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Review

Together we sync: a systematic qualitative and quantitative review of fMRI hyperscanning studies

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Abstract

Social interaction relies on neurocognitive processes that support mutual prediction and coordination. Traditional neuroimaging investigates brain activity at the individual level, limiting insight into the reciprocal nature of social exchange. Hyperscanning overcomes this by simultaneously recording brain activity from interacting individuals. We conducted a systematic review of 28 functional magnetic resonance imaging (fMRI) hyperscanning studies examining inter-brain coupling during interactive tasks. We assessed study features and examined whether paradigms included four key properties that make the use of hyperscanning particularly valuable over single-brain designs: real-time reciprocity, mutual information flow, unpredictability, and irreproducibility. Substantial methodological heterogeneity was observed, and only a few studies incorporated all four theoretically relevant features. To identify consistent spatial neural patterns of inter-brain coupling, we performed coordinate-based hierarchical clustering on residual (task-independent) and task-evoked coupling data. The latter was further analysed in relation to the complexity of the interaction. Residual coupling consistently involved the right posterior superior temporal gyrus, overlapping with the anterior temporo-parietal junction (TPJ), suggesting a role in spontaneous alignment. Task-evoked coupling differed by interactional complexity, with posterior temporal regions involved in low-complexity tasks, and medial frontal, mid-cingulate, and insular areas in high-complexity ones. These findings support the relevance of fMRI hyperscanning for studying inter-brain dynamics and inform future methodological development.

Keywords: hyperscanning; fMRI; inter-brain coupling; interactions; dual brain

Introduction

Human social behavior is fundamentally interactive. Whether we are collaborating, competing, or simply having a conversation, our actions are shaped by the presence and responses of others. This responsiveness depends on our capacity to understand what others are thinking, anticipate their actions, and adjust our behavior accordingly – a set of processes broadly referred to as social cognition (Frith and Frith 2006). Social cognitive mechanisms support a wide range of outcomes, from joint action and cooperation (Sebanz et al. 2006) to manipulation and strategic behavior (Decety et al. 2004), underscoring their relevance across diverse social contexts.

Recent decades have seen growing interest in methods that better capture the complexity of real-world social interactions (Ochsner and Lieberman 2001, Frith and Frith 2010), driven in part by the limitations of traditional laboratory paradigms, which often isolate participants and overlook core features of everyday naturalistic social contexts (Richardson et al. 2008).

This methodological shift has given rise to the so-called ‘second-person neuroscience’, a field that examines the neural basis of social cognition as it emerges through dynamic, reciprocal interaction between individuals. Rather than focusing solely on intra-individual brain activity, this perspective emphasizes real-time inter-brain coupling as a core mechanism of social interaction (Schilbach et al. 2013, Redcay and Schilbach 2019).

The emphasis on reciprocity and neural coupling has prompted researchers to reconsider how social interaction is operationalized in neuroscientific research. To address this, Redcay and Schilbach (2019) proposed a continuum of experimental designs varying in their degree of reciprocal engagement. At the least interactive end is the third-person single-brain approach, in which a participant passively observes another person while only the participant’s brain activity is recorded. A step closer to interaction is the second-person single-brain approach, where the participant engages with a partner, yet only the participant’s brain is scanned, limiting the analysis to intra-individual processes. Moving into ‘true’ second-person territory, the sequential dual-brain design involves recording both participants’ brain activity in separate, turn-taking sessions. Finally, the simultaneous dual-brain approach, known as *hyperscanning*, captures real-time neural dynamics between interacting individuals, offering the most ecologically valid framework for investigating social exchange.

Defining hyperscanning

Hyperscanning can be implemented through different techniques, including electroencephalography (EEG), magnetoencephalography (MEG), functional near-infrared spectroscopy (fNIRS), and functional magnetic resonance imaging (fMRI). Over the past decade,

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the number of publications has steadily increased (Fig. 1a), with EEG and fNIRS dominating due to portability, affordability, and ease of implementation (Dumas et al. 2011). EEG provides unmatched temporal resolution, making it ideal to study fast interpersonal dynamics such as synchrony and turn-taking, but its signals are highly susceptible to artifacts from eye blinks, facial muscles, and body movements. fNIRS, although slower and restricted to cortical surfaces, offers greater tolerance to movement, enabling paradigms with higher ecological validity, such as during theatrical live performance (Greaves et al. 2022), nine-person ensemble drumming (Liu et al. 2021), breastfeeding (Bembich et al. 2024), or free play (Papoutselou et al. 2024).

In contrast, fMRI-based hyperscanning remains less common, possibly due to its higher technical demands, as well as the limited availability of multiple synchronized MRI scanners. These challenges are even more pronounced for MEG-based hyperscanning, which remains rare (Fig. 1b).

Researchers have also begun to combine hyperscanning with neurostimulation techniques such as transcranial alternating current stimulation (tACS) and transcranial direct current stimulation (tDCS) (Novembre et al. 2017, Szymanski et al. 2017, Liu et al. 2023, Long et al. 2023, Lu et al. 2023), neurofeedback (for a review, see Konrad et al. 2024), and biofeedback of autonomic signals such as heart rate, respiration, and skin conductance (Müller and Lindenberger 2011).

Importantly, all these techniques should not be viewed as alternatives but as complementary tools: only a multimodal perspective that integrates different methods, such as combining fNIRS with EEG to balance spatial and temporal resolution (Fronda and Balconi 2022; Balconi and Angioletti 2024), or MEG with EEG to exploit their complementary strengths (Ahn et al. 2018), can capture both the anatomical specificity, the temporal precision, and the ecological validity needed to address the full range of questions in social neuroscience.

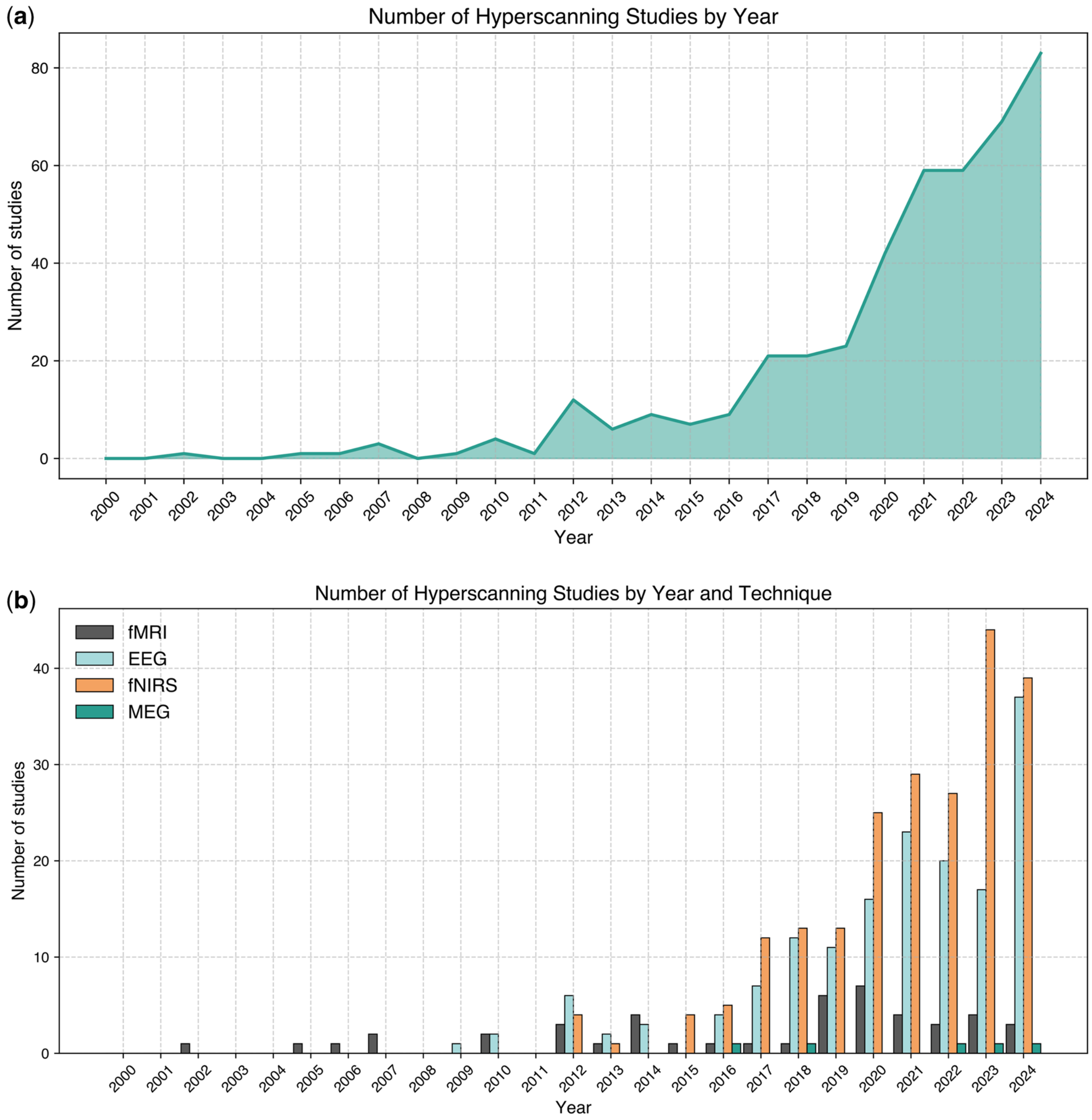

Figure 1. (a) Number of original hyperscanning studies published by year. (b) Number of original hyperscanning studies published by year and by techniques. These plots are based on the literature screening we conducted.

Rationale and criteria for using hyperscanning

Despite its promise, hyperscanning presents a core methodological challenge: distinguishing genuine inter-brain coupling that reflects reciprocal social interaction from spurious synchrony driven by shared sensory input, joint attention, or motor mirroring (Czeszumski et al. 2020, Holroyd 2022, Hakim et al. 2023). Addressing this issue requires careful consideration of both experimental design and analytical strategy.

To ensure that observed neural coupling reflects meaningful social exchange rather than parallel processing, several authors have proposed pivotal criteria to guide the conceptualization of experimental paradigms most suitable for making hyperscanning data theoretically meaningful.

A central requirement is the presence of real-time, reciprocal interaction in which individuals experience mutual engagement and recognize their actions as being directed toward and relevant for the other (Schilbach et al. 2013, Redcay and Schilbach 2019).

Tsoi et al. (2022) also emphasized the necessity of an active and dynamic social exchange, where individuals continuously adjust their behavior based on shared prior experiences and actively attempt to anticipate each other's thoughts and actions.

Bilek et al. (2022) further stressed that hyperscanning studies should aim to uncover causal relationships between brains, to explore the causal influence one brain may have on another. This includes investigating whether brain states are genuinely shared during interaction, the direction and timing of these shared activities, and how these processes are shaped by individual- and interaction-related factors.

Crucially, the focus should be on mutual adaptation and complementarity within social interactions, where neural signals from individual A serve as an input for individual B (and, possibly, vice-versa), influencing their thoughts, decisions, behavior, and eliciting corresponding neural responses (Przyrembel et al. 2012, Hasson and Frith 2016).

Finally, Misaki et al. (2021) highlighted the role of the unpredictability and of the dynamic nature of interactions, which give rise to transient and non-reproducible patterns of brain-to-brain coupling. These two features, incorporated into the task, may contribute to making the exchange more akin to everyday interactions, which are often characterized by unscripted, unpredictable, unique, and constantly evolving mutual influence.

In the absence of such features, the use of fMRI hyperscanning may be less meaningful, and simpler approaches such as sequential dual brain paradigms may be sufficient (see fMRI pseudo-hyperscanning studies such as Schippers et al. 2010, Dikker et al. 2014, Su et al. 2024).

Challenges and heterogeneity in fMRI-based hyperscanning

While EEG and fNIRS have dominated inter-brain research due to their accessibility and portability, fMRI offers unique advantages for investigating social interaction at the whole-brain level. Its high spatial resolution and ability to detect activity in deep and distributed brain networks enable a detailed mapping of the neural architecture underlying social processes, offering a degree of anatomical specificity not achievable with other modalities.

Since the first dual-scanner study (Montague et al. 2002), fMRI hyperscanning has demonstrated technical feasibility but remains methodologically demanding. Key challenges include low temporal resolution, susceptibility to motion artifacts, and logistical constraints such as synchronizing two scanners or maintaining a stable high-bandwidth connection across scanning sites. These limitations are further compounded by the limited ecological validity of the scanner environment, which can restrict the realism of face-to-face interaction.

Beyond technical constraints, the field is marked by considerable heterogeneity in both experimental paradigms and analytic strategies. Studies vary widely in the types of social behaviors they examine, from joint attention and mimicry to complex negotiation and cooperation. They also differ in how inter-brain coupling is quantified, using methods such as residual or task-based time-series correlation, beta-series correlation, cross-correlation with time lags, coherence analysis, and dynamic causal modeling.

This methodological diversity raises key conceptual and empirical questions. Do current fMRI hyperscanning studies truly capture the interactive dynamics they aim to investigate? How often do they meet the key features that fully exploit the fMRI hyperscanning's potential over single-brain designs? And can consistent spatial patterns of inter-brain coupling be identified across such varied paradigms?

This review aims to address these questions through an integrated qualitative and quantitative synthesis, offering a systematic classification of the existing literature.

Aim of the review and expected results

While different reviews on hyperscanning are already available, our contribution offers a distinct perspective. Previous works have mostly adopted narrative and conceptual approaches, discussing the promises and limitations of hyperscanning (e.g. Dumas et al. 2011, Koike et al. 2015, Wang et al. 2018, Czeszumski et al. 2020, Nam et al. 2020, Hamilton 2021). Others have focused on analytic methods (Hakim et al. 2023) or used scientometric bibliographical tools – such as citations, authorship, keywords – to map the field (Carollo and Esposito 2024). A few recent reviews have addressed fMRI hyperscanning more specifically, outlining its feasibility and constraints (Misaki et al. 2021, Tsoi et al. 2022). Yet, only one quantitative meta-analysis has gone beyond narrative approaches, synthesizing inter-brain findings from fMRI hyperscanning studies and directly comparing them with dual-fNIRS studies (Lotter et al. 2023). However, no prior work has systematically categorized fMRI hyperscanning studies based on the critical features of the interactive task and setting, nor provided a quantitative synthesis of inter-brain findings across fMRI studies by differentiating analysis types and evaluating the modulatory role of interactional complexity. This review addresses these gaps through a combined qualitative and quantitative approach. From a qualitative perspective, we first classified the studies according to their sample characteristics, task design, and analytical strategy, with particular attention to features shaping the nature of the social interaction, such as shared goals, role asymmetry, dyad composition, task/interaction complexity, visual access, and familiarity between participants.

We then examined the extent to which each study's paradigm incorporated the four key criteria defined above, which are thought to enhance the relevance of hyperscanning for studying social exchanges. We expected this classification to show that only a subset of existing fMRI hyperscanning studies fully meet the criteria for a second-person, dual-brain approach, particularly in capturing the unpredictable and irreproducible nature of social interaction as it unfolds during the task.

Importantly, this review is not intended as a critique of prior work, which has laid essential groundwork for the development of fMRI hyperscanning. Rather, our aim is to identify gaps that remain in the literature, to help guide future research toward task designs that better approximate real-world social interactions – those that are dynamic, evolving, and less constrained by predefined structures (Przyrembel et al. 2012, Hamilton 2021). By highlighting these areas, we hope to encourage further methodological innovation that builds on, rather than replaces, the valuable contributions of previous studies.

From a quantitative perspective, we used coordinate-based hierarchical clustering algorithms to identify brain regions that consistently exhibited inter-brain coupling. We also examined whether coupling patterns may vary based on the type of analysis employed and the complexity of the social exchange. By 'complexity of the interaction' we refer to the degree of cognitive, communicative, and strategic demands embedded in the interaction as operationalized in the experimental design. Based on this criterion, we divided the studies into two groups: one including tasks characterized by a low level of complexity, and the other comprising tasks with a higher degree. This classification was informed by theoretical accounts suggesting that more complex social interactions engage higher-order processes – such as mentalizing, high-level inferential processing, strategic and decisional adaptation, and socio-affective regulation – that are likely supported by distinct neural systems (Frith and Frith 2012, Schilbach et al. 2013). Categorizing tasks along this complexity axis enabled us to test whether inter-brain synchrony patterns vary as a function of low- vs. high-complex interactions.

We anticipated identifying a core set of brain regions consistently involved in inter-brain synchronization across studies, particularly in residual (spontaneous) coupling, with the right temporo-parietal junction (TPJ) as a likely candidate given its established role in social alignment (Redcay and Schilbach 2019).

For task-evoked coupling, we expected variability depending on the complexity of the interaction elicited by the task. Specifically, tasks eliciting simpler social interactions were expected to engage posterior temporal regions associated with perceptual and sensorimotor processes.

In contrast, tasks eliciting more complex and strategic social exchanges were anticipated to engage higher-order regions (medial prefrontal cortex, mid-cingulate cortex, anterior insula), reflecting greater inferential demands. Alternatively, inter-brain synchrony patterns might remain relatively consistent across levels of interactional complexity, indicating the presence of a robust core inter-brain coupling network even in minimal social contexts.

Materials and methods

This review was conducted in accordance with the PRISMA guidelines (Page et al. 2021). A detailed protocol was developed a priori to guide the review process, including eligibility criteria, search strategy, study selection, data extraction, and synthesis procedures (see *Data availability statement* section).

