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Relational neuroscience: Insights from hyperscanning research

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ABSTRACT

Humans are highly social, typically without this ability requiring noticeable efforts. Yet, such social fluency poses challenges both for the human brain to compute and for scientists to study. Over the last few decades, neuroscientific research of human sociality has witnessed a shift in focus from single-brain analysis to complex dynamics occurring across several brains, posing questions about what these dynamics mean and how they relate to multifaceted behavioural models. We propose the term '*Relational Neuroscience*' to collate the interdisciplinary research field devoted to modelling the inter-brain dynamics subserving human connections, spanning from real-time joint experiences to long-term social bonds. Hyperscanning, i.e., simultaneously measuring brain activity from multiple individuals, has proven to be a highly promising technique to investigate inter-brain dynamics. Here, we discuss how hyperscanning can help investigate questions within the field of Relational Neuroscience, considering a variety of subfields, including cooperative interactions in dyads and groups, empathy, attachment and bonding, and developmental neuroscience. While presenting Relational Neuroscience in the light of hyperscanning, our discussion also takes into account behaviour, physiology and endocrinology to properly interpret inter-brain dynamics within social contexts. We consider the strengths but also the limitations and caveats of hyperscanning to answer questions about interacting people. The aim is to provide an integrative framework for future work to build better theories across a variety of contexts and research subfields to model human sociality.

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1. Introduction

Humans are highly social. Yet, how is such high social proficiency achieved and implemented? We can navigate complex real-time interactions and form long-term relationships, engage in successful communication, understand others' actions, intentions and beliefs as distinct from our own, and make decisions based on this knowledge. While 'being social' and forming social bonds looks and feels relatively effortless, it is a computationally complex phenomenon. Scholars have been interested in how humans interact since the earliest records of human activity, from ancient philosophers to modern scientists. Despite this long-standing interest, methodological challenges have significantly limited the scientific advancement in building a robust understanding of how minds interact and, in particular, how people form, engage in and maintain social relationships, both in the short and long-term. Recently, the advance of experimental, computational and neuroimaging methods, as well as a shift towards multiple-brain analysis (see e.g., Hari and Kujala, 2009; Konvalinka and Roepstorff, 2012; Redcay and Schilbach, 2019; Schilbach et al., 2013), has created a particularly propitious environment for the exploration and expansion of knowledge on the neuroscience of interacting minds (Wheatley et al., 2023). As such, research has started to be increasingly more interested in the interpersonal dynamics that arise from shared social experiences (for more recent accounts, see e.g., Koban et al., 2019; Konvalinka et al., 2023; Novembre et al., 2023; Verga et al., 2023), including how people co-construct and co-interpret the world around them. In this paper, we propose the term '*Relational Neuroscience*' to refer to the overarching area of neuroscientific research that aims to model human sociality, with a specific focus on how people form, engage in and maintain social relationships. To do so, hyperscanning – simultaneously measuring brain activity from multiple people – is viewed as a highly promising tool, which has proven advantageous for understanding the neural mechanisms of how humans exist (and co-exist) in a social world (see e.g., Czeszumski et al., 2020; Koike et al., 2015; Mu et al., 2018; Tsoi et al., 2022).

We first define the term Relational Neuroscience and discuss some key concepts within this field (Section 2). In Section 3, we illustrate hyperscanning as a promising technique for investigating Relational Neuroscience questions, offering an overview of its application in various subfields including cooperative interactions and communication in dyads and groups, empathy, attachment and bonding, and developmental neuroscience. When considering these subfields, we adopt a focused lens on relational aspects of human cognition. In Section 4, we move beyond hyperscanning to include complementary fields of research to be used in conjunction with hyperscanning to achieve a better understanding of inter-brain dynamics in the context of Relational Neuroscience. Lastly, we conclude with a discussion on the major theories and future directions in Relational Neuroscience research.

2. Relational neuroscience: what, why and how?

We propose the term Relational Neuroscience to refer to the overarching and ongoing research effort devoted to identifying both the causes and consequences of inter-brain dynamics as they occur across different groups and contexts. The ultimate goal of Relational Neuroscience is twofold: to model the patterns of brain dynamics arising across interacting individuals, and to understand their meaning. As such, Relational Neuroscience is highly interdisciplinary in that it combines multimodal signals (brain, physiology, movement, speech etc.) and psychological constructs (e.g., attachment, social closeness etc.) to model interpersonal dynamics. Specifically, Relational Neuroscience investigates the association between brain signals as a function of social interaction (*what*) to model human-to-human sociality (*why*), adopting hyperscanning as its core methodology in conjunction with complementary research tools and measures across a variety of contexts, groups and time-dependent inter-personal dynamics summarised by the two dimensions of interpersonal closeness and interactivity (*how*). Accordingly, the word 'Relational' mainly refers to the relationship between interacting individuals (i.e., interpersonal closeness) and the interaction settings and dynamics (i.e., interactivity) within which those interactions unfold. For more details, please refer to Section 2.1 and Fig. 1.

