

3.2.2 Phase coherence during expecting-load vs. enduring-load - 2 x 6 repeated measures ANOVA

Phase coherence was significantly lower while enduring load than while expecting load, $F(1, 23) = 7.966$, $p = 0.010$, $\eta^2_p = 0.257$ for tapping, and $F(1, 23) = 4.820$, $p = 0.039$, $\eta^2_p = 0.173$ for ticking (see Figure 5B). This indicates that, when performing the periodic tapping and ticking tasks simultaneously, coordination stability decreased when participants were concurrently matching patterns compared to when they were only expecting to match patterns. Across load levels 1 to 6, phase coherence was not significantly different for tapping, $F(5, 115) = 1.233$, $p = 0.298$, $\eta^2_p = 0.051$, but it was significantly different for ticking, $F(5, 115) = 2.690$, $p = 0.024$, $\eta^2_p = 0.105$. Post hoc tests with Bonferroni correction revealed phase coherence of ticking to be significantly lower for load level 3 compared to level 1, $t(23) = 4.445$, $p = 0.003$. With no correction, compared to load level 1, phase coherence of ticking was significantly lower for level 3, $t(23) = 4.445$, $p < 0.001$, for level 4, $t(23) = 2.186$, $p = 0.039$, for level 5, $t(23) = 2.501$, $p = 0.020$, and for level 6, $t(23) = 2.832$, $p = 0.009$. No significant interaction was found between load condition and load level, $F(5, 115) = 0.951$, $p = 0.451$, $\eta^2_p = 0.040$ for tapping, and $F(5, 115) = 1.390$, $p = 0.233$, $\eta^2_p = 0.057$ for ticking.

3.2.3 Phase coherence during pre-load, expecting-load and post-load: one-way repeated measures ANOVA with eight within-subject levels

Phase coherence did not significantly differ between pre-load dual task, expecting-load (levels 1 to 6), and post-load dual task conditions, $F(7, 161) = 0.382$, $p = 0.912$, $\eta^2_p = 0.016$ for tapping, and $F(7, 161) = 1.720$, $p = 0.108$, $\eta^2_p = 0.069$ for ticking (see Figure 5C). This indicates that the effect of expecting load on coordination stability between tapping and ticking was similar to that of no such expectation.

3.2.4 Phase coherence during pre-load, enduring-load and post-load: one-way repeated measures ANOVA with eight within-subject levels

Phase coherence did not significantly differ between pre-load dual task, enduring-load (levels 1 to 6), and post-load dual task conditions, $F(7, 161) = 1.410$, $p = 0.205$, $\eta^2_p = 0.058$ for tapping; it differed significantly for ticking, $F(7, 161) = 2.162$, $p = 0.040$, $\eta^2_p = 0.086$ for ticking (see Figure 5D). However, post hoc comparisons with Bonferroni correction revealed no significant difference for ticking. This indicates that concurrent visual pattern-matching did not affect coordination stability between tapping and ticking.

3.2.5 Phase coherence of tapping with walking and ticking - 2 x 2 repeated measures ANOVAs

Phase coherence of tapping, relative to walking and ticking, was significantly higher during dual task compared to single task, $F(1, 23) = 102.496$, $p < 0.001$, $\eta^2_p = 0.817$ for pre-load stage, and $F(1, 23) = 63.960$, $p < 0.001$, $\eta^2_p = 0.736$ for post-load stage. This indicates that tapping was more coordinated with walking and ticking when performed simultaneously than separately. Phase coherence of tapping was significantly higher with ticking compared to with walking, $F(1, 23) = 8.265$, $p = 0.009$, $\eta^2_p = 0.264$ for pre-load stage, and $F(1, 23) = 4.445$, $p = 0.046$,