Information sources and search strategy

We systematically searched three electronic databases: PubMed, Embase, and Scopus. Final searches were completed in October 2024. Additional records were identified via citation tracking during the screening process.

We used a targeted yet inclusive search strategy to retrieve all studies referring to hyperscanning or to dual-fMRI approaches specifically. This allowed us to identify a comprehensive set of records, from which fMRI-specific studies were selected during screening. Search strategies were tailored to each database to optimize recall and precision.

- PubMed. We entered the following keywords: Hyperscanning [All Fields] OR ('dual-fMRI'[All Fields]) OR ('dual fMRI'[All Fields]). The search yielded 526 records.
- Embase. We entered the Emtree term 'hyperscanning'/exp, to include all narrower terms related to 'hyperscanning,' combined with a free-text search for 'hyperscanning.' The final query was: 'hyperscanning'/exp OR 'hyperscanning' OR 'dual-fMRI' OR 'dual fMRI.' The search yielded 539 records.
- Scopus: ALL (hyperscanning OR 'dual-fMRI' OR 'dual fMRI') AND (LIMIT-TO (SRCTYPE, 'j')) AND (LIMIT-TO (PUBSTAGE, 'final')) AND (LIMIT-TO (DOCTYPE, 'ar')) AND (LIMIT-TO (SUBJAREA, 'neur') OR LIMIT-TO (SUBJAREA, 'psyc') OR LIMIT-TO (SUBJAREA, 'soci')) AND (LIMIT-TO (LANGUAGE, 'english')). The search yielded 1213 records.

These queries identified a raw dataset of 2278 records. It was observed that the use of a hyphen in the keyword *dual fMRI* did not affect the number of records extracted. Therefore, for simplicity and clarity in the PRISMA flowchart (Fig. 2), only the term 'dual fMRI' is reported.

Selection process

The first screening phase involved reading titles and abstracts, including all articles written in English where hyperscanning was the main topic or where the approach involved simultaneous neurofunctional or physiological data acquisition, regardless of the specific technique used. This process also allowed us to differentiate between review articles, meta-analyses, and other types of non-empirical studies, such as methodological papers, opinion articles, commentaries, and conference proceedings. Records of interest were included if they met the following criteria:

- Design: Original empirical research;
- Language: Published in English;
- Population: Human participants;

Subsequently, from the empirical studies identified, a further selection process was conducted to pinpoint the fMRI hyperscanning studies, the focus of this review. Records were included according to the following criteria:

- Paradigm: Simultaneous dual-brain imaging (i.e. hyperscanning);
- Modality: Included or focused on fMRI-based hyperscanning;
- Analysis: Reported inter-brain connectivity or coupling analysis.

Studies were excluded if they used pseudo-hyperscanning paradigms (e.g. sequential scanning or simulated interaction), focused solely on feasibility without results, or lacked analytical treatment of inter-brain measures.

All search results were imported into Rayyan (https://www.rayyan.ai/) for deduplication and screening. Two independent authors (T.B., M.C.) conducted the initial screening. Disagreements were resolved through discussion or consultation with a third author (L.Z.). The same procedure was applied to full-text eligibility assessment. A PRISMA flow diagram (Fig. 2) outlines the selection process.

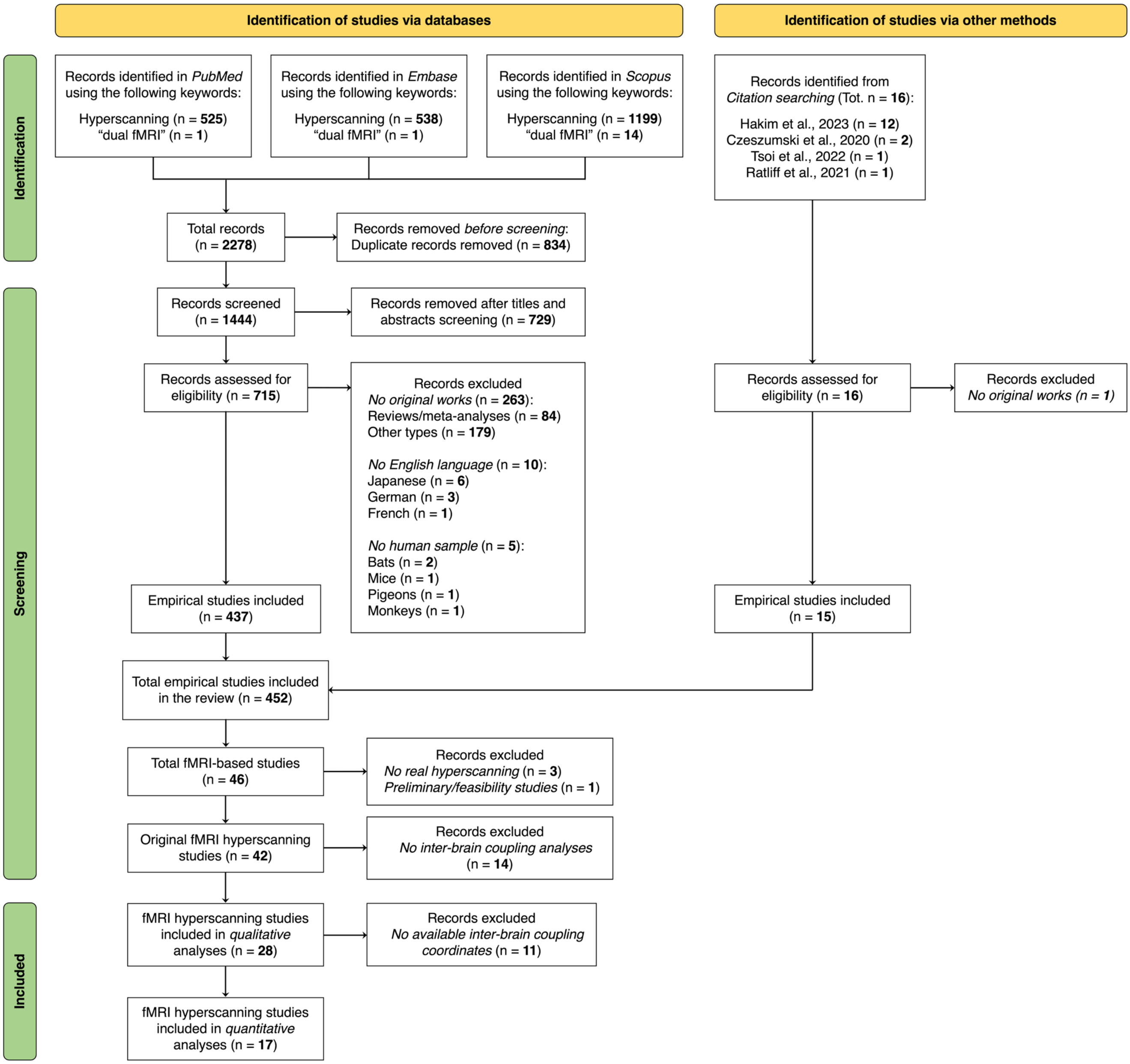

Figure 2. PRISMA flowchart, adapted from (Page et al. 2021), illustrating the identification, screening, and selection process for studies included in the qualitative and quantitative synthesis.

Results of search and final dataset

Of the 2278 records retrieved, 1444 remained after removing duplicates. Of these, 729 were excluded during title and abstract screening for not addressing hyperscanning or not involving simultaneous data acquisition. A further 278 were excluded after full-text review: 263 for not being original empirical studies (including 84 reviews or meta-analyses and 179 other types such as commentaries, methodological papers, pilot studies, conference papers, and abstracts); 10 for being in a language other than English; and 5 for involving non-human participants. This resulted in 437 empirical studies.

An additional 16 records were identified through citation tracking, one of which was later excluded, yielding a total of 452 studies.

From this pool, we selected fMRI-based hyperscanning studies. Forty-six records met initial inclusion criteria. One study (Montague et al. 2002) was excluded for focusing solely on feasibility, and three more for using pseudo-hyperscanning paradigms (e.g. sequential scanning). Only studies reporting inter-brain coupling analyses were retained, resulting in a final set of 28 studies for inclusion. Of these, 17 provided stereotactic coordinates and were included in the quantitative synthesis.

For each study we conducted a qualitative analysis of sample characteristics, task design, and analytic strategies. Two authors (T.B., M.C.) independently extracted key data, including publication details, sample size, imaging modality, paradigm, analysis methods, and stereotactic coordinates when available.

Qualitative assessment

Each study was systematically reviewed and categorized according to five main thematic domains:

1. **Characteristics of the experimental sample**. For each study, we recorded the final sample size used in inter-brain analyses (excluding outliers where applicable), gender composition, and whether participants were healthy or from clinical populations, specifying diagnoses where applicable. We also noted if samples overlapped with previous publications.
2. **Description of the experimental task**. Studies were classified based on the cognitive domain and the specific task used. We also categorized tasks as either naturalistic (e.g. face-to-face conversation) or computer-based, and described control conditions. A brief summary of task procedures was also included.
3. **Characteristics of the social interaction**. We documented whether the interaction involved a *shared goal*, the presence of *informational and/or role asymmetries* (e.g. sender–receiver), *visual access* to the partner (e.g. full face, eye contact, or no visibility), and whether any *verbal communication* was permitted. Additional variables included group size (e.g. dyads, triads), gender composition, prior acquaintance between participants, and – when available – the type of relationship (e.g. friends). Studies were also categorized based on how transparently participants could access the partner's outcome generation process, such as words, decisions, gaze movements: (a) direct observation of actions (e.g. seeing the partner actually playing a card); (b) indirect representations (e.g. seeing an avatar actually playing a card); (c) outcome-only scenarios (e.g. seeing a card appearing on the screen); and (d) no observable interaction (e.g. passive video viewing of others playing with no real-time interaction). Finally, we classified each study according to whether the task elicited a low or high level of interactional complexity.
4. **fMRI settings and inter-brain analyses**. We categorized each study based on scanner specifications, the specific analytical approach adopted to assess inter-brain dynamics (e.g. time-series correlation, cross-correlation, effective connectivity), and the eventual validation procedures used to assess the real brain synchronization within the interactive participants (e.g. re-randomized or permuted pairing). We also considered whether the analyses were conducted at a whole-brain level or focused on regions of interest (ROIs). In the latter case, we listed the specific ROIs. Characteristics of MRI scanners used in each study, scanning site information, and details on analytical validation procedures are reported in the online supplementary material.
5. **Added theoretical value of hyperscanning as a function of the interactive task.** Each experimental paradigm was assessed based on whether it met key features that make the use of hyperscanning over single-brain approaches particularly meaningful. As discussed in the introduction, these include real-time reciprocal engagement, mutual information inflow, and interaction dynamics inherently unpredictable and irreproducible. By real-time reciprocal engagement, we refer to online, ongoing interaction in which participants are actively involved and mutually responsive to each other's behavior. By mutual information inflow, we mean that individuals have access to behaviorally relevant signals from their partner, ensuring a continuous exchange of information – even if implicit (e.g. simply through visual access to the partner's face). By unpredictable, we mean the dynamic, non-deterministic, and unprogrammable influence of one's behavior on that of the other. This renders the course of the exchange inherently emergent, such that it cannot be fully anticipated or pre-scripted by task design constraints, allowing participants at least some degree of freedom in how they respond to, and are influenced by, each other's behavior. By irreproducible in repeated sessions we refer to the impossibility of replicating the same interaction across sessions, as each exchange is influenced by its unique temporal dynamics and the participants' relational history (Przyrembel et al. 2012, Schilbach et al. 2013, Hasson and Frith 2016, Redcay and Schilbach 2019, Misaki et al. 2021, Bilek et al. 2022, Tsoi et al. 2022, Hamilton 2021).

Quantitative assessment

We included the 17 studies reporting stereotactic coordinates and performed coordinate-based hierarchical clustering to identify regions showing inter-brain synchrony. Studies were classified as using either residual or task-based coupling analyses, and activation peaks were extracted accordingly. For task-based data, we also tested whether patterns of inter-brain synchrony varied as a function of social interaction complexity.

Analytical classification

To account for methodological differences, the dataset was divided into two groups based on the analytical approach:

- *Residual time-series correlation analyses*, also known as innovations analyses (Saito et al. 2010), which assess synchronization after removing task-related variance. The resulting residual signals are assumed to reflect spontaneous, intrinsic and shared neural dynamics that are per se not evoked by task characteristics.
- *Task-based coupling analyses*, which assess inter-brain synchronization directly tied to specific task conditions.

Data extraction

For each study, we extracted stereotactic coordinates of regions showing significant inter-brain coupling. All coordinates were reported in Montreal Neurological Institute (MNI) space. Three studies (Krueger et al. 2007, Wang et al. 2022, 2024) originally reported Talairach coordinates, which we converted to MNI space using the GingerALE transformation tool (version 3.0.2). Given the limited number of studies and activation peaks, we included all reported coordinates, regardless of whether they were derived from whole-brain or ROIs-based analyses.

Hierarchical clustering analysis

We used the unique-solution clustering algorithm developed by Cattinelli et al. (2013), implemented in the CluB MATLAB toolbox (Berlingeri et al. 2019).

This approach was selected for two main reasons. First, the limited number of fMRI hyperscanning studies with stereotactic coordinates reduces the feasibility of meta-analytic methods like Activation Likelihood Estimation (ALE). Second, hierarchical clustering enabled us to examine whether inter-brain coupling patterns varied by interaction complexity. Although it does not account for sample size or spatial uncertainty, it offers a pragmatic and theoretically grounded alternative suited to our aims.

CluB calculates squared Euclidean distances between reported foci and merges them recursively using Ward's criterion (Ward 1963), minimizing intra-cluster variance while maximizing the between-cluster sum of squares (Cattinelli et al. 2013). We set the maximum mean spatial variance within each cluster to 7.5 mm in all three spatial dimensions to approximate the typical spatial resolution of neuroimaging results (Berlingeri et al. 2019). Resulting cluster centroids were labeled using the Automatic Anatomical Labeling atlas (AAL, Rolls et al. 2020) and visualized in MRIcron (version 1.0.20190902).

Cluster composition analysis

To examine whether inter-brain coupling patterns varied with the complexity of the interaction elicited by the task, we performed a cluster composition analysis limited to the subset of studies that employed task-based coupling analyses. This restriction was necessary, as only task-based designs explicitly manipulated or measured features of interactional complexity.

Each task-based study was classified as eliciting either low- or high-complexity interactions. Tasks classified as low-complexity primarily elicited perceptual and reactive behaviors, with minimal engagement of inferential mechanisms (e.g. simple imitation or basic joint attention). In contrast, tasks classified as high-complexity elicited higher-order processes such as mentalizing, intention attribution, and socio-affective evaluation (e.g. trust-based decision-making).

For each cluster identified through hierarchical clustering, we calculated the proportion of foci associated with each level of interactional complexity and compared it to the expected distribution across the full task-based dataset. Binomial tests were then used to assess whether these proportions significantly deviated from chance, indicating whether specific brain regions were differentially recruited as a function of the complexity of the interaction.

Results

Qualitative assessment

This section includes detailed information on all key aspects of the included studies. For a more concise yet comprehensive overview, readers can refer to the corresponding tables and figures.

Characteristics of the experimental sample

The final sample across the selected fMRI hyperscanning studies comprised 1502 participants, including 469 males and 614 females (in 419 cases, gender was not reported), based on post-exclusion data. Of these, 1401 were healthy individuals (1366 adults and 35 adolescents), while 101 were from clinical populations. The clinical groups consisted of 21 individuals with autism spectrum disorder (Tanabe et al. 2012), 40 individuals with borderline personality disorder (17 in remission; Bilek et al. 2017), and 40 individuals with fibromyalgia (Ellingsen et al. 2020, 2022, 2023). See Table 1 and Fig. 3 for details.

Description of the experimental task

The included studies explored a broad range of cognitive and behavioral phenomena through diverse experimental paradigms. We classified tasks by cognitive domain, spanning from basic perceptual exchanges to more complex, goal-directed interactions such as cooperation, competition, and pain-related dynamics in patient–clinician contexts. See Table 2 and Fig. 3 for an overview.

Mutual gazing

Two studies examined mutual gaze as a foundational form of social interaction, in which participants simply looked at each other's faces. Koike et al. (2016) investigated whether joint attention training following mutual gaze enhances inter-brain synchronization and creates a pair-specific social memory trace. Koike et al. (2019a) compared neural and behavioral responses during live eye contact

Table 1. Demographic characteristics of each study, including sample size, gender distribution, and clinical conditions.