Crucially, we appreciate, and would like to make our readers aware, that many of our considerations associated with the concept of Relational Neuroscience are informed by the seminal work of others within the areas of social and second-person neuroscience that we reference throughout our manuscript. Nonetheless, we note that while other terms, such as social neuroscience and second-person neuroscience, refer to a somewhat broader research field devoted to modelling the social brain as it interacts with the external world (including, but not limited to, other social agents), Relational Neuroscience more precisely focuses on *the interpersonal dynamics that arise from shared social experiences*. It is also worth mentioning that the term *Relational Neuroscience* by itself is not completely new to neuroscientific literature. However, its usage has been sporadic and mainly in relation to therapeutic interventions and psychiatric disorders of the social brain (see e.g., Hass-Cohen and Clyde Findlay, 2018; Hass-Cohen, 2016; Holmes and Slade, 2019; Mizen and Hook, 2020). Here, we adopt this term as one that can represent a growing body of research work devoted to model human-to-human sociality from a neuroscientific perspective to facilitate theoretical, experimental and technological advancements.

The idea that two brains align under certain circumstances was first demonstrated using sequential scanning with functional magnetic resonance imaging (fMRI). In their seminal work, Hasson and colleagues showed that during natural sequential movie watching, people's brains exhibit similar neural responses (Hasson et al., 2004). These results have been convincingly replicated using fMRI in a variety of tasks including story listening (Yeshurun et al., 2017) and memory recall (J. Chen et al., 2017) as well as with electroencephalography (EEG) during solo video watching, when participants were asked to learn information from recorded videos (Madsen and Parra, 2022). Importantly, these studies provide evidence that different individuals' brains *conform* to the external world, i.e., respond similarly to the same external signals and associated internal perceptual experiences. This is relatively unsurprising: similarly to how two individual digestive systems process the same meal through roughly the same digestive processes, so would two individual brains show comparable responses to the same stimulus (e.g., a movie). However, this work does not tell us much about whether and how such neural conformity (or alignment) arises as a function of social contact. One of the first studies trying to explore the role of social contact in neural conformity was the study by Parkinson et al. (2018). Using sequential fMRI scanning, the authors demonstrated that participants who were also friends, when exposed to the same movie, exhibited brain responses that were more similar to each other than those of participants who were not friends. In other words, social network proximity modulates how similarly people process the world. This work tells us something about long-term social bonds (e.g., friendships) and how these impact on people's perception and interpretation of external experiences. However, it cannot tell us much about *real-time* social interactions.

Real-time human sociality has often been modelled in terms of signal coordination and alignment in the context of motor behaviour and verbalisations (see e.g., Konvalinka et al., 2023; Verga et al., 2023; Vinciarelli, 2017). Over the last few decades, the idea that such types of individuals' signals can progressively align to one another through social connection has generated questions about whether the same phenomenon emerges at the neural level. However, sequential scanning techniques used in studies like in Parkinson et al.'s (2018) can only test the effect of interpersonal closeness (or social network proximity), i.e., a social dimension that is context *in*dependent and *un*related to the timing of the inter-personal dynamic – as they, by definition, measure brain signals from individual brains *sequentially* (i.e., one by one and one after the other). While interpersonal closeness is an important dimension of