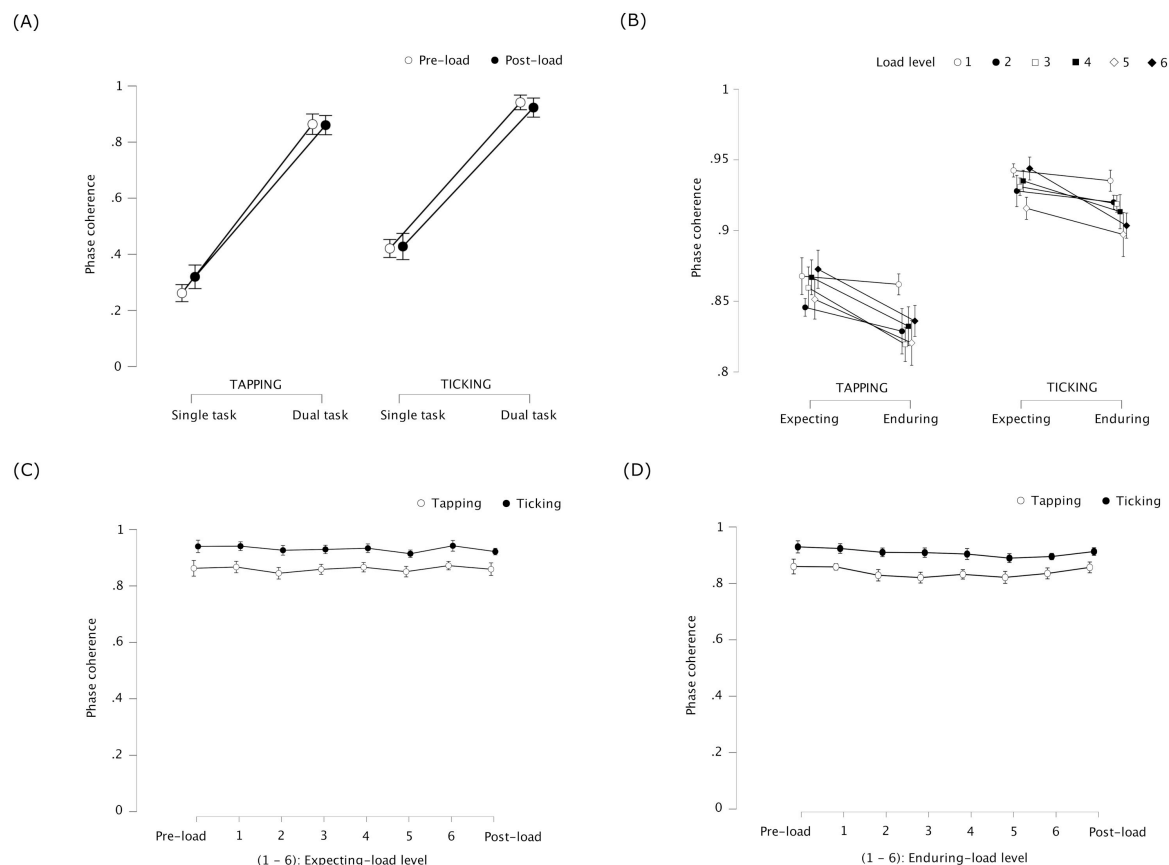


FIGURE 5

Experiment 2: phase coherence of tapping and ticking representing coordination stability between the periodic tasks – (error bars indicate standard error). **(A)** Single task / Dual task × pre-load stage / post-load stage – coordination stability increased between tapping and ticking when performed simultaneously (dual task) compared to separately (single task); coordination before cognitive load was introduced (pre-load) did not differ significantly from the same after load was removed (post-load). **(B)** Expecting-load / enduring-load × load level (1 to 6) – coordination stability decreased in the tapping-ticking dual task while enduring load compared to expecting load; the decrease did not significantly differ across load levels 1 to 6 (matching patterns of 4–9 blocks, respectively), except during level 3 when the coordination stability of ticking was significantly lower compared to level 1. **(C)** Pre-load dual task / expecting-load (level 1 to 6) / post-load dual task – coordination stability was similar in the tapping-ticking dual task between expecting cognitive load compared to not expecting load (pre-load and post-load). **(D)** Pre-load dual task / enduring-load (level 1 to 6) / post-load dual task – coordination stability was similar in the tapping-ticking dual task while enduring cognitive load compared to not (pre-load and post-load).

$\eta^2_p = 0.162$ for post-load stage. This indicates that tapping was more coordinated with ticking than with walking. There was a significant interaction between task condition (single task, dual task) and co-periodic task (walking, ticking), $F(1, 23) = 23.044$, $p < 0.001$, $\eta^2_p = 0.500$ for pre-load stage, and $F(1, 23) = 10.217$, $p = 0.004$, $\eta^2_p = 0.308$ for post-load stage. This indicates that tapping was more coordinated during dual task (compared to single task) with ticking than with walking.