First author	Year	Final sample	Gender M/F	Condition	First author	Year	Final sample	Gender M/F	Condition
Koike	2019a	30 healthy adults	18/12	-	Ratliff	2021	35 healthy adults (parents) 35 adolescents	13/57	-
Koike	2016	94 healthy adults	44/50	-	Shaw	2020	54 healthy adults	54/0	-
Bilek	2015	76 healthy adults[a]	10/66	-	Špiláková	2020	38 healthy adults	22/16	-
Bilek	2017	80 healthy adults 40 BPD adults	0/120	Borderline Personality Disorder (current and remission)	Stolk	2014	54 healthy adults	54/0	-
Bilek	2022	84 healthy adults[b]	Ns	-	Xie	2020	36 healthy adults	20/16	-
Goelman	2019	54 healthy adults	0/54	-	Shaw	2018	38 healthy adults	38/0	-
Koike	2019b	See Koike, 2016		-	King-Casas	2005	96 healthy adults	Ns	-
Saito	2010	38 healthy adults	38/0	-	Tomlin	2006	136 healthy adults[d]	Ns	-
Tanabe	2012	21 healthy adults 21 ASD adults[c]	32/10[c]	High-functioning ASD	Krueger	2007	44 healthy adults	22/22	-
Yoshioka	2021	44 healthy adults	20/24	-	Wang	2022	66 healthy adults	Ns	-
Miyata	2021	32 healthy adults	10/22	-	Wang	2024	78 healthy adults	42/36	-
Abe	2019	37 healthy adults	Ns	-	Ellingsen	2020	17 healthy adult clinicians 17 adult patients	5/29	Chronic pain (fibromyalgia)
Spiegelhalder	2014	22 healthy adults	0/22	-	Ellingsen	2022	22 healthy adult clinicians 23 adults patients	7/38	Chronic pain (fibromyalgia)
Salazar	2021	40 healthy adults	20/20	-	Ellingsen	2023	See Ellingsen, 2022		Chronic pain (fibromyalgia)

Note. If gender information is not available (Ns = not specified), it is because the gender distribution was not reported in the final sample (after excluding outliers).
[a] The sample consisted of 26 participants from a preliminary discovery experiment and 50 from a subsequent replication experiment.
[b] In addition to the 84 participants, the authors also included 36 additional adults who had participated in a previous study (Bilek et al. 2017).
[c] In the study, the sample also included 19 additional pairs of healthy adults from Saito et al. (2010), who were subtracted from the counts of males and females.
[d] This study also included the 96 participants from King-Casas et al. (2005), which are not included in this count.

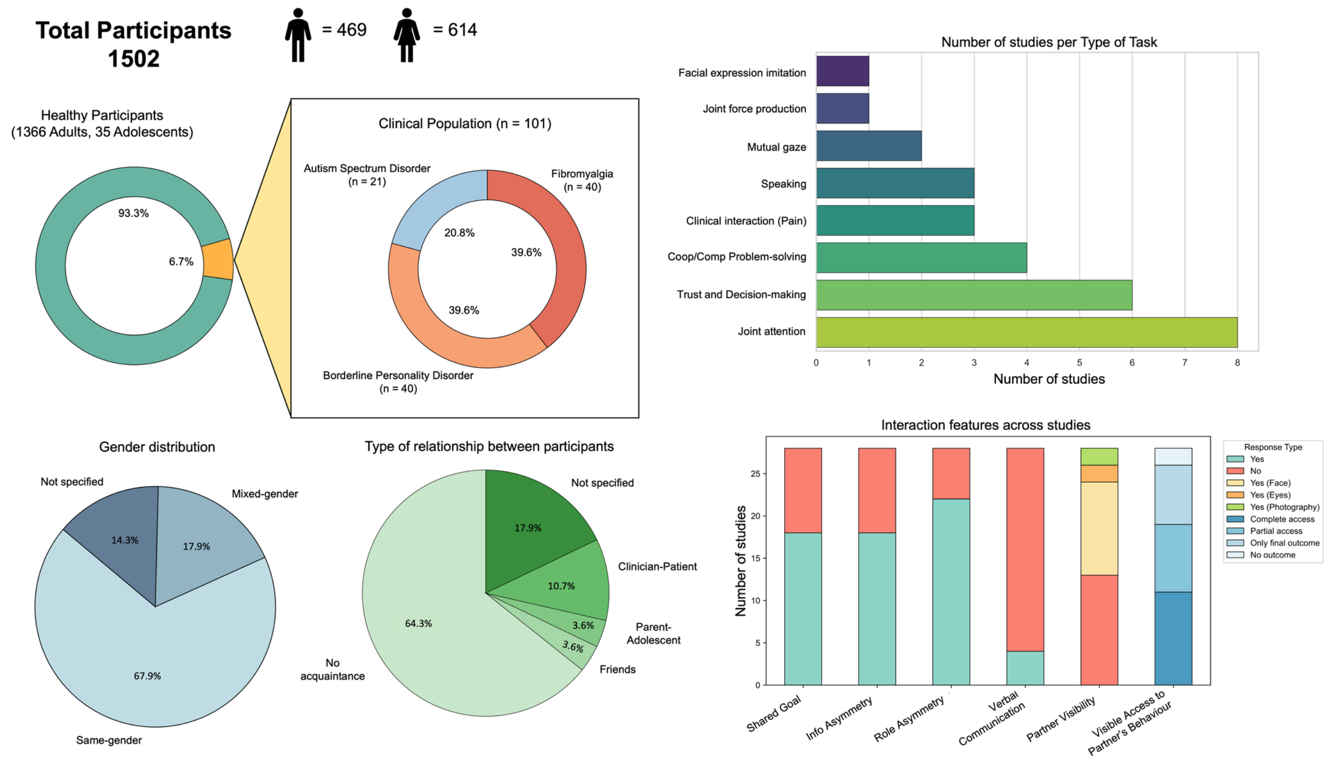

Figure 3. Summary of key qualitative features extracted from the included fMRI hyperscanning studies. The top left panel shows the total number of participants, their gender distribution, and the breakdown between healthy individuals and clinical populations. The two pie charts below summarize the gender composition of dyads and the type of relationship between participants. The top right bar chart reports the number of studies per type of experimental task. The bottom right panel illustrates the distribution of specific interaction features across studies, including shared goals, information and role asymmetries, verbal communication, partner visibility and the degree of access to the partner's behavior.

versus a delayed, non-interactive replay, isolating the effects of real-time mutual engagement.

Gaze-oriented and verbal-oriented Joint Attention

Eight studies explored joint attention as a non-verbally or verbally mediated mechanism for coordinating shared attention between individuals. Most employed gaze-based paradigms in which dyads alternated roles as sender and receiver: the former directed attention by looking at a target, while the latter inferred the target based on gaze cues (Saito et al. 2010, Tanabe et al. 2012, Bilek et al. 2015, 2017, 2022, Goelman et al. 2019, Koike et al. 2019b). These tasks were used to investigate clinical populations, including borderline personality disorder (Bilek et al. 2017) and autism spectrum disorder (Tanabe et al. 2012). In contrast, Yoshioka et al. (2021) employed a verbal joint attention task, where participants coordinated attention through spoken instructions rather than gaze, targeting spatial locations or object features.

Reciprocal imitation of facial expressions or joint force production

Two studies examined distinct forms of reciprocal imitation. Miyata et al. (2021) investigated real-time imitation of facial expressions with emotional valence (happy, sad, neutral), as participants alternated between expressing and mimicking their partner's facial cues. Abe et al. (2019) used a joint force-production task, where dyads had to match the average of their grip forces to a target in real time, adjusting one's own force based on their partner's input.

Speaking interaction

Three studies examined spoken social interaction, ranging from natural conversation to structured communicative games. Spiegelhalder et al. (2014) involved close female friends in live autobiographical storytelling. Ratliff et al. (2021) investigated parent–adolescent dyads engaged in conflict-resolution dialogues. Salazar et al. (2021) employed the 'Say the Same Thing' task, a joint-action game where participants aimed to say the same word simultaneously across rounds, fostering mutual prediction and semantic alignment.

Cooperative and/or competitive problem-solving

Four studies investigated goal-directed social interaction, spanning both cooperative and competitive contexts. Xie et al. (2020) used a multiplayer Pictionary-style game, where participants first drew action words individually and then collaborated by viewing each other's real-time sketches. Stolk et al. (2014) designed a communication task in which a Communicator guided an Addressee to recreate a target configuration on a digital board, involving both familiar (pre-trained) and novel (negotiated) signal mappings. Shaw et al. (2020) and Špiláková et al. (2020) employed the Pattern Game (Decety et al. 2004), in which a Builder reproduces a configuration of tokens either assisted by a Helper (cooperative condition) or sabotaged by a Hinderer (competitive condition).

Trust and decision-making

Six studies focused on trust, reciprocity, and strategic decision-making in interactive contexts. King-Casas et al. (2005)

Table 2. Overview of interactive experimental paradigms used in each fMRI hyperscanning study.

First author	Year	Domain	Task	Format	Task description	Control condition
Koike	2019a	Passive observation	Mutual gazing task	Naturalistic task	Participants watched their partner's face through a live video feed and were instructed to gaze at their partner's eyes and imagine what their partner was thinking	Delayed video of the partner's face
Koike	2016					No previous JA task and Video condition
Bilek	2015	Attention	Gaze-guided joint attention task	Naturalistic task	The Initiator (or Sender) spontaneously selected and fixated one of four target objects, while the Responder (or Receiver) followed the initiator's gaze to the same object	No joint interaction
Bilek	2017					No joint interaction
Bilek	2022					No joint interaction
Goelman	2019					Ns[a]
Koike	2019b					Designated-choice JA task and No joint interaction
Saito	2010				Participants viewed each other's eyes and two ball targets, and shifted their gaze either in response to their partner's eye movement or based on a change in ball colour. They were instructed to produce either concordant (same side) or discordant (opposite side) gaze shifts	Non-sharing attention Eye contact condition
Tanabe	2012					Non-sharing attention Eye contact condition
Yoshioka	2021		Verbal-guided joint attention task	Naturalistic task	One participant provided verbal cues to direct the other's attention toward a spatial location or object feature, which the responder then confirmed and identified	No joint interaction (Solo)
Miyata	2021	Reciprocal imitation	Partner's facial expression imitation task	Naturalistic task	One participant was assigned the role of Initiator and asked to display a happy, sad, or neutral facial expression; the other, as Responder, was instructed to imitate the Initiator's expression	Simultaneous facial expression (No imitation)
Abe	2019		Joint force production task	Computer-based task	Participants cooperatively matched their average grip forces to a target value by adjusting their individual force levels based on visual feedback	No joint interaction (Solo) and Watch-solo and watch-joint conditions
Spiegelhalder	2014	Speaking interaction	Live verbal interaction task	Naturalistic task	Participants alternately speak about autobiographical life events or listen to their partner speaking	Imagining autobiographical events
Salazar	2021		Say the same thing game		Participants independently selected and simultaneously spoke a word, aiming to progressively converge on the same word as their partner through iterative exchanges based solely on prior verbal responses	Last Letter game
Ratliff	2021		Conflict discussion task		Parent–adolescent dyads discussed their most frequent conflicts, describing the issues and collaboratively generating solutions	Ns
Shaw	2020	Cooperative competitive problem-solving	Pattern game	Computer-based task	Participants either cooperated or competed to recreate geometric patterns by sequentially placing coloured tokens on a board, alternating roles as Builder and either Helper, Hinderer, or Observer	No joint conditions (Solo and Observation)
Špiláková	2020					
Stolk	2014		Token movement communication task		The Communicator knew the target configuration and could only use token movements to guide the Addressee, who had to infer where and how to place her token to achieve the shared goal	Known interactions
Xie	2020		Drawing task (Pictionary)		Participants first independently drew assigned action words, then evaluated each other's drawings, and finally collaborated to redraw the words on a shared screen, taking turns and viewing each other's contributions in real time	Drawing control words (spirals)
Shaw	2018	Trust and decision-making	Iterated ultimatum game	Computer-based task	The Proposer selected one of two possible ways to divide a sum of money and offered it to the Responder, who then decided whether to accept or reject the offer within a time limit	No monetary exchanges/consequences
King-Casas	2005		Investment game		The Investor decided how much money to invest; the amount was then tripled and transferred to the Trustee, who determined how much to return to the Investor	Neutral investor reciprocity
Tomlin	2006					Motor and sensory tasks
Krueger	2007				Participants alternated roles as First Mover (deciding whether to trust) and Second Mover (deciding whether to reciprocate or defect) making monetary decisions within a binary game tree structure	No interaction condition
Wang	2022		Strategic cheap talk game		The Sender, knowing the reward probabilities for two boxes, advised the Receiver on which box to open. Rewards were shared in the cooperative condition or given only to the winner in the competitive condition	Ns
Wang	2024		Trust game		Participants jointly aimed to maximize rewards by alternating who received the larger payoff, through an initial communication stage followed by a final decision	Within-group non-interactive pairs
Ellingsen	2020	Pain and patient-clinician interaction	Pressure pain anticipation and treatment (acupuncture)	Naturalistic task	Patients received moderately painful and non-painful cuff-pressure stimuli to the left leg, while clinicians either applied or not remotely controlled electroacupuncture treatment	No previous clinical intake
Ellingsen	2022					No treatment and sham conditions
Ellingsen	2023		Pressure pain processing		Patients received a series of non-painful and moderately painful leg pressure stimuli, either alone or while interacting with a clinician via live video link	No interaction condition (Solo)

Note. Studies are categorized by cognitive domain, specific task, and experimental format, either naturalistic or computer-based. Each entry includes a brief description of the task procedure and the corresponding control condition. Ns = not specified.

[a] In Goelman et al. (2019), the implementation of a control condition is not specified; however, the study adopts the same paradigm used by Bilek et al., who did include a No-Interaction condition.

and Tomlin et al. (2006) employed multi-round trust games where one participant invested money and the other decided how much to return, enabling the examination of evolving patterns of cooperation and betrayal. Shaw et al. (2018) adapted an iterated Ultimatum Game, where participants alternated roles across rounds and adjusted offers based on prior outcomes. Krueger et al. (2007) used a sequential trust paradigm in which participants decided whether to trust or reciprocate, modeling turn-based contingency. Wang et al. (2022) implemented a strategic communication task based on a 'cheap talk' game, contrasting cooperative and competitive conditions where the sender could either guide or deceive the receiver in finding the reward inside one of two boxes. Wang et al. (2024) used a coordination game with asymmetric payoffs, requiring dyads to align decisions through an initial communicative phase followed by an outcome phase, allowing the study of strategic planning and achievement of balanced reciprocity.

Pain and patient-clinician interaction

Ellingsen et al. (2020) investigated inter-brain dynamics between fibromyalgia patients and acupuncturists, comparing conditions with or without a prior clinical intake to establish rapport. During scanning, patients received pain stimuli while clinicians either delivered real or sham electroacupuncture or remained passive. The study assessed how therapeutic relationship influenced behavioral mirroring and neural synchrony during pain anticipation. In a subsequent study (Ellingsen et al. 2022), the authors examined the role of facial expressions during treatment in shaping interpersonal concordance. The third study (Ellingsen et al. 2023) focused on the stimulation phase itself, comparing pain responses in solo versus interactive conditions and assessing how the presence of a trusted clinician shaped inter-brain synchrony during direct pain experience.

Characteristics of the social interaction

Group division, gender distribution, acquaintance, and type of relationship

Most studies involved dyadic interactions, with two exceptions: Xie et al. (2020), who examined triads during a joint drawing task, and Wang et al. (2024), who investigated trust dynamics among four participants interacting in rotating pairs (three scanned simultaneously, one unscanned).

Of the 28 studies, 19 (67.9%) controlled for gender when forming participant pairs. Some studies (e.g. Ellingsen et al. 2020, 2022, 2023, Xie et al. 2020, Ratliff et al. 2021) deliberately used mixed-gender dyads, while others (King-Casas et al. 2005, Tomlin et al. 2006, Wang et al. 2022, 2024) did not report gender composition.

In terms of prior acquaintance, over half the studies (64.3%) involved unfamiliar participants. Notable exceptions included parent–adolescent dyads (Ratliff et al. 2021), friend pairs (Spiegelhalder et al. 2014), and cases where a therapeutic alliance was established pre-experiment (Ellingsen et al. 2020, 2022, 2023). A few studies (e.g. Stolk et al. 2014, Bilek et al. 2015, Goelman et al. 2019, Xie et al. 2020, Wang et al. 2022) did not report on participants' prior familiarity. See Table 3 and Fig. 3.

Shared goals, information/role asymmetry, verbal communication, partner visibility, access to others' behavior, verbal communication and interaction complexity

We first assessed whether the task involved an explicit shared goal, defined as a collaborative outcome requiring coordinated contributions from all the agents involved in the interaction and that could not be achieved by single individuals. In 18 out of 28 studies (64.3%), the interaction was structured around such goals. These included gaze- and verbally guided joint attention tasks, where success depended on accurately aligning attention to a shared target; collaborative drawing tasks, where participants worked together to represent or guess a word; cooperative problem-solving tasks involving spatial or symbolic coordination; and joint motor tasks requiring synchronized effort (e.g. matching average grip force). No explicit shared goal was present in mutual gaze paradigms (Koike et al. 2016, 2019a), where participants simply looked into each other's eyes without pursuing an outcome. The same applies to simple storytelling tasks, based on alternating personal narratives, and to economic games (e.g. Trust Game, Investment Game, Ultimatum Game), in which each player aims to maximize their own monetary gain, potentially leading to conflicting interests or decisions based on distrust (King-Casas et al. 2005, Tomlin et al. 2006, Krueger et al. 2007, Shaw et al. 2018). Finally, an absence of an explicit shared goal is also evident in studies involving pain processing and anticipation in patient–clinician interactions (Ellingsen et al. 2020, 2023).

We also assessed information asymmetry, defined as a structural imbalance in knowledge that necessitates communication or inference. This feature was central to many joint attention tasks, either mediated by gaze (e.g. Bilek et al. 2015, Koike et al. 2019b) or verbal cues (Yoshioka et al. 2021), as well as narrative tasks, imitation, and semantic coordination (e.g. Salazar et al. 2021). More complex forms were evident in interactive games requiring spatial guidance (Stolk et al. 2014) or strategic decisions affecting joint outcomes (e.g. trust games). In contrast, studies based on mutual gaze (Koike et al. 2016, 2019a), joint force production (Abe et al. 2019), or the Pattern Game (Shaw et al. 2020, Špiláková et al. 2020) involved symmetrical information and shared access to task parameters.