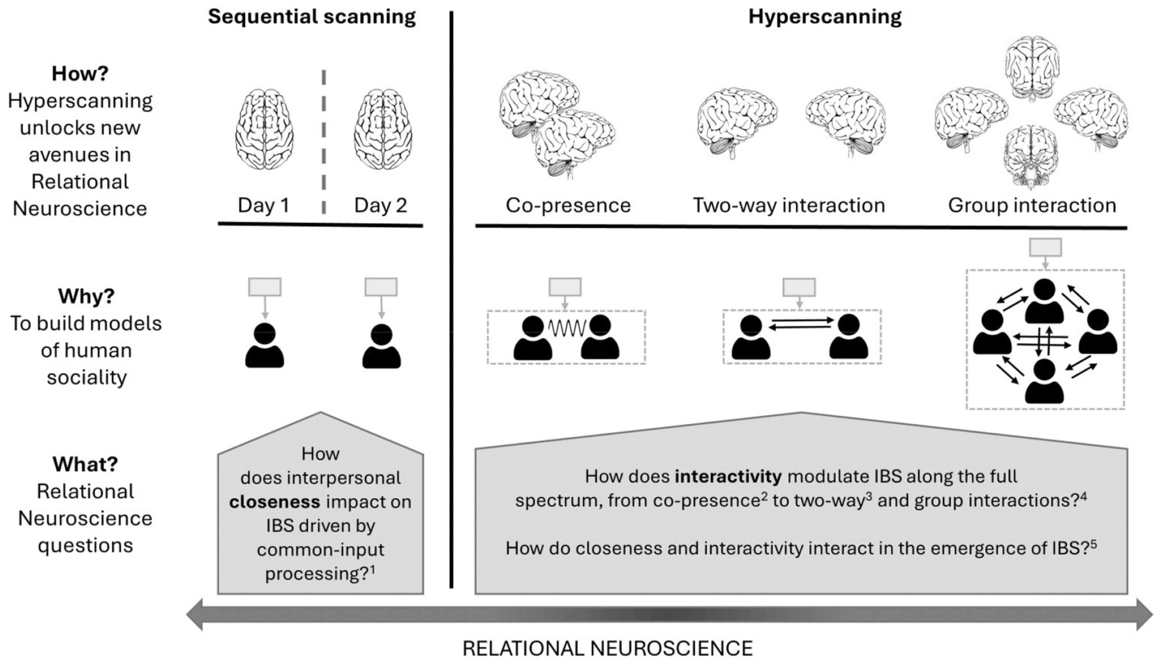

Fig. 1. Relational Neuroscience: what, why and how? From bottom to top: *What?* Considering the two dimensions of Relational Neuroscience, namely interpersonal closeness and interactivity (see main text Section 2.1), Relational Neuroscience questions how these modulate interpersonal dynamics, both independently and together; examples of studies answering these questions are: 1. (Parkinson et al., 2018), 2. (Pan et al., 2017), 3. (T. Nguyen et al., 2021), 4. (T. Liu et al., 2021) and 5. (Azhari et al., 2020). *Why?* Answering Relational Neuroscience questions allows us to build models of human sociality. Such models describe signals coming from different individuals and how these couple across a wide range of relational dynamics, beyond common-input processing (grey box). *How?* While sequential scanning may be used to answer the question of how interpersonal closeness modulates inter-brain synchrony (IBS) driven by common-input processing, hyperscanning is necessary to study a range of other questions related to real-time social dynamics varying in their degree of interactivity and, in turn, how these form, maintain and are modulated by interpersonal closeness.

human sociality (see Section 2.1), it does not provide the full picture. People regularly interact in real-time, including (but not only) to form long-term social bonds, and are able to coordinate with one another (Konvalinka et al., 2023). This makes 'social timing', i.e., mutual adaptation in time, an important dimension of human sociality (see e.g., Novembre et al., 2023; Verga et al., 2023). Therefore, fully understanding whether and how individual signals align as a function of social contact must also involve investigation of *real-time* social interactions. Hyperscanning – i.e., simultaneously measuring brain activity from multiple individuals (see Fig. 1 and Section 2) – allows researchers to study real-time interpersonal dynamics between interacting agents. This technique has been successfully used with fMRI (Montague et al., 2002), EEG (Balconi et al., 2023), magnetoencephalography (MEG) (Hirata et al., 2014), and functional near-infrared spectroscopy (fNIRS) (Cui et al., 2012) (for a review see Hakim et al., 2023). In doing so, research has revealed synchronisation patterns across *interacting* individual brains – referred to as inter-brain synchrony (IBS) – when people jointly engage in a variety of tasks, beyond what would be expected by simply attending to the same external stimuli (Hasson et al., 2004). Specifically, IBS has been demonstrated to emerge when people complete cooperative tasks together (see e.g., Cui et al., 2012; T. Liu et al., 2021), engage in conversation (see e.g., T. Nguyen et al., 2021), co-attend to the same content (e.g., movie watching, De Felice et al., 2024; and learning, Dikker et al., 2017) and share emotional experiences (see e.g., Deng et al., 2023; also see Section 3 for a review on IBS studies). We call such an emergence of brain dynamics between interacting individuals, above and beyond what can be explained by shared perceptual input, the '*hyperscanning effect*', because it requires hyperscanning (beyond sequential scanning) to capture it (see also Fig. 1).