4 Discussion

The current study investigated whether the stability of spontaneous intrapersonal coordination between periodic behaviors decreased more when walking was involved. In the dual task condition, at preferred rates, the stability of spontaneous coordination between finger-tapping and walking was significantly lower than that between finger-tapping and repetitive vocalization of the word “tick” (ticking). This finding is similar to that by Qi

et al. (2019), where no evidence of coordination was found between tapping and walking, although spontaneous coordination occurred between tapping and foot movements; in that study, tapping was at an unrelated given rate. Therefore, at both preferred as well as given rates, spontaneous coordination of tapping is lower with walking than with other periodic tasks. This finding supports the categorization of walking as a more complex cognitive task compared to other periodic tasks (Sheridan and Hausdorff, 2007; Hausdorff et al., 2005), as the additional attentional load involved in walking could have resulted in lower coordination stability between tapping and walking.

In both experiments conducted in the current study, spontaneous intrapersonal coordination between the periodic tasks was significantly higher when the tasks were performed simultaneously than separately, in line with past findings. Although the direction of change in coordination stability across conditions was similar in both experiments, the effect sizes indicated that the magnitude of such change was different. In the dual task condition, the coordination stability increased less

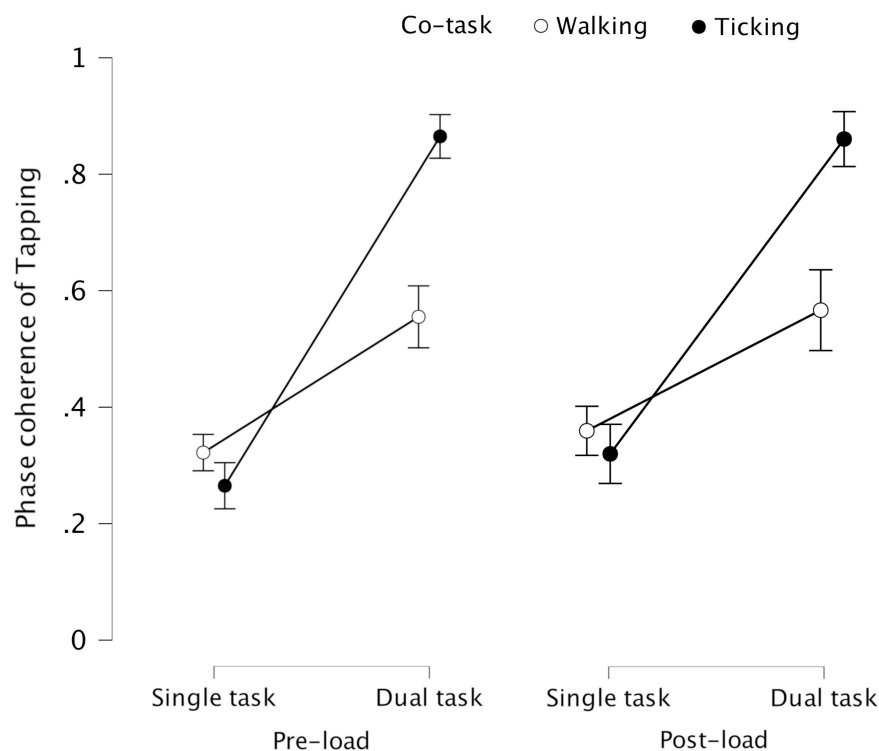


FIGURE 6

Phase coherence of tapping representing its coordination stability with walking and ticking in single task and dual task conditions across pre-load and post-load stages – (error bars indicate standard error) – The increase in coordination stability of tapping during dual task compared to single task was significantly greater with ticking than with walking, possibly due to higher attentional cost of walking.

between tapping and walking than between tapping and ticking (see Figure 6). This could have been due to additional attentional cost of walking rendering tapping-walking coordination more difficult to achieve. Also, with additional load through concurrent cognitive task, the coordination stability decreased more between tapping and walking than between tapping and ticking. This could be due to backward counting being more efficient than visual pattern-matching in causing task interference: tapping-walking coordination decreased more with concurrent backward counting in 7's than in 3's, whereas tapping-ticking coordination was unaffected by the difficulty level of concurrent pattern-matching. Alternatively, this could again be due to additional attentional cost of walking causing tapping-walking coordination to be more susceptible to task interference, implying the possibility of cognitive overload.