Role asymmetry was present when participants had functionally distinct roles, as in clinician–patient (Ellingsen et al. 2020, 2023), parent–adolescent (Ratliff et al. 2021), or Builder–Helper/Hinderer dynamics in structured tasks (Shaw et al. 2020). At variance from the previous case, these asymmetries existed even when both parties had equivalent access to task information.

Verbal communication was allowed in only 4 of the 28 studies (14.3%) – specifically, in three speaking tasks (Spiegelhalder et al. 2014, Ratliff et al. 2021, Salazar et al. 2021) and one verbal joint attention task (Yoshioka et al. 2021). All other studies relied on nonverbal or indirect communication.

Partner visibility was permitted in 13 studies (42.4%), particularly in gaze-based interactions, imitation, and patient–clinician dyads. In contrast, decision-making studies often limited visibility, sometimes providing only a photo of the partner (e.g. Tomlin et al. 2006, Krueger et al. 2007).

Access to partner behavior also varied across studies. In some (39.2%), participants had full visibility into their partner's actions and responses in real time; in others, they saw only the outcomes (e.g. monetary decisions; 25%) or received indirect cues (e.g. via cursor movements or audio input; 28.6%).

Finally, tasks were classified as characterized low or high interaction complexity based on whether tasks primarily involved perceptual alignment or low-level inferential processes, versus higher-order inferential, strategic, or socio-affective demands. See Table 4 and Fig. 3 for a detailed overview.

fMRI settings and inter-brain analyses

Characteristics of MRI scanners used in each study, scanning site information, and details on analytical validation procedures are reported in the Supplementary Materials.

Table 3 Classification of each study based on key features of the social interaction embedded in the experimental design: number of participants interacting in real time, each group's gender division, acquaintance among participants, and the eventual type of relationship.

First author	Year	N° group members	Group division	Acquaintance between members	Type of relationship	First author	Year	N° group members	Group division	Acquaintance between members	Type of relationship
Koike	2019a	2	Same-gender	No	-	Ratliff	2021	2	Mixed-gender	Yes	Parent - Adolescent
Koike	2016	2	Same-gender	No	-	Shaw	2020	2	Same-gender[b]	No	-
Bilek	2015	2	Same-gender	Ns	-	Špiláková	2020	2	Same-gender	No	-
Bilek	2017	2	Same-gender[a]	No	-	Stolk	2014	2	Same-gender[b]	Ns	-
Bilek	2022	2	Same-gender	No	-	Xie	2020	3	Mixed-gender	Ns	-
Goelman	2019	2	Same-gender[a]	Ns	-	Shaw	2018	2	Same-gender[b]	No	-
Koike	2019b	See Koike, 2016		No	-	King-Casas	2005	2	Ns	No	-
Saito	2010	2	Same-gender[b]	No[e]	-	Tomlin	2006	2	Ns	No[d]	-
Tanabe	2012	2	Same-gender	No	-	Krueger	2007	2	Same-gender	No	-
Yoshioka	2021	2	Same-gender	No	-	Wang	2022	2	Ns	Ns	-
Miyata	2021	2	Same-gender	No	-	Wang	2024	4[c]	Ns	No	-
Abe	2019	2	Same-gender	No	-	Ellingsen	2020	2	Mixed-gender	Yes	Previous clinical intake
Spiegelhalder	2014	2	Same-gender[a]	Yes	Friendship	Ellingsen	2022	2	Mixed-gender	Yes	Previous clinical intake
Salazar	2021	2	Same-gender	No	-	Ellingsen	2023	See Ellingsen, 2022		Yes	Previous clinical intake

[a] Study sample composed of only female participants.

[b] Study sample composed of only male participants.

[c] Four participants—playing simultaneously but interacting in rotating pairs—three of whom were inside the scanners while the fourth was outside.

[d] In the personal version of the trust game, although participants were previously unacquainted, they met before the task, were instructed together, viewed a photo of their partner during each round, and saw each other again after the task when payments were made in each other's presence. In contrast, in the impersonal version, participants never met, had no opportunity for future interaction, and received no information about their counterpart.

[e] Participants were unacquainted with each other, except for 4 pairs whose members had prior exposure to one another. Ns = not specified.

Table 4. Classification of each study based on characteristics of the interactive setting, including the presence of a shared goal, informational and role asymmetries, type of role differentiation, partner visibility, verbal communication, and visible access to the partner's behavior and the level of interaction complexity characterizing the experimental task.

First author	Year	Shared goal	Info asymmetry	Role asymmetry	Type of role asymmetry	Partner visibility	Verbal communication	Visible access to partner's behaviour	Interaction complexity	Motivation
Koike	2019a	No	No	No	-	Yes (Face)	No	No outcome	Low	Mutual gaze paradigm characterised by high reliance on perceptual and nonverbal cues, with minimal engagement of inferential, strategic/decisional, or socio-affective processes.
Koike	2016	No	No	No	-	Yes (Face)	No	No outcome	Low	
Bilek	2015	Yes	Yes	Yes	Sender - Receiver	Yes (Face)	No	Complete access	Low	Gaze- and verbal-guided joint attention tasks primarily relied on perceptual alignment, with minimal demands for higher-order inferential processes such as advanced mentalizing, strategic reasoning, or socio-affective coordination.
Bilek	2017	Yes	Yes	Yes	Sender - Receiver	Yes (Face)	No	Complete access	Low	
Bilek	2022	Yes	Yes	Yes	Sender - Receiver	Yes (Face)	No	Complete access	Low	
Goelman	2019	Yes	Yes	Yes	Sender - Receiver	Yes (Face)	No	Complete access	Low	
Koike	2019b	Yes	Yes	Yes	Initiator - Responder	Yes (Face)	No	Complete access	Low	
Saito	2010	Yes	Yes	Yes	Ns	Yes (Eyes)	No	Complete access	Low	
Tanabe	2012	Yes	Yes	Yes	Ns	Yes (Eyes)	No	Complete access	Low	
Yoshioka	2021	Yes	Yes	Yes	Initiator - Responder	No	Yes	Partial access	Low	
Miyata	2021	Yes	Yes	Yes	Initiator - Responder	Yes (Face)	No	Complete access	Low	Facial expression imitation and joint force production tasks primarily engaging sensorimotor alignment and low-level perceptual processes. Structured nature of the tasks and minimal involvement of higher-order inferential, strategic, or socio-affective mechanisms.
Abe	2019	Yes	No	No	-	No	No	Partial access	Low	
Spiegelhalder	2014	No	Yes	Yes	Speaker - Listener	No	Yes	Partial access	Low	Storytelling task with alternating speaker and passive listener roles. Interaction followed a fixed structure, with minimal strategic adaptation or mutual behavioural adjustment and limited engagement of inferential or socio-affective mechanisms.
Salazar	2021	Yes	Yes	No	-	No	Yes	Only final outcome	High	Verbal cooperative task involving spontaneous, turn-based exchanges to converge on a shared concept. Engages mutual adaptation, semantic alignment, and perspective-taking, supporting inferential and interactive complexity.
Ratliff	2021	Yes	No	Yes	Adolescent - Parent	No	Yes	Partial access	High	Conflict discussion task involving alternating self-disclosure and active listening. Interaction was open-ended and emotionally meaningful, requiring affective engagement, empathy, and perspective-taking. High socio-affective demands with reciprocal adaptation to partner's verbal and emotional content.
Shaw	2020	Yes	No	Yes	Builder - Helper/Hinderer	No	No	Partial access	High	Strategic turn-based and concurrent interaction with mutual influence, requiring real-time mutual adaptation and mentalizing. High inferential and socio-cognitive demands beyond low-level perceptual alignment.
Špiláková	2020	Yes	No	Yes	Builder - Helper/Hinderer	No	No	Partial access	High	
Stolk	2014	Yes	Yes	Yes	Communicator - Addressee	No	No	Partial access	High	
Xie	2020	Yes	No	No	-	No	No	Partial access	High	

(Continued)

Table 4. Continued.

First author	Year	Shared goal	Info asymmetry	Role asymmetry	Type of role asymmetry	Partner visibility	Verbal communication	Visible access to partner's behaviour	Interaction complexity	Motivation
Shaw	2018	No	Yes	Yes	Proposer - Responder	No	No	Only final outcome	High	Trust- and reciprocity-based paradigms involving repeated reciprocal decisions, requiring intention attribution, strategic adaptation, and role-specific responses. The iterative structure and focus on partner-specific feedback engaged high-level inferential reasoning linked to high uncertainty and behavioural interdependence.
King-Casas	2005	No	Yes	Yes	Investor - Trustee	No	No	Only final outcome	High	
Tomlin	2006	No	Yes	Yes	Investor - Trustee	Yes (Photography)	No	Only final outcome	High	
Krueger	2007	No	Yes	Yes	Mover1 - Mover2	Yes (Photography)	No	Only final outcome	High	
Wang	2022	Yes	Yes	Yes	Sender - Receiver	No	No	Only final outcome	High	
Wang	2024	Yes	Yes	No	-	No	No	Only final outcome	High	
Ellingsen	2020	No	No	Yes	Patient-Clinician	Yes (Face)	No	Complete access	High	Paradigm involving real-time patient–clinician interaction during pain delivery, with emphasis on therapeutic alliance, empathy, and affective understanding. Required socio-affective evaluation and perspective-taking.
Ellingsen	2022	No	No	Yes	Patient-Clinician	Yes (Face)	No	Complete access	High	
Ellingsen	2023	No	No	Yes	Patient-Clinician	Yes (Face)	No	Complete access	High	

Note. 'Visible access to partner's behavior' refers to what participants can perceive of their experimental partner's actions: 'Complete access' indicates full visual access to the partner's behavior; 'Partial access' refers to indirect or mediated cues, such as cursor movements, token displacements, or auditory information from speech (e.g. hearing the partner's voice with its natural timing, pauses, hesitations or corrections, even in the absence of visual contact); 'Only final outcome' indicates access only to the partner's final choice or result; 'No outcome' indicates the absence of any observable behavior from the partner (e.g. during simple eye contact). Ns = Not specified: In Saito et al. (2010) and Tanabe et al. (2012), a role asymmetry is present, but the authors did not provide explicit labels (such as 'Sender' and 'Receiver') to define the roles of the participant who sends the information and the one who receives it.

Analytical approaches

This section outlines the analytical strategies used to assess inter-brain coupling, highlighting how they differ in processing time-series data, modeling neural dynamics, and quantifying between-brain relationships. Note that some studies employed multiple methods, contributing to more than one analytical category.

The most common was **time-series correlation analysis**, applied in 13 studies (46.4%). Of these, seven focused on *residual time-series* correlation, where task-related activity and nuisance regressors were modeled out to isolate task-independent fluctuations. The remaining residuals, or 'innovations,' were interpreted as reflecting spontaneous, potentially socially meaningful neural activity. Statistically, these residuals reflect structured variance unexplained by the task model. If consistently correlated across interacting pairs, they may capture endogenous neural alignment driven by shared internal states or implicit social processes (Saito et al. 2010, Tanabe et al. 2012). Five of these studies used a whole-brain approach (Saito et al. 2010, Tanabe et al. 2012, Koike et al. 2019a, Xie et al. 2020, Yoshioka et al. 2021), while two used ROI-based strategies. Abe et al. (2019) targeted the right anterior TPJ, and Koike et al. (2016) focused on the right middle temporal gyrus and the right inferior frontal gyrus to test whether the inter-individual neural synchronization, found through task-related time-series analysis, was merely due to eye-blink related brain activation while looking at the partner's face.

The remaining studies in this category used *task-related time-series*, rather than residuals, to examine inter-brain dynamics. These included whole-brain analyses (Koike et al. 2016, Shaw et al. 2018) and data-driven approaches based on spatial or temporal components from principal component analysis and group independent component analysis, rather than anatomical landmarks (Bilek et al. 2017, Shaw et al. 2020, Špiláková et al. 2020, Salazar et al. 2021). In contrast, Krueger et al. (2007) used an anatomically constrained ROI approach targeting the paracingulate cortex, septal area, and ventral tegmental area. Another set of studies employed **beta-series correlation analyses**, using whole-brain approaches (Koike et al. 2019b, Miyata et al. 2021, Yoshioka et al. 2021) or focusing on regions identified through prior whole-brain analyses (i.e. the right superior temporal gyrus; Stolk et al. 2014). In this method each trial is modeled separately using a distinct regressor, yielding trial-specific beta estimates for every voxel. These beta images are compiled into time series preserving the experiment's temporal structure. Pearson correlations are then computed voxel-wise across dyads and normalized via Fisher's r-to-z transformation.

Three studies by Ellingsen et al. (2020, 2022, 2023) employed a method known as **dynamic concordance**. In this approach, trial-by-trial parameter estimates (Z-statistics) were extracted from predefined ROIs in one participant and used as regressors in a second-level whole-brain GLM of their partner's data. This allowed the identification of brain regions in one individual whose activity dynamically predicted the trial-by-trial ROI activity of the other member of the dyad, capturing interpersonal neural alignment over time.

Six studies employed **time-lagged cross-correlation**, aligning one participant's brain signal with their partner's across temporal lags. This approach captures both simultaneous and delayed synchronization, reflecting the natural timing of social cues and responses. The approaches included ROI-based analyses directly targeting the cingulate and paracingulate cortex (Tomlin et al. 2006), or focusing on regions identified through prior General Linear Model analyses, as in King-Casas et al. (2005), who concentrated on the middle and anterior cingulate cortex and on the caudate nucleus. Other works employed whole-brain seed-to-voxel analyses, starting from the bilateral pre- and motor areas of the speaker (Spiegelhalder et al. 2014) or from the bilateral anterior insula, bilateral dorsolateral and ventrolateral prefrontal cortex, and bilateral amygdala (Ratliff et al. 2021). Another study adopted a more data-driven approach based on group independent component analysis (Bilek et al. 2015).

Coherence-based methods were also used in four studies, which examined inter-brain coupling in the frequency domain. Coherence reflects the consistency of phase and amplitude between two time-series across specific frequency bands. ROI-to-ROI coherence analyses targeted regions such as the right superior temporal gyrus (Stolk et al. 2014, Wang et al. 2022), right TPJ and left precuneus (Wang et al. 2022), while seed-to-voxel methods used regions such as the right TPJ as seeds (Wang et al. 2022, 2024). Additionally, Goelman et al. (2019) used an advanced coherence-based method combining wavelet transforms and nonlinear multivariate analysis, identifying directed information flows across four-node cortical networks during a joint attention task. This study focused on specific bilateral seeds, including the dorsomedial and ventromedial prefrontal cortex, TPJ, posterior cingulate cortex, superior temporal sulcus (STS), fusiform gyrus, and precuneus.

Finally, one study applied **hyperscanning Dynamic Causal Modeling** (Bilek et al. 2022) to assess effective connectivity between brains during a gaze-guided joint attention task. Each dyad's model included four nodes (right TPJ and medial prefrontal cortex from both participants), capturing within- and between-brain dynamics. Task role asymmetries were modeled as modulatory inputs, and Bayesian estimation with Parametric Empirical Bayes revealed consistent cross-brain connectivity patterns. See Table 5.

Added theoretical value of hyperscanning as a function of the interactive task

We assessed whether each experimental task embedded the features that make hyperscanning data most suitable for providing theoretically meaningful information on the neurophysiological correlates of inter-subjective social processes. These features include real-time mutual engagement, bidirectional information inflow, unpredictable behavioral dynamics, and irreproducibility of the interaction. According to the classification proposed by

Table 5. Summary of analytical methods used to assess inter-brain coupling across hyperscanning studies, categorized by type of analysis and listing representative studies.

Type of inter-brain analysis	Studies
Residual time-series correlation	Saito et al. (2010), Tanabe et al. (2012), Koike et al. (2016), Abe et al. (2019), Koike et al. (2019a), Xie et al. (2020), Yoshioka et al. (2021)
Task-related time-series correlation	Krueger et al. (2007), Koike et al. (2016), Bilek et al. (2017), Shaw et al. (2018, 2020), Špiláková et al. (2020), Salazar et al. (2021)
Beta-series correlation	Stolk et al. (2014), Koike et al. (2019b), Miyata et al. (2021), Yoshioka et al. (2021)
Dynamic concordance	Ellingsen et al. (2020, 2022, 2023)
Time-lagged cross-correlation	King-Casas et al. (2005), Tomlin et al. (2006), Spiegelhalder et al. (2014), Bilek et al. (2015), Ratliff et al. (2021)
Coherence-based analyses	Stolk et al. (2014), Goelman et al. (2019), Wang et al. (2022, 2024)
Hyperscanning Dynamic Causal Modeling	Bilek et al. (2022)

previous authors, such features are considered necessary to fully harness the unique potential of dual-brain imaging (Przyrembel et al. 2012, Schilbach et al. 2013, Hasson and Frith 2016, Redcay and Schilbach 2019, Misaki et al. 2021, Bilek et al. 2022, Tsoi et al. 2022).

Only the experimental paradigms from seven studies (25%) met al. four criteria. Notably, all included tasks incorporated the first two features – real-time reciprocal engagement and mutual information inflow. The aspects that appeared less consistently implemented were interaction unpredictability and irreproducibility in repeated sessions.