The discovery of this effect has sparked substantive theoretical debate relating to its potential mechanisms and functions (see e.g., Hamilton, 2021; Holroyd, 2022; Kingsbury and Hong, 2020; Konvalinka et al., 2023; Novembre et al., 2023). Importantly, the hyperscanning effect emerging as part of IBS data acquisition may reflect different mechanisms, such as bonding, affiliation and attachment (see e.g., Azhari et al., 2021; Pan et al., 2017; Zheng et al., 2020), mutual prediction (see e.g., Hamilton, 2021; Kingsbury et al., 2019) and joint planning (see e.g., Nguyen et al., 2023). These mechanisms are not necessarily mutually exclusive, and it is likely that they overlap and intertwine in naturalistic interactions (see Section 5 for a more detailed discussion). This overlap makes modelling the individual contributions methodologically and computationally challenging (see e.g., Hamilton, 2021; Holroyd, 2022). For example, does IBS emerge from, or result in, closer social bonds (Zheng et al., 2020), or both? Is IBS an epiphenomenon of mutual understanding and prediction (Hamilton, 2021) or is it a causal mechanism in itself (Novembre et al., 2023; Novembre and Iannetti, 2021), playing an important role in, e.g., social learning (Pan et al., 2021), motor coordination (Lu et al., 2023; Novembre et al., 2017) and communication (J. Liu et al., 2023)? Are there individual factors, such as age (M. Yang et al., 2023), attractiveness (Yuan et al., 2022), leadership (Jiang et al., 2015a; Reinero et al., 2020) and/or familiarity (De Felice et al., 2024), that modulate such dynamics? And what are the neural, physiological and behavioural consequences of such processes? These are some of the questions that pertain to Relational Neuroscience research. Trying to conclusively answer such questions is beyond the scope of this review (but see the Discussion in Section 5), and many interesting theoretical discussions have been published recently on these topics (see e.g., Hamilton, 2021; Holroyd, 2022; Kingsbury and Hong, 2020; Konvalinka et al., 2023; Novembre et al., 2023). Here, we aim to provide an alternative framework, complementing others, to conceptualise and organise Relational Neuroscience questions into clear methodological approaches, which can hopefully lead to more interpretable results, with the ultimate goal of developing better theoretical models. In doing so, we take a closer look at hyperscanning research.

An important consideration to make at this point relates to the spectrum of interpersonal dynamics that fall into the interest of

Relational Neuroscience. Below, we consider two core dimensions: *interpersonal closeness* and *interactivity*.

2.1. Relational neuroscience dimensions: interpersonal closeness and interactivity

The study of social dynamics in Relational Neuroscience covers a wide range of scenarios. Accordingly, social contact – defined here as any form of interaction or communication between individuals, encompassing physical, verbal, or shared experiences that contribute to social connections and relationships – can take many forms. It spans from real-time contingent interaction between strangers (see e.g., T. Liu et al., 2021; Novembre et al., 2016; Yang et al., 2023) to long-term relationship bonds (see e.g., Pan et al., 2017; Zhang et al., 2023). Furthermore, it includes both situations where *active exchange* is kept to almost zero while sharing an experience (e.g., during movie co-watching, Azhari et al., 2021; De Felice et al., 2024), as well as situations where people are highly interactive. In turn, highly interactive scenarios can encompass either balanced interactions, with different social agents who (can) contribute equally to the interaction (e.g., naturalistic conversations, Nguyen et al., 2021, 2023; group decision-making, J. Yang et al., 2020), or more *a-priori* unbalanced social dynamics with clearly defined roles (e.g., teacher-student interactions, De Felice et al., 2021, 2023; Zheng et al., 2020; therapist-client interactions, Fachner et al., 2019; Y. Zhang et al., 2018; leader-follower interactions, Jiang et al., 2015b; H. Zhang et al., 2023). Based on our literature review on hyperscanning research (see Section 3), we propose that all these scenarios can be classified along a spectrum

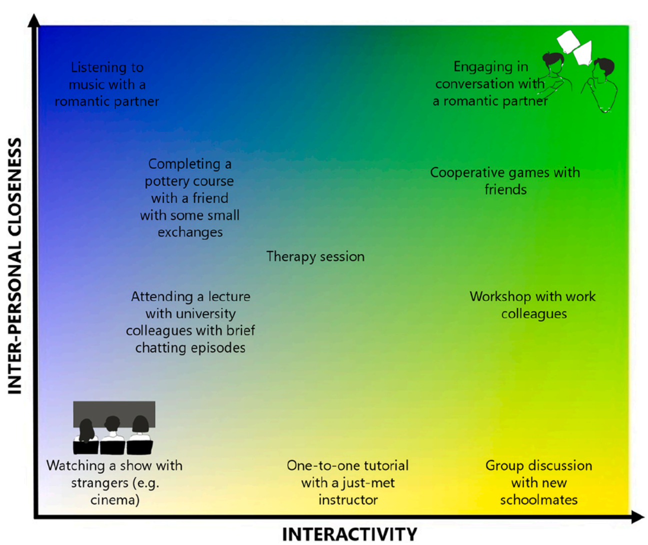

Fig. 2. Examples of real-world social dynamics along the two dimensions of Relational Neuroscience Starting from the origin (depicted in white), interactivity progresses on the x-axis (yellow), and interpersonal closeness progresses on the y-axis (blue). Intensity in colour represents how far a given social context is mapped on either of these dimensions. The right-top quadrant is green (blue+yellow) to represent social contexts high on both interactivity and interpersonal closeness. Note that the closeness and interactivity dimensions are depicted here as orthogonal for illustration purposes, but these can (and often do) overlap - although they don't *have to* overlap (see text for a discussion on how these dimensions relate to each other in real-world social exchanges). We acknowledge that examples included in the graph are simplifications of real-world social exchanges: in reality, their exact position on the interactivity and/or interpersonal closeness dimension can vary substantially. For example, interactivity during a therapy session may vary between individuals and/or therapeutic approaches, as well as within individuals across different days. Similarly, as one progresses with the therapeutic journey, the patient-therapist relationship will inevitably evolve and thus vary in terms of interpersonal closeness.