Cognitive overload occurs when cognitive load imposed by processing demands exceeds the available resources, and this happens in three scenarios (Mayer and Moreno, 2003). Firstly, overload can be due to excessive demands in “essential processing” relevant to the core demands of the task; this is equivalent to Cognitive Load Theory’s “intrinsic cognitive load” that is imposed by the nature of the presented task, such as an arithmetic problem (Sweller et al., 1998; Sweller, 2011). In the current study, counting backward in 3's and 7's as well as matching visual patterns may have caused cognitive overload, either on their own or in conjunction with maintaining periodic tasks at a constant rate, which also may need cognitive resources. Secondly, demands in “incidental processing” irrelevant to the core task, on top of the

essential processing demands, can cause overload; this is in line with Cognitive Load Theory’s “extraneous cognitive load” on top of “intrinsic cognitive load,” causing overload, where extraneous cognitive load is imposed by demands irrelevant to the core task, such as instructions that are hard to follow, or manner of task presentation, such as an illegible font in a reading comprehension task (Sweller et al., 1998; Sweller, 2011). In the current study, there were no obvious elements that fall into this category. Although participants needed to remember task instructions (e.g., to stay near to the microphone during ticking), these were not intentionally made to be difficult. Also, there were no coordination differences between the expecting-load condition and the pre-load or post-load stage, although they needed to remember additional task instructions while expecting load. Any extraneous load imposed by incidental processing demands are common in research, and seem reasonable enough not to be considered a cognitive overload risk. However, the possibility cannot be ruled out. Lastly, cognitive overload can be due to demands in “representational holdings” that refer to visual or auditory representations held in working memory (Mayer and Moreno, 2003). In the current study, the counting backward task required the participants to remember the current number in working memory (representational holding), until the next number was computed by applying the negative counter (essential processing); the visual pattern-matching task required them to remember the first pattern which was removed after a brief presentation (representational holding), until the second one was presented for comparison between the two patterns (essential processing). In both cognitive tasks, the combination of the

two demands, posed by essential processing and representational holdings, could have caused cognitive overload, rendering the required resources for coordination unavailable.

Intrapersonal coordination may involve similar processes to interpersonal synchronization. One system related to interpersonal synchronization is the error monitoring / correction system under the predictive coding framework (Shamay-Tsoory et al., 2019; Gebauer et al., 2016; Koban et al., 2019). In particular, interpersonal synchronization minimizes “coding costs by reducing the mismatch between the representations of observed and own motor behavior” (Koban et al., 2019, p.1). Based on this postulate, high cognitive load should increase spontaneous interpersonal synchronization (2019) to relieve cognitive resources to support the cognitive task. The converse of this prediction is supported by previous findings: interpersonal synchronization imposed intentionally improves cognitive performance on problem-solving and memory tasks (Miles et al., 2017; Valdesolo et al., 2010; Von Zimmermann and Richardson, 2016; Woolhouse et al., 2016). In the current study, though, intrapersonal coordination stability decreased overall under additional cognitive load, suggesting that this prediction about interpersonal synchronization may not extend to intrapersonal coordination. However, it is important to consider that coordination stability between tapping and walking was significantly lower during enduring load compared to expecting load, but not compared to dual task with no such expectation. This suggests a possible increase in coordination stability during expecting load compared to dual task with no such expectation (see Figure 4C). Such an increase would be in line with the aforesaid postulate by Koban et al. (2019) in which case, our findings could have been due to cognitive overload. It would therefore be interesting to test cognitive loads that tax the limited resources but avoid overload.