In Stolk et al. (2014), participants worked in pairs to collaboratively recreate a target configuration of tokens on a digital board. One participant (the 'Communicator') had access to the target layout and conveyed this information through spatial token movements, which the 'Addressee' interpreted and replicated. Crucially, there were no pre-defined signals or correct solutions; instead, each dyad developed spontaneous, pair-specific signal-meaning mappings, leading to the emergence of 'conceptual pacts' (i.e. shared interpretations negotiated and refined over time).

Ratliff et al. (2021) implemented a conflict discussion and resolution task involving parent–adolescent dyads. The interaction was open-ended and emotionally dynamic. Behavioral exchanges evolved in real time, shaped by each participant's responses and their prior relational history, resulting in an inherently unpredictable and non-replicable social interaction.

Other five studies focused on trust-based dynamics, primarily using investment games to explore how players' decisions were influenced by their partner's prior behavior, such as perceived fairness and the partner's past actions (Shaw et al. 2018), the gradual reputation-building between participants (King-Casas et al. 2005, Tomlin et al. 2006, partnership formation and maintenance between interacting agents (Krueger et al. 2007), or the development and achievement of perfect reciprocity through repeated decisions (Wang et al. 2024). They featured real-time, highly engaging interactions in which participants respond dynamically to one another; constant mutual information inflow; exhibited behavioral unpredictability shaped by mutual adaptation; and were irreproducible, as each interaction unfolded uniquely based on the dyad's evolving history and context. Table 6 summarizes which interaction features were included in each study.

Quantitative assessment

Residual time-series correlation analysis studies

We conducted a quantitative, coordinate-based hierarchical clustering analysis on six fMRI hyperscanning studies that examined residual (task-independent) inter-brain coupling. These included two studies on mutual gaze (Koike et al. 2016, 2019a), three on joint attention (two gaze-based; Saito et al. 2010, Tanabe et al. 2012; and one verbal-guided; Yoshioka et al. 2021), and one study on joint force coordination (Abe et al. 2019).

All but two studies used whole-brain approaches; Abe et al. (2019) employed a ROI analysis targeting the right anterior TPJ, and Koike et al. (2016) focused on the right middle temporal gyrus and right inferior frontal gyrus, regions identified in their previous task-related time-series correlation analyses. Notably, we included the study by Tanabe et al. (2012), which examined inter-brain coupling in both healthy dyads and mixed dyads composed of one participant with ASD and one neurotypical partner. We included the coordinate peak as it was found to be significant only in the healthy–healthy dyads compared to mixed dyads. The latter, moreover, did not exhibit significant inter-brain synchronization relative to pseudo-pairs.

Together, these studies reported 21 activation peaks reflecting significant inter-brain coupling.

The hierarchical clustering analysis revealed six clusters, each composed of 2–8 peaks. The average SD across clusters was 4.68 mm (x), 6.32 mm (y), and 6.86 mm (z), indicating spatial coherence of the identified clusters. These values indicate how much activation peaks spread and deviate from the cluster centroid along each spatial axis.

Two main inclusion criteria were applied to determine which of the identified clusters would be retained for interpretation. First, the spatial dispersion of activation peaks within each cluster was evaluated by calculating the mean + 1.5 SD along each axis. Clusters showing a dispersion value outside this range on any axis were excluded. Second, only clusters comprising activation peaks from at least two independent studies were retained for interpretation. This approach identified one anatomically coherent cluster in the right posterior portion of the superior temporal gyrus (3 peaks), falling within the anterior TPJ, and included contributions from different studies: anecdotally, these were on mutual gaze (Koike et al. 2016), joint force production (Abe et al. 2019), and verbal-guided joint attention (Yoshioka et al. 2021; see Table 7a and Fig. 4a). As the analysis was based on residual time series, task labels are reported for illustration only and do not imply causal links with clustering.

Despite the limited number of peaks, these findings suggest that residual coupling consistently emerges in temporo-parietal regions, supporting their role in spontaneous neural alignment related to shared internal states, social attention, and self–other distinction.

Task-based coupling analyses studies

We conducted a quantitative, coordinate-based hierarchical clustering analysis on 13 fMRI hyperscanning studies that examined task-related inter-brain coupling. These included studies using beta-series correlation (Koike et al. 2019b, Miyata et al. 2021, Yoshioka et al. 2021), task-based time-series correlation (Krueger et al. 2007, Koike et al. 2016, Shaw et al. 2018), cross-correlation (King-Casas et al. 2005, Tomlin et al. 2006, Spiegelhalder et al. 2014, Ratliff et al. 2021), and coherence analysis (Stolk et al. 2014, Wang et al. 2022, 2024). Notably, Yoshioka et al. (2021) and Koike et al. (2016) contributed to both residual and task-related datasets and were therefore included in both analyses.

Among these studies, three employed ROI-based analyses (Tomlin et al. 2006, Krueger et al. 2007, Stolk et al. 2014), three used seed-to-voxel approaches (Spiegelhalder et al. 2014, Ratliff et al. 2021, Wang et al. 2024), and one study combined ROI-to-ROI and seed-to-voxel analyses (Wang et al. 2022). Collectively, these studies yielded 214 activation peaks.

The hierarchical clustering analysis revealed 37 clusters, each composed of 2–16 peaks. The mean spatial dispersion across clusters was 7.32 mm (x-axis), 7.55 mm (y-axis), and 6.22 mm (z-axis), respectively.

As with the clustering of residual analyses, two inclusion criteria were applied for further interpretation: (i) spatial dispersion thresholds were calculated for each axis, retaining only clusters whose dispersion on each axis fell within the range of mean spatial dispersion + 1.5 SD; and (ii) clusters had to comprise activation peaks reported by at least two independent studies. Based on those criteria, we identified 27 clusters.

For the binomial analysis, studies were grouped by the level of interaction complexity. Low-complexity paradigms included mutual gaze, joint attention (gaze- or verbal-guided), facial imitation, joint force production, and simple storytelling. High-complexity

Table 6. Assessment of the added theoretical value of fMRI hyperscanning for each study based on key interaction features.

First author	Year	Domain	Task	Real-time reciprocal engagement	Mutual information inflow	Unpre-dictability	Irreproducibility across repeated sessions	Motivation
Koike	2019a	Passive observation	Mutual gazing task	Yes	Yes	No	No	The mutual gazing tasks employed in these studies fulfil the criteria of real-time reciprocal engagement and continuous mutual information flow, as participants interact online and have sustained access to each other's gaze and facial cues. However, the interaction remains highly structured and offers limited room for spontaneous behavioural adaptation or emergent dynamics. Consequently, it may not fully meet the criteria of unpredictability or irreproducibility across sessions, as the interaction follows a fixed and symmetrical script that does not allow participants' behaviors to dynamically shape or influence one another in an open-ended way.
Koike	2016			Yes	Yes	No	No	
Bilek	2015	Attention	Gaze-guided joint attention task	Yes	Yes	No	No	The gaze-guided joint attention tasks meet the criteria of real-time reciprocal engagement and mutual information inflow, as participants - with complementary roles - actively coordinate their gaze in real time, accessing behaviourally relevant cues from their partner. However, the structure of the task limits the emergence of unpredictable interaction dynamics.
Bilek	2017			Yes	Yes	No	No	
Bilek	2022			Yes	Yes	No	No	
Goelman	2019			Yes	Yes	No	No	
Koike	2019b			Yes	Yes	No	No	
Saito	2010			Yes	Yes	No	No	
Tanabe	2012			Yes	Yes	No	No	
Yoshioka	2021		Verbal-guided joint attention task	Yes	Yes	No	No	The verbal-guided joint attention task involves real-time interaction, in which one participant directs the other's attention through verbal cues, ensuring a mutual exchange of information. However, the interaction structure is constrained, with clearly defined roles and outcomes across trials. As a result, the communicative patterns and behavioural responses tend to be predictable and easily reproduced across sessions. While the task does require coordination, it lacks the spontaneous adaptation and dynamic evolution that characterize more naturalistic interactions.
Miyata	2021	Reciprocal imitation	Partner's facial expression imitation task	Yes	Yes	No	No	The facial expression imitation task features real-time engagement, complementary role dynamics, and mutual information exchange, with participants alternating between expressing and imitating emotional facial expressions. Nevertheless, the interaction remains highly structured, as the sequence of expressions is predetermined and therefore predictable. Opportunities for spontaneous adaptation or emergent behaviour are limited, reducing the degree of unpredictability in the interaction. Furthermore, the task appears to be standardized and replicable across sessions, which – while advantageous for experimental control – may reduce its sensitivity to more nuanced or context-dependent interaction dynamics.
Abe	2019		Joint force production task	Yes	Yes	No	No	The joint force production task requires real-time mutual adjustments and a shared motor goal, resulting in an engaging interaction characterized by reciprocal adaptation and mutual information exchange. Participants continuously monitor and adjust their force output in response to their partner's input to maintain a joint target, effectively simulating aspects of real-world motor cooperation. While the task offers strong experimental control and reproducibility across trials, its structured and time-locked nature may limit the emergence of spontaneous behavioural variability beyond the mechanical adjustments required by the task itself.

(Continued)

Table 6. Continued.

First author	Year	Domain	Task	Real-time reciprocal engagement	Mutual information inflow	Unpre-dictability	Irreproducibility across repeated sessions	Motivation
Spiegelhalder	2014	Speaking interaction	Live verbal interaction task	Yes	Yes	No	No	The task entails real-time verbal communication between partners, with alternating speaker and listener roles that foster engagement and a structured form of complementary exchange. While this setup allows for interpersonal coordination, the interaction structure remains relatively constrained, as participants follow a predetermined script with limited reciprocal influence or adaptive flexibility. As the interaction is prompted and consistent across sessions, it may prioritize reproducibility over spontaneity, potentially limiting open-ended behavioral variability.
Salazar	2021		Say the same thing game	Yes	Yes	Yes	No	The task involves dynamic and reciprocal verbal interaction, requiring participants to engage in real-time communication and achieve semantic convergence on the same word. It supports mutual prediction and continuous adaptation to the partner's behavior, thus clearly fulfilling the criteria of real-time reciprocal engagement and mutual information exchange. Its deliberately loose structure introduces variability and limits the extent to which responses can be pre-scripted, fostering a degree of interactional unpredictability. Nevertheless, the overarching structure and the strategic convergence process tend to remain relatively consistent across sessions, which may reduce overall irreproducibility.
Ratliff *	**2021**		Conflict discussion task	Yes	Yes	Yes	Yes	The conflict discussion task is real-time and highly engaging, as participants discuss emotionally relevant topics with immediate back-and-forth dialogue. The exchange is complementary allowing a constant information inflow, with asymmetric pre-established (parent-child) and more informal roles emerging naturally through turn-taking and perspective sharing. The interaction is inherently unpredictable, as the content and tone of the discussion are shaped moment by moment by the participants' responses. Finally, the task is irreproducible: each conversation reflects the unique relational history and dynamics of the dyad, and the emotional and behavioral trajectories cannot be identically recreated across sessions.
Shaw Špiláková	2020 2020	Cooperative competitive problem-solving	Pattern Game	Yes Yes	Yes Yes	Yes Yes	No No	The task entails real-time interaction and active engagement, as participants dynamically coordinate or interfere with one another's actions depending on the assigned condition. The interaction is complementary and role-dependent, requiring mutual behavioural adaptation and continuous information exchange. It retains a certain degree of unpredictability, as each player's actions directly influence their partner's decisions in real time. Nonetheless, the structure and objectives of the task remain stable and replicable across rounds and sessions, which may constrain the influence of relational history and limit the emergence of unique, context-dependent dynamics.
Stolk *	**2014**		Token movement communication task	Yes	Yes	Yes	Yes	The interaction is real-time and highly engaging, requiring participants to continuously interpret and respond to their partner's behaviour. It features asymmetrical yet complementary roles and fosters ongoing mutual adaptation and rich information exchange. The lack of predefined signals enhances unpredictability and necessitates the joint construction of meaning. As a result, each interaction becomes inherently irreproducible, shaped by the unique history of the dyad and the evolving conceptual pacts formed during the exchange.
Xie	2020		Drawing task (pictionary)	Yes	Yes	Yes	No	The collaborative drawing task entails real-time interactive engagement, as participants take turns contributing to a shared drawing while observing each other's input in real time. The alternating structure and shared goal foster complementary roles and mutual information exchange. The task supports reciprocal adaptation and joint improvisation. However, the influence of relational history is minimal, and the task can be reliably replicated across sessions with only minor variation.

(Continued)

Table 6. Continued.

First author	Year	Domain	Task	Real-time reciprocal engagement	Mutual information inflow	Unpre-dictability	Irreproducibility across repeated sessions	Motivation
Shaw *	**2018**	Trust and decision-making	Iterated Ultimatum Game	Yes	Yes	Yes	Yes	The iterated Ultimatum Game used represents a real-time and engaging social exchange, in which participants' decisions directly influence their partner's subsequent behaviour. The task features clear role asymmetry (Proposer vs. Responder) and complementary actions, with both participants adapting their strategy in response to prior outcomes. The interaction unfolds dynamically across multiple rounds, promoting the emergence of both positive and negative reciprocity. This mutual behavioural adaptation, shaped by the history of past choices and the perceived partner's fairness, introduce both unpredictability and irreproducibility.
King-Casas * **Tomlin** * **Krueger** *	**2005** **2006** **2007**		Investment game	Yes Yes Yes	Yes Yes Yes	Yes Yes Yes	Yes Yes Yes	The task involves real-time decision-making and continuous behavioural adaptation, with clearly asymmetrical roles (investor vs. trustee) that shape complementary and reciprocal actions. Participants' decisions evolve over repeated rounds, influenced by the partner's previous behaviors, allowing for the progressive construction of mutual expectations, reputations and partnership. The interaction is inherently unpredictable and irreproducible, as each round is shaped by prior outcomes, generating a unique dyadic history that cannot be exactly replicated across sessions.
Wang	2022		Strategic cheap talk game	Yes	Yes	Yes	No	The task involves real-time, engaging interaction with asymmetrical roles, as participants alternate between Sender and Receiver across trials. It features complementary exchanges, where one participant provides probabilistic suggestions and the other makes decisions accordingly. While the competitive condition introduces a certain degree of behavioural variability through strategic deception – thus partially fulfilling the unpredictability criterion – the cooperative condition remains more structured, with aligned interests and a fixed reward probability. Moreover, the task structure is highly consistent across sessions, placing limited emphasis on relational history and reducing the extent to which unique, context-dependent dynamics can emerge.
Wang *	**2024**		Trust game	Yes	Yes	Yes	Yes	The interaction is real-time and highly engaging, requiring participants to anticipate, coordinate with, and adapt to their partner's actions. It involves complementary roles in the decision-making process, with continuous mutual information inflow during both strategic planning and execution. The task exhibits a high degree of unpredictability, as outcomes emerge from dynamic mutual adaptation and strategy shifts over time. Crucially, it also meets the criterion of irreproducibility: the history of interaction significantly shapes future decisions, with participants' behaviour being uniquely influenced by fluctuating levels of trust and the gradual development of reciprocal expectations, rendering each session context-dependent and non-repeatable.
Ellingsen Ellingsen	2020 2022	Pain and patient-clinician interaction	Pressure pain anticipation and treatment (acupuncture)	Yes Yes	Yes Yes	Yes Yes	No No	The task features real-time reciprocal engagement via face-to-face nonverbal communication, primarily through spontaneous facial expressions. It enables continuous mutual information exchange, as patients' affective displays dynamically shape clinicians' responses. The interaction is inherently unpredictable, driven by individual variability in emotional expressivity, empathy, and pain communication styles. Nevertheless, the task remains highly structured and protocol-driven, with fixed roles and controlled timing, which may limit its irreproducibility across sessions.

(Continued)

Table 6. Continued.

First author	Year	Domain	Task	Real-time reciprocal engagement	Mutual information inflow	Unpre-dictability	Irreproducibility across repeated sessions	Motivation
Ellingsen	2023		Pressure pain processing	Yes	Yes	Yes	No	The task involves real-time, reciprocal engagement, as patients and clinicians interact via live video during pain stimulation, allowing for mutual responsiveness and exchange. Mutual information inflow is present, with patients conveying pain responses and clinicians dynamically modulating their empathic appraisal. The interaction supports a degree of unpredictability, as the clinician's reactions and patients' pain experiences vary depending on the ongoing social context and non-verbal cues. Nevertheless, the overall protocol is relatively standardized across sessions, with consistent procedures and interaction settings that may limit the emergence of unique, context-dependent dynamics and thus reduce irreproducibility.

Note. Each study was evaluated according to four key interaction features considered essential to fully exploit the potential of fMRI hyperscanning: (i) real-time reciprocal engagement, (ii) mutual information inflow, (iii) unpredictability, and (iv) irreproducibility across repeated sessions. The rightmost column provides a concise explanation of why each study did or did not include the interaction features in the task design. First authors' names of studies fulfilling all criteria are reported in **bold ***.