of two core dimensions (Fig. 2): interpersonal closeness and interactivity. Here, we define interpersonal closeness as the degree of social proximity between interacting agents, often measured in terms of relationship duration and/or intimacy. Interpersonal closeness thus increases when moving, e.g., from strangers to friends and romantic partners. Additionally, we define interactivity as the level of reciprocity and richness of multisensory mutual exchange during a social interaction. Therefore, interactivity increases, e.g., from co-watching a movie to actively and reciprocally engaging in a conversation. Note that, in contrast to closeness, which changes slowly and is relatively context-independent, the interactivity dimension is heavily context dependent. Furthermore, these two dimensions are not meant to be exhaustive, but they rather have been proposed here as they encompass the vast majority of research done in Relational Neuroscience to date, and provide a comprehensive framework within which different past and new experimental studies can be placed, classified and interpreted.

When it comes to the *interpersonal closeness* dimension, a growing body of evidence suggests that the level of intimacy between two or more people is related to the degree of IBS (see e.g., Azhari et al., 2019, 2020; Bizzego et al., 2020; Yuan et al., 2022; Pan et al., 2017; Song et al., 2024; Q. Zhang et al., 2023; W. Zhang et al., 2023). For example, Pan et al. (2017) measured IBS in three types of female-male dyads including lovers, friends, and strangers, as they engaged in a computerised cooperative task. The authors found that lover dyads showed stronger increase in IBS in the right superior frontal cortex compared to both friend and stranger dyads, and such IBS increase selectively covaried with lovers' task performance. Similarly, a positive relationship was found between student-teacher IBS and students' reported feelings of closeness to their teacher (Bevilacqua et al., 2019). Taken together, these findings suggest that long-term social dynamics can impact on real-time synchrony at the brain level.

As for the *interactivity* dimension, existing work seems to have predominantly focused on one side of the spectrum. Thus, the study of between-person synergy (of brain, behavioural and/or physiological signals) has largely considered person-to-person dynamics in the context of *rich exchange of social signals*, the latter being related to verbal (e.g., Nguyen et al., 2021, 2023; Templeton et al., 2022), affective (e.g., Peng et al., 2021; Prochazkova & Kret, 2017), motor (e.g., Kruppa et al., 2021; T. Liu et al., 2021; Pan et al., 2021) and/or attentive signals, e.g., through eye-gaze (e.g., Gumilar et al., 2022; Hirsch et al., 2017; Luft et al., 2022; Marriott Haresign et al., 2023). These studies show that IBS reflects inter-personal dynamics arising during active mutual social exchanges. However, more recent evidence suggests that merely sharing an experience with another person may also modulate interpersonal dynamics, even when such shared experience involves minimal or no explicit exchange – for example, during movie co-watching (e.g., Azhari et al., 2021; De Felice et al., 2024) or co-listening to audio stimuli (e.g., Azhari et al., 2020). Along these lines, De Felice et al. (2024) showed that pairs of adults (all knowing each other) who watched a movie together – but did *not* interact during co-watching – exhibited greater IBS within parietal and frontal regions (compared to randomly shuffled pairs who watched the same movies separately). These data therefore suggest that sharing an experience, even when such experience does not involve any active interaction, may modulate interpersonal dynamics at the brain level, in ways that differ from solo-experiences, possibly via physiological co-regulation and/or inter-personal dynamics of body consciousness and ownerships (Blanke, 2012).

According to the above, we suggest that the spectrum of interpersonal dynamics studied within the field of Relational Neuroscience should include dynamics that develop both as part of long-term social bonds – with longitudinal evidence of the evolution of parent-child behavioural interactional synchrony from infancy to early adulthood already documented across twenty years (see e.g., Ulmer Yaniv et al., 2021) – as well as one-time interactions between strangers, for example, when comparing IBS during social interactions between romantic couples versus friends versus strangers (see e.g., Kinreich et al., 2017;

Djalovski et al., 2021). Equally, we propose that assessed dynamics should span from sharing the same experience without rich interaction to fully interactive contexts where people proactively and mutually exchange verbal, affective and/or motor signals (see references mentioned above). While Relational Neuroscience is interested in both dimensions, and the use of hyperscanning can clearly be advantageous for studying all the scenarios described above, distinguishing between these different situations is important to build accurate models of interconnected minds.