Furthermore, under the predictive coding framework, error correction activates the reward system (Shamay-Tsoory et al., 2019) and triggers dopamine / oxytocin release (Gvirts and Perlmutter, 2020) that may, in turn, improve interpersonal synchrony by increasing the salience of social cues between interacting partners (Gvirts Probolovski and Dahan, 2021). This reasoning is supported by oxytocin improving interpersonal synchronization (Gebauer et al., 2016), and dopaminergic deficits impairing interpersonal synchronization, for example, as in Attention Deficit Hyperactivity Disorder (ADHD) (Probolovski et al., 2021). Extending this to intrapersonal coordination, one could compare whether ADHD reduces intrapersonal coordination stability. In the current study, details of ADHD diagnosis were not collected from the participants, precluding any such comparison.

4.1 Limitations

The choice to use different cognitive tasks across the two experiments was due to the incompatibility of backward counting with repetitive vocalization. However, because of that, we could not meaningfully compare tapping-walking and tapping-vocalization in terms of coordination stability with concurrent cognitive tasks. Cognitive overload could have influenced the findings in the current study, masking any increase in spontaneous intrapersonal coordination under high cognitive load that is within the individual

cognitive capacities of the participants. A tailored approach could have improved cognitive load manipulation, where load levels for each participant would be titrated to their individual ability. Also, given that spontaneity was the primary focus of investigation in the study, a balanced split of musicians and non-musicians would have allowed us to examine whether formal music training affected spontaneous intrapersonal coordination.

4.2 Future directions

It would be interesting to examine the effects of age and music training on spontaneous intrapersonal coordination. The ability to synchronize with external stimuli, key to interpersonal synchronization, is not affected by aging (Turgeon et al., 2011), but it is helped by music training (Repp, 2010; Scheurich et al., 2018). Whether these results on aging and music training apply to spontaneous intrapersonal coordination as well would be a logical inquiry to make. To address the cognitive overload issue, a follow-up using cognitive tasks with lower processing demands would be informative. To reduce the cognitive demands of a task, minimizing the need for representational holding by presenting the task information simultaneously instead of sequentially has been recommended (Mayer and Moreno, 2003). This can be applied in the visual pattern-matching task by presenting both patterns simultaneously instead of sequentially. Another possibility is to use pre-experiment individualized assessment of cognitive load capacity for each participant (Mayer and Moreno, 2003; Elliott et al., 2009). Also, individual differences in cognitive load capacity could be used to predict individual differences in spontaneous intrapersonal coordination. Extending this to interpersonal interactions that involve individuals with a wide range of cognitive capacities, it would be interesting to test if individual cognitive capacities predict the level of interpersonal coordination. Given how intra- and interpersonal coordination may have the same underlying sensorimotor control mechanisms at the sub-movement level (Nazzaro et al., 2023), it would be reasonable to evaluate if such a chain of predictions is viable. While it is reasonable to intuit intrapersonal coordination stability to transfer to interpersonal coordination, it is also important to consider findings that show that the strength of intrapersonal coupling interferes with what is potentially an aspect in interpersonal coordination: Learning of unfamiliar coordination patterns (Annand et al., 2020); although this interference is more in individuals than in dyads, and manageable with training, it is a factor that needs consideration. Overall, it will be interesting to see if and how intrapersonal coordination unfolds as a microcosm of its interpersonal counterpart.

5 Conclusion

Spontaneous intrapersonal coordination appears to increase between periodic behaviors when performed simultaneously compared to separately, and this increase is less pronounced between tapping and walking than between tapping and ticking.

Also, additional cognitive load through a concurrent cognitive task decreases spontaneous intrapersonal coordination, and this decrease is more pronounced between tapping and walking than it is between tapping and ticking. Walking may be more cognitively demanding than ticking, thus more difficult to coordinate under additional cognitive load. Spontaneous intrapersonal coordination appears to be sensitive to the attentional costs of periodic behaviors and their coordination, thus may index cognitive capacity. Overall, the study demonstrates spontaneous intrapersonal coordination as a viable area of investigation into spontaneous coordination in general, and opens the door to further inquiry into how periodic behaviors interact within individuals.

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 humans were approved by Western University Non-Medical Research Ethics Board. The studies were conducted in accordance with the local legislation and institutional requirements. The participants provided their written informed consent to participate in this study.

Author contributions

RJ: Conceptualization, Formal Analysis, Investigation, Methodology, Project administration, Software, Visualization, Writing – original draft, Writing – review and editing. JG: Conceptualization, Formal Analysis, Funding acquisition, Methodology, Resources, Supervision, Writing – review and editing.

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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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