Table 7 Results of hierarchical clustering and cluster composition analyses of activation peaks associated with inter-brain coupling.

a. Hierarchical clustering of residual time-series correlation analysis studies

Centroid label	Left hemisphere			Right hemisphere			x SD	y SD	z SD	Number of studies	Number of peaks
	x	y	z	x	y	z					
Posterior superior temporal gyrus/ anterior temporo-parietal junction	-	-	-	61	−41	21	5.77	8.19	7.55	3	3

b. Hierarchical clustering and cluster composition of task-based coupling analyses studies

Centroid label	Left hemisphere			Right hemisphere			x SD	y SD	z SD	Number of studies	Number of peaks
	x	y	z	x	y	z					
Medial orbital superior frontal gyrus	−1	42	−7	-	-	-	10.07	2.65	8.08	3	3
Medial superior frontal gyrus	-	-	-	1	41	29	6.89	12.88	8.65	4	8
Middle frontal gyrus	-	-	-	36	39	34	6.89	7.15	4.14	3	6
Dorsolateral superior frontal gyrus	-	-	-	15	25	49	8.14	5.57	7	2	3
Anterior insula	-	-	-	42	24	1	5.85	9.21	6.03	5	16
Anterior insula	−41	19	−2	-	-	-	6.33	6	5.63	3	8
Middle cingulate cortex	−7	16	41	-	-	-	7.75	5.95	6.63	4	8
Precentral gyrus	-	-	-	46	1	42	5.01	9.04	9.15	3	8
Thalamus	-	-	-	1	−1	6	7.14	12.95	5.44	3	4
Middle insula	-	-	-	38	−2	11	6.22	5.45	7.15	3	10
Postcentral gyrus	-	-	-	64	−4	17	3.65	11.43	3.59	2	4
Precentral gyrus	−41	−6	51	-	-	-	1.29	4.11	2.22	4	3
Middle cingulate cortex	−2	−9	41	-	-	-	3	8.6	2.63	2	4
Postcentral gyrus	−53	−18	31	-	-	-	10.39	4.69	4.57	3	4
Superior temporal gyrus	-	-	-	54	−33	8	3.38	7.4	6.05	4	8
Middle temporal gyrus	-	-	-	60	−34	−13	2.16	5.32	7.09	4	4
Inferior parietal gyrus	-	-	-	41	−38	48	5.94	10.93	9.89	3	5
Supramarginal gyrus	-	-	-	60	−39	39	6.93	6.31	4.11	2	7
Middle cingulate cortex	−3	−41	36	-	-	-	5.18	7.7	7.34	3	7
Superior temporal gyrus	-	-	-	59	−49	20	5.43	3.18	6.54	4	7
Praecuneus	−9	−51	52	-	-	-	9.6	8.86	7.53	3	5
Middle temporal gyrus	-	-	-	48	−57	5	5.99	2.42	5.32	2	6
Superior parietal gyrus	-	-	-	16	−58	53	1.73	5.51	6.43	3	2
Superior occipital gyrus	-	-	-	28	−75	45	9.64	6.77	6.94	3	10
Middle occipital gyrus	-	-	-	42	−77	8	4.16	5.52	8.3	3	10
Inferior occipital gyrus	−26	−81	−7	-	-	-	9.95	5.69	9.93	4	11
Lingual gyrus	-	-	-	19	−82	−2	5.31	8.03	4.31	4	8

Note. For each cluster, the following information is reported: the anatomical label according to the AAL atlas, the centroid coordinates in MNI stereotaxic space (with SD), the number of activation peaks (foci) within the cluster, and the number of independent studies (≥2) contributing to the cluster. The areas identified through the binomial analysis are highlighted in **bold**.

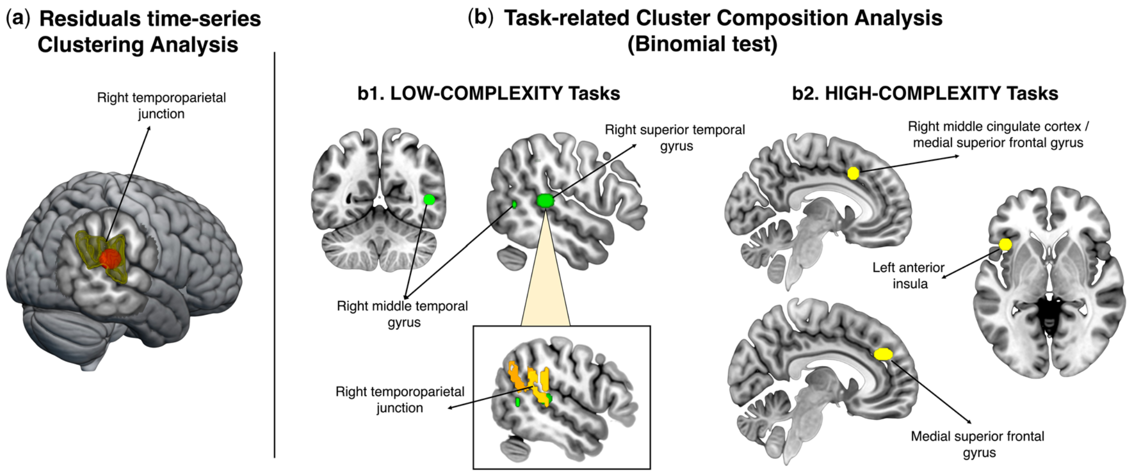

Figure 4. (a) Anatomical localization of the cluster identified through hierarchical clustering of activation peaks reported in residual time-series correlation studies. The cluster is located in the posterior portion of the right superior temporal gyrus, overlapping with the anterior part of the right TPJ (yellow). For the TPJ mask, we used the parcellation provided by Mars et al. (2012;https://www.rbmars.dds.nl/CBPatlases.htm). Visualization was performed using 3D render maps in MRIcroGL (version 12.6). (b) Clusters emerged from the binomial analysis. (b1) The clusters in the middle and superior temporal gyri were systematically associated with tasks involving lower social exchange complexity. The second cluster partially overlaps with the ventral portion of the anterior right TPJ (in yellow). (b2) Clusters became more involved as interaction complexity increased, including the medial superior frontal gyrus, the middle cingulum and the left anterior insula. Notably, all these clusters met both the inclusion criteria employed in the initial hierarchical cluster analysis. Visualizations were rendered using MRIcroGL (version 12.6) with the MNI152 template.

paradigms involved conflict resolution, cooperative or competitive problem-solving, trust, and strategic decision-making. See Table 4.

The binomial analysis revealed five clusters whose composition significantly reflected interaction complexity. To ensure robustness, we considered only those clusters that included activation peaks from at least two studies classified within the same level of complexity factor, toward which the cluster showed systematic recruitment. A cluster in the right posterior middle temporal gyrus showed a greater-than-expected proportion of peaks from low-complexity interactions (6 out of 6 peaks; prior likelihood = .318, *P* = .001), with contributions from two studies, including Koike et al. (2016) and Yoshioka et al. (2021). A second cluster in the right posterior superior temporal gyrus – in part overlapping with the ventral part of the anterior TPJ – (6 out of 8 peaks, prior likelihood = .318, *P* = .015), extending into the superior temporal sulcus, showed contribution from three studies (Spiegelhalder et al. 2014, Koike et al. 2016, Yoshioka et al. 2021). In contrast, three clusters were systematically recruited as interaction complexity increased and were exclusively composed of peaks derived from high-complexity interactions. The first cluster was located in the middle cingulate cortex (8 out of 8 peaks; prior likelihood = .682, *P* = .047), with contributions from four studies (King-Casas et al. 2005, Tomlin et al. 2006, Ratliff et al. 2021, Wang et al. 2022). The second cluster is located in the left mid-anterior insular cortex (8 out of 8 peaks; prior likelihood = .682, *P* = .047): the cluster contained peaks from three studies (Shaw et al. 2018, Ratliff et al. 2021, Wang et al. 2024). Finally, the third cluster was identified in the posterior part of the superior medial frontal gyrus (8 out of 8 peaks; prior likelihood = .682, *P* = .047), with contributions from four studies (Tomlin et al. 2006, Shaw et al. 2018, Ratliff et al. 2021, Wang et al. 2022). See Table 7b and Fig. 4b.

Discussion

This review offers an integrated synthesis of fMRI hyperscanning studies on inter-brain coupling during social interaction. Combining a systematic qualitative assessment with quantitative clustering analyses, we evaluated how current paradigms operationalize real-time interaction and whether consistent neural coupling patterns emerge across studies.

Our findings reveal increased attention to ecological validity, alongside substantial variability in task design and theoretical framing. In the following sections, we outline key neural convergence patterns, discuss differences in task interactivity, and highlight conceptual and methodological issues relevant for future research.

Neural convergence across paradigms: insights from hierarchical clustering analyses

Our hierarchical clustering analysis revealed patterns of spatial convergence that varied according to the type of inter-brain analysis and the complexity of the social interaction.

A central hub repeatedly identified is the right TPJ, encompassing the ventral supramarginal gyrus, angular gyrus, inferior parietal lobule, and posterior superior temporal sulcus (Mars et al. 2012, Bzdok et al. 2013, Quesque and Brass 2019). The right TPJ appeared both as a core cluster in residual analyses and as part of clusters associated with task-related studies, underscoring its pivotal role in neural alignment during social interaction.

This region is implicated in a wide range of cognitive functions (Eddy 2016), including multisensory integration (Matsuhashi et al. 2004), perspective-taking and imitation (Santiesteban et al. 2015), stimulus-driven attentional reorienting (Corbetta et al. 2008), external attribution of agency (Sperduti et al. 2011), self-other distinction (Quesque and Brass 2019), and higher-level theory of mind and social cognitive processes (Schurz et al. 2014, Donaldson et al. 2015, Redcay and Schilbach 2019). The same region is the core lesion site for the spatial neglect syndrome (Bisiach et al. 2000).

A recent meta-analysis (Merchant et al. 2025) suggests a functional subdivision within the TPJ: the anterior-ventral portion appears to be more strongly associated with social interaction – namely, contingent and reciprocal exchanges between individuals in which each partner's actions influence the other – whereas the dorsal-posterior TPJ is more engaged during social engagement, defined as the subjective emotional experience of being involved with, and aware of, a social partner, whether real or perceived. The predominance of anterior-ventral TPJ involvement in our results suggests that the observed inter-brain coupling may reflect processes of active interpersonal coordination rather than mere social engagement.

The TPJ is part of the Default Mode Network (DMN; Schilbach et al. 2008), a network consistently implicated in inter-brain coupling during social interaction. For instance, during communication tasks such as storytelling or teaching, DMN activity becomes synchronized between speaker and listener – an effect that is stronger when communication is effective and when participants share social closeness (Yeshurun et al. 2021). Moreover, the central role of the right TPJ in interpersonal neural synchronization is reinforced by Lotter et al. (2023), who identified it as part of a broader co-activation network including bilateral frontotemporal cortices, the insulae, dorsolateral prefrontal cortices, supplementary motor areas, and the thalami – regions collectively implicated in theory of mind, action observation, attention, and social interaction. These converging findings suggest that posterior right TPJ engagement during inter-brain coupling may support the alignment of cognitive states necessary for effective communication and coordinated behavior.

Aside from its significant involvement highlighted from the quantitative analyses, it is worth mentioning that this region emerges as a central hub of inter-brain coupling in several hyperscanning studies that were not included in the clustering analyses because they lacked information about peak stereotactic coordinates (Bilek et al. 2015, 2017, 2022, Goelman et al. 2019, Špiláková et al. 2020, Xie et al. 2020, Salazar et al. 2021). Notably, this area (61, −41, 21) also overlaps with the cluster identified in the previous fMRI hyperscanning ALE meta-analysis (62, −48, 16; Lotter et al. 2023), underscoring strong convergence across approaches. However, in the same work, Lotter et al. (2023) also reported an fNIRS-based TPJ cluster located more anteriorly, encompassing more anterior portions of the middle and superior temporal gyri.

Binomial analyses revealed the involvement of the posterior portion of the middle and superior temporal gyri in interaction contexts characterized by low levels of complexity. The second cluster included the superior temporal sulcus and, in part, overlaps with the ventral part of the anterior TPJ. These regions appear to overlap with areas implicated in attentional processes dedicated to interpreting overt social cues, such as actions and behaviors, making them key components of a social attention system that monitors and aligns with social partners (Arioli and Canessa 2019, Merchant et al. 2025). Moreover, these areas are thought to integrate both sensory inputs from the partner's behavior and efference copies of one's own actions, thereby enabling the detection of contingency between self- and other-generated behavior (Redcay et al. 2010, Koike et al. 2016, 2019a).

The convergence in posterior temporal regions observed in low-complexity interactions within our dataset is consistent with their role in processing externally available social information from a 'social space,' particularly in contexts where interaction is structured, predictable, or turn-based. The engagement of these regions likely reflects participants' reliance on overt behavioral cues in order to guide attention, actions, and low-order mentalizing mechanisms (David et al. 2008, Bzdok et al. 2013).

With the increase in interaction complexity, inter-brain coupling reliably engages higher-order regions such as the posterior superior medial frontal cortex and the anterior mid-cingulate cortex. These areas are implicated in adaptive cognitive control and performance monitoring, particularly in response to errors and unexpected outcomes (Ridderinkhof et al. 2004), as well as in distinguishing between self- and other-generated actions during social exchanges (King-Casas et al. 2005, Tomlin et al. 2006). These regions are also sensitive to task contingencies, including outcome evaluation and reward uncertainty (Rushworth and Behrens 2008, Shaw et al. 2018), and are functionally linked to the posterior superior temporal sulcus, supporting the integration of social information in dynamic contexts (Apps et al. 2013). Their consistent involvement in high-complexity paradigms may thus reflect the cognitive demands of strategic coordination, dynamic goal monitoring, and mutual adaptation under conditions of unpredictability.

Another brain region associated with higher social interaction complexity is the left anterior insula. This region is involved in the affective aspects of reciprocity during social decision-making (Shaw et al. 2018), in processing both cognitive and emotional stimuli to promote emotion regulation (Ratliff et al. 2021), and in general, insular regions represent a critical hub for empathy, facilitating the understanding and sharing of others' emotional experiences and social affects (Golland et al. 2017, Uddin et al. 2017, Corradi-Dell'Acqua et al. 2020). Taken together, these findings point to the insula's potential as a bridge between cognitive and affective domains of inter-brain coupling, helping to sustain the shared emotional context that supports effective social interaction.

Beyond identifying convergent brain regions, it is crucial to integrate these findings with insights from studies that incorporated all key features of interaction, as they provide compelling evidence on the cognitive mechanisms underlying social exchanges. Experimental paradigms based on trust and reciprocity games (King-Casas et al. 2005, Tomlin et al. 2006, Krueger et al. 2007) show that inter-brain coupling in cingulate and striatal circuits supports key social processes, including monitoring reciprocity, tracking reputation, detecting expectation violations, and adapting flexibly to a partner's intentions.

In communicative interaction settings, Stolk et al. (2014) showed that neural coherence in the right superior temporal gyrus reflects the joint negotiation of shared meanings. Their findings suggest that mutual understanding does not arise from isolated signals but from pair-specific brain synchronization that builds across interactions, supporting the view that successful communication relies on shared conceptualizations rather than simple signal priming.

Extending to economic decision-making, Shaw et al. (2018) showed that in repeated exchanges, reciprocity is supported by inter-brain alignment in the anterior insula and cingulate, reflecting neural mechanisms that sustain fairness evaluations and guide adaptive responses to a partner's behavior.

Within family interactions, Ratliff et al. (2021) showed that parent–adolescent cross-brain connectivity in socio-emotional networks, particularly the anterior insula, relates to emotion regulation and adolescent internalizing symptoms, highlighting the role of synchrony in affective development. At the level of dyadic coordination, Wang et al. (2024) reported that right TPJ-related coupling tracked reciprocal exchanges and predicted higher joint rewards, pointing to interpersonal dynamics as a mechanism for achieving shared benefits and emphasizing the TPJ's central role in sustaining alignment.

Taken together, these studies converge on a set of regions – including the anterior insula and cingulate for socio-emotional evaluation and regulation, temporo-parietal areas (right superior temporal gyrus, right TPJ) for communication and alignment during cooperation – that anchor the neural computations underlying social exchanges. In this way, fMRI hyperscanning emerges not merely as a methodological extension of single-brain research but as a theoretical framework that reveals the interpersonal computations at the core of human social cognition.

While previous efforts have begun to address consistent spatial patterns of inter-brain coupling across hyperscanning studies (Lotter et al. 2023), our quantitative synthesis represents an additional step forward in identifying consistent spatial patterns of neural coupling, though several limitations must be acknowledged. First, our hierarchical clustering analyses included only a subset of eligible studies, which limits the generalizability of the findings. Second, considerable heterogeneity across studies – in terms of task design, interaction features, and analytic strategies (e.g. inter-brain coupling methods, ROI vs. whole-brain approaches) – introduces variability that may limit spatial convergence. Third, our classification of interaction complexity, while grounded in theoretical considerations, remains partly subjective and will benefit from further refinement as the field evolves. Notably, the binary classification adopted here likely oversimplifies the multidimensional nature of social interaction, an unavoidable constraint given the current limited number of studies. Fourth, while we reviewed a broad range of analytical techniques, it is important to acknowledge that some of these methods were originally developed for modalities with higher temporal resolution than fMRI. The relatively slow sampling rate of the BOLD signal may limit the temporal precision required to interpret inter-brain synchrony or causality claims robustly. As such, findings based on these techniques should be interpreted cautiously and ideally integrated with complementary evidence from higher-temporal-resolution modalities such as EEG. Moreover, while inter-brain coupling is a valuable index of shared neural activity, it typically reflects undirected associations and does not imply causality. Only one study (Bilek et al. 2022) used hyperscanning Dynamic Causal Modeling to examine directed influences between brains – a promising yet underused approach that deserves further exploration. On a final note, although we included all eligible studies regardless of outcome, potential publication bias remains a concern and should be addressed in future meta-analytic efforts.