Also, although the interpersonal closeness and interactivity dimensions can be considered as two separate, non-mutually exclusive dimensions, they can (and often do) interact. For example, engaging in a conversation may be related to different neural patterns compared to sharing an experience with little interaction, which in turn may differ from solo-experience, and these patterns may additionally differ depending on whether either of these situations occurs between strangers, acquaintances or long-term friends or lovers. A similar account of three interactive experimental dimensions comprising the factors "experience" (i.e., differentiating between detachment versus engagement), "participation" (i.e., differentiating between the observation of inert stimuli versus structured or dynamic interaction) and "data collection & analysis" (i.e., differentiating between the measurement of data from single versus multiple individuals) has been previously postulated (Schilbach et al., 2013), emphasising that high interactivity often correlates with unstructured environments, whereas low interactivity often aligns with more structured settings.

Furthermore, while we suggest that the spectrum of interpersonal dynamics studied within the field of Relational Neuroscience can be nicely captured by the two dimensions of interpersonal closeness and interactivity, we appreciate that there are other variables reflecting individual variability that may also be related to IBS. These variables comprise age, sex/gender, race, education and sociodemographic status, amongst others. Although many studies control for (at least some of) these variables or sometimes perform explicit comparison analyses – e.g., by assessing sex-differences in both parents and children in the context of parent-child interaction (Nguyen et al., 2024) –, more data is needed to provide a richer understanding of their potential influences.

Before presenting recent examples of hyperscanning research to answer Relational Neuroscience questions (Section 3), in Section 2.2 we define some core terms used in the Relational Neuroscience literature.

2.2. How to call what?

In the previous section, we introduced the concept of Relational Neuroscience, defining its scope, methodologies and dimensions. This section aims to clarify what the primary sources of Relational Neuroscience data are, and which specific terminology is used within the field when describing data assessment and analysis methods.

Although we mainly focus on hyperscanning data derived from brain measures within the present Relational Neuroscience framework, we appreciate that interpersonal dynamics between two (or more) individuals during the free exchange of signals unfold within (at least) three additional modalities: behavioural markers, physiological/endocrinological signals, and higher-level systems, such as beliefs. An illustration of all these four modalities of interpersonal dynamics is provided in Fig. 3. We further elaborate on the usefulness of including the behavioural, physiological/endocrinological, and higher-level systems modalities in hyperscanning experiments to not only assess their relations with brain measures, but also associations between each other, in Section 4.

In recent decades, as the interest in Relational Neuroscience has steadily grown, multiple terms have been employed to describe interpersonal dynamics across neural, behavioural, physiological, and conceptual levels. However, there remains ambiguity regarding precise definitions, appropriate analysis contexts, and the information each term conveys. This lack of clarity has resulted in confusion and inconsistencies across studies, hindering cohesion among researchers interested in Relational Neuroscience. In Table 1, we therefore categorize the most common terms used in Relational Neuroscience research based on the interpersonal dynamics described and the extent of information provided by each of them. To do so, we consider each term based on the level of measurement – i.e., the specific modality – at which it is used (e.g., brain, physiology etc.) and include some examples of work from scientific literature (note that these are representatives and are not meant to be exhaustive). We distinguish between terms that generally indicate the existence of an interpersonal dynamic versus those that delve deeper into characterising the specific nature of this dynamic. Specifically, we consider whether the term includes information about similarity: i.e., how one signal looks like the other; direction, i.e., whether one signal influences the other, or if they are bidirectional in their influence; frequency, i.e., the number of oscillations or cycles of a periodic signal that occur in a unit of time; time, i.e., temporal dynamics

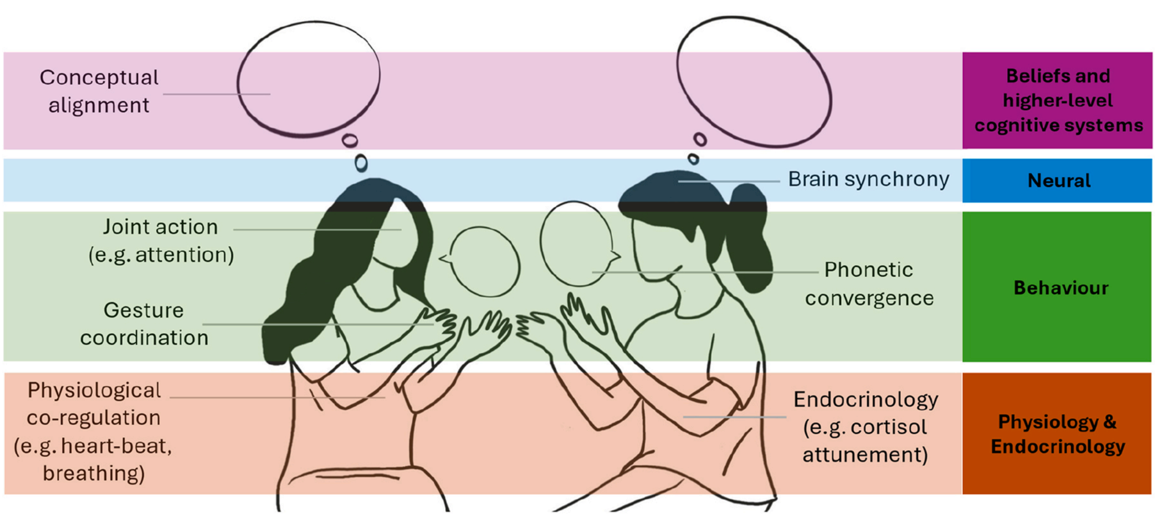

Fig. 3. | Interpersonal dynamics across different modalities during naturalistic interaction Relational Neuroscience is interested in modelling the interpersonal dynamics between at least two individuals during the free exchange of signals. Such signals come from different modalities, giving rise to convergence across physiological/endocrinological, behavioural, neural signals, and high-level cognitive systems, such as beliefs. Please note that this figure is meant only as a schematic representation of the intricate intra- and interpersonal dynamics at play during social interactions: in fact, there can be, and often are, complex associations between these modalities in various ways.

between two signals, including lags between signal peaks; and order, i.e., how one signal leads or lags the other.

Please note that within our Relational Neuroscience framework, we do not assume that the four modalities – i.e., neural signals, behavioural markers, physiological/endocrinological signals, and higher-level systems – as depicted in Fig. 3 and further described in Table 1 represent separate and independent units. Many studies (as outlined in more detail in Sections 3 and 4) not only show tight associations between neural signals and signals from the other three modalities, but also between signals from the behavioural and physiological/endocrinological signal modalities. Both intra- and interpersonal dynamics across modalities can be modulated in social interactions, hinting at the complexities of brain-body dynamics both within (Criscuolo et al., 2022) and between individuals (Reindl, et al., 2022).

In Box 1 **(Glossary)**, we furthermore present full definitions for a selection of these terms, focusing on those most commonly used and that are most distinctive, either at their level of analysis and/or for their informativeness. Note that many of these terms are often employed interchangeably in many studies.

In Section 3 below, we present a selective and illustrative overview of recent hyperscanning research within the realm of Relational Neuroscience clustered into different sub-fields.

3. Hyperscanning to answer Relational Neuroscience questions

Hyperscanning approaches represent an important paradigm shift from single/first-person neuroscience to two/second-person neuroscience (Schilbach et al., 2013). The applied technique simultaneously records neural activity from two or more brains and thereby enables a major step forward in understanding the mechanisms of inter-brain dynamics during socially shared experiences. In contrast to sequential scanning (see e.g., Hasson et al., 2004; M. Nguyen et al., 2019) assessing one single participant at a time, hyperscanning studies can grasp the unique effect of real-time interactive minds. This particularly holds true when hyperscanning is used in relatively unconstrained and naturalistic settings with mobile measures of brain activity (see e.g., Czeszumski et al., 2020). Hyperscanning approaches are still in their infancy, but the field is growing rapidly (see e.g., Carollo and Esposito, 2024). This section provides a selective and illustrative narrative overview of the literature where hyperscanning has been used to answer research questions within the realm of Relational Neuroscience. To do so, it non-exhaustively considers several different sub-fields separately and discusses the state of the art of each of them. Namely, we will consider studies on i) cooperation and communication in dyads and groups, ii) empathy for pain, iii) attachment and bonding and iv) developmental neuroscience. For each of these subfields, we also highlight which Relational Neuroscience dimension is of particular interest: this is meant to showcase the importance of that dimension for a specific field, although overlaps can and often do exist between dimensions and many experiments are likely to include both dimensions in their paradigms.

3.1. Cooperation and communication in dyads and groups

Social interactions involve a series of mutual and joint decisions by two or more individuals to complete a task, solve a problem, move in synchrony whilst playing music and dancing, and engaging in conversations while exchanging communicative signals. All these decisions can be summarised under the umbrella term of cooperation. In the following, we consider evidence showing that IBS is a marker of successful cooperation and communication, by reviewing both dyadic and group studies. With regards to the Relational Neuroscience dimensions (see Section 2.1*), of particular interest for cooperation studies is the interactivity dimension.*

At a very basic level, dyadic cooperation necessitates successful transfer of verbal and nonverbal information as part of interpersonal communication. To do so, people engaging in interaction need to coordinate their behaviours in order to facilitate such exchanges (e.g., turn-taking within conversations). Several studies have identified IBS as a neural correlate of these coordinating processes, suggesting that IBS may be a marker of (successful) communication and cooperation. Hyperscanning research has revealed increased IBS over frontal and temporal brain areas during verbal communication (e.g., T. Nguyen et al., 2020), gestural communication (e.g., Dumas et al., 2010; Schippers et al., 2009), and social touch (e.g., Goldstein et al., 2018). Research also showed a link between heightened IBS and visual contact during direct real-time interaction (e.g., Jiang et al., 2015b; Koul et al., 2023).