Despite these constraints, we believe this work represents a step towards a more cumulative and integrative perspective on fMRI hyperscanning. In particular, the observed dissociation between clusters as a function of interaction type and analytical approach may encourage future studies to integrate these dimensions, through whole-brain or data-driven methodologies capable of capturing the distinct neurofunctional mappings underlying social interaction.

How interactive are current hyperscanning paradigms

Our qualitative review revealed considerable variability in the extent to which current fMRI hyperscanning studies engage participants in genuinely interactive social exchanges. Only a subset of paradigms fully incorporated the four key features defined above (Schilbach et al. 2013, Hasson and Frith 2016, Redcay and Schilbach 2019, Tsoi et al. 2022). The studies that met these criteria often involved open-ended communication (Ratliff et al. 2021), strategic decision-making (King-Casas et al. 2005, Tomlin et al. 2006, Krueger et al. 2007, Shaw et al. 2018), or iterative cooperation (Stolk et al. 2014, Wang et al. 2024), where participants could continuously influence each other's behavior. In these contexts, mutual responsiveness and co-regulation were central to task performance, creating the kind of dynamic coupling that hyperscanning is uniquely positioned to capture (Misaki et al. 2021).

By contrast, other studies have employed tasks that emphasized structured or mirrored behaviors, such as synchronized actions, scripted exchanges, or fixed turn-taking. While these designs ensure high experimental control and can provide valuable insights into shared cognitive processes, they may offer more limited opportunities for real-time behavioral adaptation and mutual unpredictability – features often considered central to dynamic social interaction and which contribute to making each exchange unique and unrepeatable. Considering these aspects is essential for advancing the field and for addressing key questions about the interpretive value of hyperscanning: indeed, when both participants are engaged in identical or highly structured activities without influencing each other, observed neural synchrony may simply reflect shared stimulus processing or task timing rather than true interpersonal alignment (Bilek et al. 2022, Holroyd 2022).

Another important aspect that remains relatively underexplored is the behavioral dimension of progressive co-regulation and mutual evolving influence as it unfolds during interaction. While inter-brain synchrony is frequently interpreted as a neural marker of social coordination, few studies have directly assessed the extent to which participants adapt their behavior to one another in real time. This includes dynamic adjustments such as timing, turn-taking, strategic shifts, or the gradual emergence of shared goals. Incorporating such behavioral measures could help clarify whether neural synchrony reflects not only shared task structure, but also the quality and dynamics of the social exchange itself.

Beyond current paradigms: what fMRI hyperscanning has yet to capture

Beyond task interactivity, our review highlights several underexplored areas in current fMRI hyperscanning research. Even studies with interactive features cover a limited range of social behaviors and contexts, restricting insights into inter-brain dynamics in naturalistic settings.

The majority of the available research has concentrated on a few core interaction types, primarily joint attention, where participants coordinate their focus on a common target, and trust-based decision-making, which investigates reciprocal economic or strategic exchanges. While these domains are fundamental to social cognition, they represent only a fraction of the rich repertoire of human social behavior. To deepen our understanding of interpersonal neural dynamics, it is imperative that future studies broaden the spectrum of social interactions under examination. For example, empathy-driven interactions (Tsoi et al. 2022), which involve shared emotional experiences and affective attunement, could provide invaluable insights into how neural coupling supports emotional understanding and social bonding.

Similarly, exploring the neural correlates of reciprocal social inclusion and exclusion could illuminate the dynamics of social acceptance, ostracism, and their cognitive-affective consequences. Additionally, real-time negotiation and persuasion tasks, which inherently require strategic adaptation and complex communication, represent fertile ground for investigating the interplay of higher-order cognitive and affective processes within dyads, harnessing the full potential of hyperscanning methods.

Beyond the types of social tasks studied, several contextual factors have received little attention in fMRI hyperscanning research. One such factor is the degree of prior acquaintance between interacting individuals. Although EEG and fNIRS studies have examined how inter-brain synchrony varies between strangers, friends, and romantic partners, similar investigations are scarce in fMRI hyperscanning. This is a significant gap, as familiarity likely modulates the depth and nature of neural coupling during social exchanges, influencing trust, empathy, and communication dynamics. Another pivotal but underutilized variable is the presence of hierarchical or asymmetric social roles, such as those found in teacher-student, clinician-patient, or leader-follower relationships. Understanding how status and power differentials shape inter-brain connectivity would deepen insights into real-world social interactions. Visual access to the partner during scanning also remains inconsistent. Providing participants with visual contact may reduce the artificial constraints of the MRI environment, enhancing ecological validity and enabling more naturalistic interaction studies.

Finally, fMRI hyperscanning has seen limited application to clinical populations or studies explicitly targeting social dysfunction. Aside from a few pioneering works focusing on pain processing and treatment in patient–clinician dyads (Ellingsen et al. 2020, 2022, 2023), only a handful of studies have explored altered social cognition in clinical groups. For instance, Bilek et al. (2017) demonstrated reduced inter-brain synchrony in individuals with borderline personality disorder, despite no detectable anomalies in individual brain structure or function. This finding underscores the added value of two-person neuroscience in capturing social deficits that might be invisible to traditional single-subject approaches or the dyadic dynamics in patient-to-clinician relationships. Expanding hyperscanning research in clinical contexts may hold important potentials for translational neuroscience.

Beyond current paradigms: what fMRI hyperscanning cannot capture

While fMRI hyperscanning provides high spatial resolution and access to deep brain structures, it is constrained by low temporal resolution, immobility of the scanner environment, and limitations in allowing natural face-to-face engagement (Glover 2011). These factors make it challenging to investigate more ecologically valid social interactions. EEG and MEG, by contrast, offer excellent temporal resolution and, with the advent of mobile EEG and MEG systems, increasing opportunities for studying more naturalistic interactions (Melnik et al. 2017, Michel and Brunet 2019). However, EEG and MEG are associated with relatively lower spatial resolution/indeterminacy compared to fMRI. fNIRS occupies an important intermediate position: although limited to cortical surfaces and with lower spatial resolution than fMRI and lower temporal resolution than EEG or MEG, it is highly mobile, more tolerant of movement artifacts, and particularly well suited to capturing real-life, ecologically valid social exchanges (Quaresima and Ferrari 2019, Liu et al. 2021, Greaves et al. 2022, Bembich et al. 2024, Papoutselou et al. 2024). Importantly, fMRI research can build on this body of work by adopting or adapting designs already developed in fNIRS hyperscanning – such as persuasion or creativity tasks (Mayseless et al. 2019, Zhang et al. 2023) – thereby bridging ecological validity with anatomical specificity. In this way, the integration of fMRI, fNIRS, and EEG will provide a more complete framework for understanding interpersonal neural dynamics.

At the same time, it is worth noting that the broader opportunities for implementing ecologically valid, real-life paradigms with fNIRS may also contribute to differences in the neural patterns reported across modalities, thereby enriching our understanding of inter-brain coupling. For example, in their multimodal meta-analysis, Lotter et al. (2023) reported fNIRS-based activations in the left inferior frontal gyrus and in a more anterior portion of the TPJ – compared with the more posterior region identified in the present study – which did not emerge in our hierarchical clustering analysis. This anterior shift may partly reflect methodological constraints of each modality, in particular the resolution constraints of fNIRS versus fMRI with greater sensitivity for cortical surface as opposed to deeper brain structures such as the insula or the cingulate cortex, which we do find involved in our analysis. Moreover, they also highlight how the increased ecological validity afforded by fNIRS designs can uncover complementary aspects of interpersonal neural dynamics.

Conclusions

This review provides a systematic synthesis of fMRI hyperscanning studies on social interaction, combining qualitative and quantitative analyses. We identified consistent inter-brain coupling in temporo-parietal and frontal regions, modulated by interaction complexity. While many studies only partially implement features needed to exploit dual-brain imaging fully, this highlights opportunities for future research to adopt more interactive, ecologically valid designs.

Addressing underexplored dimensions will be key to advancing the field. Despite current limitations, fMRI hyperscanning uniquely captures how brains connect and coordinate during real social exchanges, offering valuable insight into the neural basis of human interaction.

Preregistration

The study was not preregistered.

CRediT statement

Tommaso Berni (Conceptualization [equal] , Data curation [equal], Formal analysis [equal], Funding acquisition [equal], Investigation [equal], Methodology [equal], Resources [equal], Software [equal], Supervision [equal], Validation [equal], Visualization [equal], Writing—original draft [equal], Writing—review & editing [equal]), Lucia Maria Sacheli (Conceptualization [equal], Data curation [equal], Formal analysis [equal], Funding acquisition [equal], Investigation [equal], Methodology [equal], Resources [equal], Software [equal], Supervision [equal], Validation [equal], Visualization [equal], Writing—original draft [equal], Writing—review & editing [equal]), Maria Cicirello (Data curation [supporting], Methodology [supporting], Visualization [supporting], Writing—original draft [supporting], Writing—review & editing [supporting]), Marco Tettamanti (Conceptualization [equal], Data curation [equal], Funding acquisition [equal], Investigation [equal], Methodology [equal], Supervision [equal], Validation [equal], Visualization [equal], Writing—original draft [equal], Writing—review & editing [equal]), Eraldo Paulesu (Conceptualization [equal], Data curation [equal], Formal analysis [equal], Funding acquisition [equal], Investigation[equal], Methodology [equal], Resources [equal], Software [equal], Supervision [equal], Validation [equal], Visualization [equal], Writing—original draft [equal], Writing—review & editing [equal]), and Laura Zapparoli (Conceptualization [equal], Data curation [equal], Formal analysis [equal], Funding acquisition [equal], Investigation [equal], Methodology [equal], Resources [equal], Software [equal], Supervision [equal], Validation [equal], Visualization [equal], Writing—original draft [equal], Writing—review & editing [equal])

Supplementary Material

Supplementary data is available at SCAN online.

Conflict of interest: The authors declare no conflicts of interest.

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Data availability

All data used in this study, comprising the full screening dataset, the list of stereotactic coordinates included in the quantitative analyses and the PRISMA protocol, are openly available on Open Science Framework (OSF) at https://osf.io/pgb3c/.

References

Abe MO, Koike T, Okazaki S *et al.* Neural correlates of online cooperation during joint force production. *Neuroimage* 2019;**191**:150–61. https://doi.org/10.1016/j.neuroimage.2019.02.003

Ahn S, Cho H, Kwon M *et al.* Interbrain phase synchronization during turn-taking verbal interaction—a hyperscanning study using simultaneous EEG/MEG. *Hum Brain Mapp* 2018;**39**:171–88. https://doi.org/10.1002/hbm.23834

Apps MA, Lockwood PL, Balsters JH. The role of the midcingulate cortex in monitoring others' decisions. *Front Neurosci* 2013;**7**:251. https://doi.org/10.3389/fnins.2013.00251

Arioli M, Canessa N. Neural processing of social interaction: coordinate-based meta-analytic evidence from human neuroimaging studies. *Hum Brain Mapp* 2019;**40**:3712–37. https://doi.org/10.1002/hbm.24627

Balconi M, Angioletti L. Inter-brain entrainment (IBE) during interoception. A multimodal EEG-fNIRS coherence-based hyperscanning approach. *Neurosci Lett* 2024;**831**:137789. https://doi.org/10.1016/j.neulet.2024.137789

Bembich S, Castelpietra E, Bua J *et al.* Cerebral synchronization between mothers and their newborns during breastfeeding. *Breastfeed Med* 2024;**19**:725–33. https://doi.org/10.1089/bfm.2023.0307

Berlingeri M, Devoto F, Gasparini F *et al.* Clustering the brain with "CluB": a new toolbox for quantitative meta-analysis of neuroimaging data. *Front Neurosci* 2019;**13**:1037. https://doi.org/10.3389/fnins.2019.01037

Bilek E, Ruf M, Schäfer A *et al.* Information flow between interacting human brains: identification, validation, and relationship to social expertise. *Proc Natl Acad Sci USA* 2015;**112**:5207–12. https://doi.org/10.1073/pnas.1421831112

Bilek E, Stößel G, Schäfer A *et al.* State-dependent cross-brain information flow in borderline personality disorder. *JAMA Psychiatry* 2017;**74**:949–57. https://doi.org/10.1001/jamapsychiatry.2017.1682

Bilek E, Zeidman P, Kirsch P *et al.* Directed coupling in multi-brain networks underlies generalized synchrony during social exchange. *Neuroimage* 2022;**252**:119038. https://doi.org/10.1016/j.neuroimage.2022.119038

Bisiach E, Vallar G. Unilateral neglect in humans. In: Boller F, Grafman J (eds.), *Handbook of neuropsychology*, Amsterdam: Elsevier, 2000, 459–502.

Bzdok D, Langner R, Schilbach L *et al.* Characterization of the temporo-parietal junction by combining data-driven parcellation, complementary connectivity analyses, and functional decoding.

Neuroimage 2013;**81**:381–92. https://doi.org/10.1016/j.neuroimage.2013.05.046

Carollo A, Esposito G. Hyperscanning literature after two decades of neuroscientific research: a scientometric review. *Neuroscience* 2024;**551**:345–54. https://doi.org/10.1016/j.neuroscience.2024.05.045

Cattinelli I, Valentini G, Paulesu E *et al.* A novel approach to the problem of non-uniqueness of the solution in hierarchical clustering. *IEEE Trans Neural Netw Learn Syst* 2013;**24**:1166–73. https://doi.org/10.1109/TNNLS.2013.2247058

Corbetta M, Patel G, Shulman GL. The reorienting system of the human brain: from environment to theory of mind. *Neuron* 2008;**58**:306–24. https://doi.org/10.1016/j.neuron.2008.04.017

Corradi-Dell'Acqua C, Ronchi R, Thomasson M *et al.* Deficits in cognitive and affective theory of mind relate to dissociated lesion patterns in prefrontal and insular cortex. *Cortex* 2020;**128**:218–33. https://doi.org/10.1016/j.cortex.2020.03.019

Czeszumski A, Eustergerling S, Lang A *et al.* Hyperscanning: a valid method to study neural inter-brain underpinnings of social interaction. *Front Hum Neurosci* 2020;**14**:39. https://doi.org/10.3389/fnhum.2020.00039

David N, Aumann C, Santos NS *et al.* Differential involvement of the posterior temporal cortex in mentalizing but not perspective taking. *Soc Cogn Affect Neurosci* 2008;**3**:279–89. https://doi.org/10.1093/scan/nsn023

Decety J, Jackson PL, Sommerville JA *et al.* The neural bases of cooperation and competition: an fMRI investigation. *Neuroimage* 2004;**23**:744–51. https://doi.org/10.1016/j.neuroimage.2004.05.025

Dikker S, Silbert LJ, Hasson U *et al.* On the same wavelength: predictable language enhances speaker–listener brain-to-brain synchrony in posterior superior temporal gyrus. *J Neurosci* 2014;**34**:6267–72. https://doi.org/10.1523/JNEUROSCI.3796-13.2014

Donaldson PH, Rinehart NJ, Enticott PG. Noninvasive stimulation of the temporoparietal junction: a systematic review. *Neurosci Biobehav Rev* 2015;**55**:547–72. https://doi.org/10.1016/j.neubiorev.2015.05.017

Dumas G, Lachat F, Martinerie J *et al.* From social behaviour to brain synchronization: review and perspectives in hyperscanning. *IRBM* 2011;**32**:48–53. https://doi.org/10.1016/j.irbm.2011.01.002

Eddy CM. The junction between self and other? Temporo-parietal dysfunction in neuropsychiatry. *Neuropsychologia* 2016;**89**:465–77. https://doi.org/10.1016/j.neuropsychologia.2016.07.030

Ellingsen DM, Duggento A, Isenburg K *et al.* Patient–clinician brain concordance underlies causal dynamics in nonverbal communication and negative affective expressivity. *Transl Psychiatry* 2022;**12**:44. https://doi.org/10.1038/s41398-022-01810-7

Ellingsen DM, Isenburg K, Jung C *et al.* Dynamic brain-to-brain concordance and behavioral mirroring as a mechanism of the patient-clinician interaction. *Sci Adv* 2020;**6**:eabc1304. https://doi.org/10.1126/sciadv.abc1304

Ellingsen DM, Isenburg K, Jung C *et al.* Brain-to-brain mechanisms underlying pain empathy and social modulation of pain in the patient-clinician interaction. *Proc Natl Acad Sci USA* 2023;**120**:e2212910120. https://doi.org/10.1073/pnas.2212910120

Frith CD, Frith U. The neural basis of mentalizing. *Neuron* 2006;**50**:531–4. https://doi.org/10.1016/j.neuron.2006.05.001

Frith CD, Frith U. Mechanisms of social cognition. *Annu Rev Psychol* 2012;**63**:287–313. https://doi.org/10.1146/annurev-psych-120710-100449

Fronda G, Balconi M. What hyperscanning and brain connectivity for hemodynamic (fnirs), electrophysiological (EEG) AND behavioral measures can tell us about prosocial behavior. *Psychology & Neuroscience* 2022;**15**:147–62. https://doi.org/10.1037/pne0000260

Frith U, Frith C. The social brain: allowing humans to boldly go where no other species has been. *Philos Trans R Soc Lond B Biol Sci* 2010;**365**:165–76. https://doi.org/10.1098/rstb.2009.0160

Glover GH. Overview of functional magnetic resonance imaging. *Neurosurg Clin N Am* 2011;**22**:133–9. https://doi.org/10.1016/j.nec.2010.11.001

Goelman G, Dan R, Stößel G *et al.* Bidirectional signal exchanges and their mechanisms during joint attention interaction–a hyperscanning fMRI study. *Neuroimage* 2019;**198**:242–54. https://doi.org/10.1016/j.neuroimage.2019.05.028

Golland Y, Levit-Binnun N, Hendler T *et al.* Neural dynamics underlying emotional transmissions between individuals. *Soc Cogn Affect Neurosci* 2017;**12**:1249–60. https://doi.org/10.1093/scan/nsx049

Greaves DA, Pinti P, Din S *et al.* Exploring theater neuroscience: using wearable functional near-infrared spectroscopy to measure the sense of self and interpersonal coordination in professional actors. *J Cogn Neurosci* 2022;**34**:2215–36. https://doi.org/10.1162/jocn_a_01912

Hakim U, De Felice S, Pinti P *et al.* Quantification of inter-brain coupling: a review of current methods used in haemodynamic and electrophysiological hyperscanning studies. *Neuroimage* 2023;**280**:120354. https://doi.org/10.1016/j.neuroimage.2023.120354

Hamilton AFDC. Hyperscanning: beyond the hype. *Neuron* 2021;**109**:404–7. https://doi.org/10.1016/j.neuron.2020.11.008

Hasson U, Frith CD. Mirroring and beyond: coupled dynamics as a generalized framework for modelling social interactions. *Philos Trans R Soc Lond B Biol Sci* 2016;**371**:20150366. https://doi.org/10.1098/rstb.2015.0366

Holroyd CB. Interbrain synchrony: on wavy ground. *Trends Neurosci* 2022;**45**:346–57. https://doi.org/10.1016/j.tins.2022.02.002

King-Casas B, Tomlin D, Anen C *et al.* Getting to know you: reputation and trust in a two-person economic exchange. *Science* 2005;**308**:78–83. https://doi.org/10.1126/science.1108062

Koike T, Sumiya M, Nakagawa E *et al.* What makes eye contact special? Neural substrates of on-line mutual eye-gaze: a hyperscanning fMRI study. *eNeuro* 2019a;**6**:ENEURO.0284-18.2019. https://doi.org/10.1523/ENEURO.0284-18.2019

Koike T, Tanabe HC, Adachi-Abe S *et al.* Role of the right anterior insular cortex in joint attention-related identification with a partner. *Soc Cogn Affect Neurosci* 2019b;**14**:1131–45. https://doi.org/10.1093/scan/nsz087

Koike T, Tanabe HC, Okazaki S *et al.* Neural substrates of shared attention as social memory: a hyperscanning functional magnetic resonance imaging study. *Neuroimage* 2016;**125**:401–12. https://doi.org/10.1016/j.neuroimage.2015.09.076

Koike T, Tanabe HC, Sadato N. Hyperscanning neuroimaging technique to reveal the "two-in-one" system in social interactions. *Neurosci Res* 2015;**90**:25–32. https://doi.org/10.1016/j.neures.2014.11.006

Konrad K, Gerloff C, Kohl SH *et al.* Interpersonal neural synchrony and mental disorders: unlocking potential pathways for clinical interventions. *Front Neurosci* 2024;**18**:1286130. https://doi.org/10.3389/fnins.2024.1286130

Krueger F, McCabe K, Moll J *et al.* Neural correlates of trust. *Proc Natl Acad Sci USA* 2007;**104**:20084–9. https://doi.org/10.1073/pnas.0710103104

Liu T, Duan L, Dai R *et al.* Team-work, team-brain: exploring synchrony and team interdependence in a nine-person drumming task via multiparticipant hyperscanning and inter-brain network topology with fNIRS. *Neuroimage* 2021;**237**:118147. https://doi.org/10.1016/j.neuroimage.2021.118147

Liu J, Zhang R, Xie E *et al.* Shared intentionality modulates interpersonal neural synchronization at the establishment of communication system. *Commun Biol* 2023;**6**:832. https://doi.org/10.1038/s42003-023-05197-z

Long Y, Zhong M, Aili R *et al.* Transcranial direct current stimulation of the right anterior temporal lobe changes interpersonal neural synchronization and shared mental processes. *Brain Stimul* 2023;**16**:28–39. https://doi.org/10.1016/j.brs.2022.12.009

Lotter LD, Kohl SH, Gerloff C *et al.* Revealing the neurobiology underlying interpersonal neural synchronization with multimodal data fusion. *Neurosci Biobehav Rev* 2023;**146**:105042.

Lu H, Wang X, Zhang Y *et al.* Increased interbrain synchronization and neural efficiency of the frontal cortex to enhance human coordinative behavior: a combined hyper-tES and fNIRS study. *Neuroimage* 2023;**282**:120385. https://doi.org/10.1016/j.neuroimage.2023.120385

Mars RB, Sallet J, Schüffelgen U *et al.* Connectivity-based subdivisions of the human right “temporoparietal junction area”: evidence for different areas participating in different cortical networks. *Cereb Cortex* 2012;**22**:1894–903. https://doi.org/10.1093/cercor/bhr268

Matsuhashi M, Ikeda A, Ohara S *et al.* Multisensory convergence at human temporo-parietal junction–epicortical recording of evoked responses. *Clin Neurophysiol* 2004;**115**:1145–60. https://doi.org/10.1016/j.clinph.2003.12.009

Mayseless N, Hawthorne G, Reiss AL. Real-life creative problem solving in teams: fNIRS based hyperscanning study. *Neuroimage* 2019;**203**:116161. https://doi.org/10.1016/j.neuroimage.2019.116161

Melnik A, Legkov P, Izdebski K *et al.* Systems, subjects, sessions: to what extent do these factors influence EEG data? *Front Hum Neurosci* 2017;**11**:150. https://doi.org/10.3389/fnhum.2017.00150

Merchant JS, Glaros S, Edakoth E *et al.* Brain bases of real-time social interaction: a meta-analytic investigation of human neuroimaging studies. *Apert Neuro* 2025;**5**. https://doi.org/10.52294/001c.138339

Michel CM, Brunet D. EEG source imaging: a practical review of the analysis steps. *Front Neurol* 2019;**10**:325. https://doi.org/10.3389/fneur.2019.00325

Miyata K, Koike T, Nakagawa E *et al.* Neural substrates for sharing intention in action during face-to-face imitation. *Neuroimage* 2021;**233**:117916. https://doi.org/10.1016/j.neuroimage.2021.117916

Misaki M, Kerr KL, Ratliff EL *et al.* Beyond synchrony: the capacity of fMRI hyperscanning for the study of human social interaction. *Soc Cogn Affect Neurosci* 2021;**16**:84–92. https://doi.org/10.1093/scan/nsaa143

Montague PR, Berns GS, Cohen JD *et al.* Hyperscanning: simultaneous fMRI during linked social interactions. *Neuroimage* 2002;**16**:1159–64. https://doi.org/10.1006/nimg.2002.1150

Müller V, Lindenberger U. Cardiac and respiratory patterns synchronize between persons during choir singing. *PLoS One* 2011;**6**:e24893. https://doi.org/10.1371/journal.pone.0024893

Nam CS, Choo S, Huang J *et al.* Brain-to-brain neural synchrony during social interactions: a systematic review on hyperscanning studies. *Appl Sci* 2020;**10**:6669. https://doi.org/10.3390/app10196669

Novembre G, Knoblich G, Dunne L *et al.* Interpersonal synchrony enhanced through 20 hz phase-coupled dual brain stimulation. *Soc Cogn Affect Neurosci* 2017;**12**:662–70. https://doi.org/10.1093/scan/nsw172

Ochsner KN, Lieberman MD. The emergence of social cognitive neuroscience. *Am Psychol* 2001;**56**:717–34. https://doi.org/10.1037//0003-066X.56.9.717

Page MJ, McKenzie JE, Bossuyt PM *et al.* The PRISMA 2020 statement: an updated guideline for reporting systematic reviews. *BMJ* 2021;**372**:n71. https://doi.org/10.1136/bmj.n71

Papoutselou E, Harrison S, Mai G *et al.* Investigating mother–child inter-brain synchrony in a naturalistic paradigm: a functional near infrared spectroscopy (fNIRS) hyperscanning study. *Eur J Neurosci* 2024;**59**:1386–403. https://doi.org/10.1111/ejn.16233

Przyrembel M, Smallwood J, Pauen M *et al.* Illuminating the dark matter of social neuroscience: considering the problem of social interaction from philosophical, psychological, and neuroscientific perspectives. *Front Hum Neurosci* 2012;**6**:190. https://doi.org/10.3389/fnhum.2012.00190

Quaresima V, Ferrari M. Functional near-infrared spectroscopy (fNIRS) for assessing cerebral cortex function during human behavior in natural/social situations: a concise review. *Organ Res Methods* 2019;**22**:46–68. https://doi.org/10.1177/1094428116658959

Quesque F, Brass M. The role of the temporoparietal junction in self-other distinction. *Brain Topogr* 2019;**32**:943–55. https://doi.org/10.1007/s10548-019-00737-5

Ratliff EL, Kerr KL, Misaki M *et al.* Into the unknown: examining neural representations of parent–adolescent interactions. *Child Dev* 2021;**92**:e1361–76. https://doi.org/10.1111/cdev.13635

Redcay E, Dodell-Feder D, Pearrow MJ *et al.* Live face-to-face interaction during fMRI: a new tool for social cognitive neuroscience. *Neuroimage* 2010;**50**:1639–47. https://doi.org/10.1016/j.neuroimage.2010.01.052

Redcay E, Schilbach L. Using second-person neuroscience to elucidate the mechanisms of social interaction. *Nat Rev Neurosci* 2019;**20**:495–505. https://doi.org/10.1038/s41583-019-0179-4

Richardson DC, Hoover MA, Ghane A. Joint perception: gaze and the presence of others. In *Proceedings of the Annual Meeting of the Cognitive Science Society* (Vol. 30, No. 30); 2008.

Ridderinkhof KR, Ullsperger M, Crone EA *et al.* The role of the medial frontal cortex in cognitive control. *Science* 2004;**306**:443–7. https://doi.org/10.1126/science.1100301

Rolls ET, Huang CC, Lin CP *et al.* Automated anatomical labelling atlas 3. *Neuroimage* 2020;**206**:116189. https://doi.org/10.1016/j.neuroimage.2019.116189

Rushworth MF, Behrens TE. Choice, uncertainty and value in prefrontal and cingulate cortex. *Nat Neurosci* 2008;**11**:389–97. https://doi.org/10.1038/nn2066

Saito DN, Tanabe HC, Izuma K *et al.* “Stay tuned”: inter-individual neural synchronization during mutual gaze and joint attention. *Front Integr Neurosci* 2010;**4**:127. https://doi.org/doi.org/10.3389/fnint.2010.00127

Salazar M, Shaw DJ, Gajdoš M *et al.* You took the words right out of my mouth: dual-fMRI reveals intra-and inter-personal neural processes supporting verbal interaction. *Neuroimage* 2021;**228**:117697. https://doi.org/10.1016/j.neuroimage.2020.117697

Santiesteban I, Banissy MJ, Catmur C *et al.* Functional lateralization of temporoparietal junction–imitation inhibition, visual perspective-taking and theory of mind. *Eur J Neurosci* 2015;**42**:2527–33. https://doi.org/10.1111/ejn.13036

Schilbach L, Eickhoff SB, Rotarska-Jagiela A *et al.* Minds at rest? Social cognition as the default mode of cognizing and its putative relationship to the “default system” of the brain. *Conscious Cogn* 2008;**17**:457–67. https://doi.org/10.1016/j.concog.2008.03.013

Schilbach L, Timmermans B, Reddy V *et al.* Toward a second-person neuroscience. *Behav Brain Sci* 2013;**36**:393–414. https://doi.org/10.1017/S0140525X12000660

Schippers MB, Roebroeck A, Renken R *et al.* Mapping the information flow from one brain to another during gestural communication. *Proc Natl Acad Sci USA* 2010;**107**:9388–93. https://doi.org/10.1073/pnas.1001791107

Schurz M, Radua J, Aichhorn M *et al.* Fractionating theory of mind: a meta-analysis of functional brain imaging studies. *Neurosci Biobehav Rev* 2014;**42**:9–34. https://doi.org/10.1016/j.neubiorev.2014.01.009

Sebanz N, Bekkering H, Knoblich G. Joint action: bodies and minds moving together. *Trends Cogn Sci* 2006;**10**:70–6. https://doi.org/10.1016/j.tics.2005.12.009

Shaw DJ, Czekóová K, Špiláková B *et al.* A neuroscientific evaluation of driver rehabilitation: functional neuroimaging demonstrates the effectiveness of empathy induction in altering brain responses during social information processing. *PLoS One* 2020;**15**:e0232222. https://doi.org/10.1371/journal.pone.0232222

Shaw DJ, Czekóová K, Staněk R *et al.* A dual-fMRI investigation of the iterated ultimatum game reveals that reciprocal behaviour is associated with neural alignment. *Sci Rep* 2018;**8**:10896. https://doi.org/10.1038/s41598-018-29233-9

Sperduti M, Delaveau P, Fossati P *et al.* Different brain structures related to self-and external-agency attribution: a brief review and meta-analysis. *Brain Struct Funct* 2011;**216**:151–7. https://doi.org/10.1007/s00429-010-0298-1

Spiegelhalder K, Ohlendorf S, Regen W *et al.* Interindividual synchronization of brain activity during live verbal communication. *Behav Brain Res* 2014;**258**:75–9. https://doi.org/10.1016/j.bbr.2013.10.015

Špiláková B, Shaw DJ, Czekóová K *et al.* Getting into sync: data-driven analyses reveal patterns of neural coupling that distinguish among different social exchanges. *Hum Brain Mapp* 2020;**41**:1072–83. https://doi.org/10.1002/hbm.24861

Stolk A, Noordzij ML, Verhagen L *et al.* Cerebral coherence between communicators marks the emergence of meaning. *Proc Natl Acad Sci USA* 2014;**111**:18183–8. https://doi.org/10.1073/pnas.1414886111

Su H, Young CB, Han ZR *et al.* Atypical child–parent neural synchrony is linked to negative family emotional climate and children's psychopathological symptoms. *Am Psychol* 2024;**79**:210–24. https://doi.org/10.1037/amp0001173

Szymanski C, Müller V, Brick TR *et al.* Hyper-transcranial alternating current stimulation: experimental manipulation of inter-brain synchrony. *Front Hum Neurosci* 2017;**11**:539. https://doi.org/10.3389/fnhum.2017.00539

Tanabe HC, Kosaka H, Saito DN *et al.* Hard to "tune in": neural mechanisms of live face-to-face interaction with high-functioning autistic spectrum disorder. *Front Hum Neurosci* 2012;**6**:268. https://doi.org/10.3389/fnhum.2012.00268

Tomlin D, Kayali MA, King-Casas B *et al.* Agent-specific responses in the cingulate cortex during economic exchanges. *Science* 2006;**312**:1047–50. https://doi.org/10.1126/science.1125596

Tsoi L, Burns SM, Falk EB *et al.* The promises and pitfalls of functional magnetic resonance imaging hyperscanning for social interaction research. *Soc Personal Psychol Compass* 2022;**16**:e12707. https://doi.org/10.1111/spc3.12707

Uddin LQ, Nomi JS, Hébert-Seropian B *et al.* Structure and function of the human insula. *J Clin Neurophysiol* 2017;**34**:300–6. https://doi.org/10.1097/WNP.0000000000000377

Wang LS, Chang YC, Liou S *et al.* When "more for others, less for self" leads to co-benefits: a tri-MRI dyad-hyperscanning study. *Psychophysiology* 2024;**61**:e14560. https://doi.org/10.1111/psyp.14560

Wang LS, Cheng JT, Hsu IJ *et al.* Distinct cerebral coherence in task-based fMRI hyperscanning: cooperation versus competition. *Cereb Cortex* 2022;**33**:421–33. https://doi.org/10.1093/cercor/bhac075

Wang MY, Luan P, Zhang J *et al.* Concurrent mapping of brain activation from multiple subjects during social interaction by hyperscanning: a mini-review. *Quant Imaging Med Surg* 2018;**8**:819–37. https://doi.org/10.21037/qims.2018.09.07

Ward J. Hierarchical grouping to optimize an objective function. *J Am Stat Assoc* 1963;**58**:236–44. https://doi.org/10.1080/01621459.1963.10500845

Xie H, Karipidis II, Howell A *et al.* Finding the neural correlates of collaboration using a three-person fMRI hyperscanning paradigm. *Proc Natl Acad Sci USA* 2020;**117**:23066–72. https://doi.org/10.1073/pnas.1917407117

Yeshurun Y, Nguyen M, Hasson U. The default mode network: where the idiosyncratic self meets the shared social world. *Nat Rev Neurosci* 2021;**22**:181–92. https://doi.org/10.1038/s41583-020-00420-w

Yoshioka A, Tanabe HC, Sumiya M *et al.* Neural substrates of shared visual experiences: a hyperscanning fMRI study. *Soc Cogn Affect Neurosci* 2021;**16**:1264–75. https://doi.org/10.1093/scan/nsab082

Zhang T, Zhou S, Bai X *et al.* Neurocomputations on dual-brain signals underlie interpersonal prediction during a natural conversation. *Neuroimage* 2023;**282**:120400. https://doi.org/10.1016/j.neuroimage.2023.120400