Communication is characterised by the inherently rhythmic or quasi-rhythmic exchange of many verbal and nonverbal signals. This likely leads to the emergence of mutual entrainment of brain rhythms of each person to the communicative rhythms of their interaction partner (e.g., Hasson et al., 2012; Hoehl et al., 2021). Therefore, neural entrainment between interacting partners emerges similarly to a radio being tuned to the correct input frequency. This bi-directional process is enhanced when interaction partners pay attention and adapt to each other, and has been associated with better mutual processing of communicative signals. Corroborating this idea, combining hyperscanning with detailed behavioural coding revealed that high levels of behavioural reciprocity and vocal turn-taking – that are indicative of mutual engagement and connection in a social exchange (e.g., Templeton et al., 2022) – relate to higher levels of IBS in mother-child pairs (e.g., T. Nguyen et al., 2020, 2021).

Further to the above, there is now convincing meta-analytic evidence (see e.g., Czeszumski et al., 2022) showing increased IBS particularly in prefrontal and temporoparietal brain regions during a variety of more advanced cooperative tasks with different amounts of complexity and motor and cognitive demands, ranging from relatively simple motor coordination (e.g., simultaneous button press; N. Liu et al., 2016) to more complex joint problem-solving (e.g., Tangram puzzles; Nguyen et al., 2020). Interestingly, IBS during cooperation does not only seem to be increased as such (compared to individual or control conditions), but also to be correlated to behavioural cooperation outcomes. For example, in an fNIRS hyperscanning study investigating cooperative problem-solving in mother-child dyads, IBS over the bilateral dorsolateral prefrontal cortex (DLPFC) and temporo-parietal junction (TPJ) during a joint Tangram puzzle task was positively correlated with the number of solved puzzles (Nguyen et al., 2020). In another fNIRS hyperscanning study in lover (versus friend and stranger) dyads, IBS over frontoparietal regions during a button-press task was positively correlated with a behavioural measure of button-press coordination (Pan et al., 2017). However, caution is advised regarding the anatomical specificity of such findings – even the meta-analytic ones –, because many studies, and particularly the ones employing fNIRS, often only assess IBS from a small number of pre-selected brain areas.

Though mainly correlative in nature so far, results of dyadic hyperscanning research thus corroborate the view that IBS is a neural correlate of successful communication and cooperation. High levels of IBS are likely indicative of high levels of mutual attention, efficient information transfer, and mutual predictability, which in turn support dyadic social coordination (also see Section 5 below).

Recent advancements within the field have enabled researchers to move beyond dyadic studies to extend the scope of multi-brain methodology to group settings. A central question thereby is whether IBS across several individuals associates with within-group coordination and cooperation. In a pioneering study conducted by Dikker and colleagues (2017), the authors utilised portable EEG devices to simultaneously record brain activity from a cohort of 12 students during regular classroom activities including group discussions. Findings revealed strongest IBS during group discussions, which the authors interpreted as reflecting shared attention. Specifically, shared attention may have enabled coordinated neural entrainment by "tuning" students' neural oscillations to the temporal structure of their shared surroundings. Another study using fNIRS hyperscanning looked at IBS during a drum beating task in groups of nine participants across a random,

Table 1
| **Terms used in Relational Neuroscience to describe the dynamics between signals originating from at least two people in a social context.** In the table, each term is considered with reference to i) the level of analysis at which it has been computed and ii) whether and how it is informative of the dynamic that it describes. Informativeness includes information about: *Similarity*: the degree to which one signal looks like the other, e.g., in terms of displaying the same behaviours or activity patterns; *Direction*: whether one signal influences the other, or if they are bidirectional in their influence; *Frequency*: number of oscillations or cycles of a periodic signal that occur in a unit of time; *Time*: temporal dynamics between two signals, including lags between signal peaks; *Order*: how one signal leads or lags the other. The label '*Not specified*' refers to the term being used with general and/or non-specific connotation.

Term	Level of measurements				Nature of the dynamic and informativeness
	Brain	**Behaviour**	**Physiology & Endocrinology**	**Higher level cognition (beliefs, goals, intentions)**	
Alignment	Neural alignment (L. Liu et al., 2020)	Verbal alignment (Campano et al., 2014); Conduct alignment (Fletcher et al., 2021)	Coital alignment (Pierce, 2000)	Conceptual alignment (Stolk et al., 2016); Linguistic alignment (Pickering and Garrod, 2006)	Similarity
Attunement	–	Motor attunement in dance (Jerak et al., 2018); Emotional attunement (Kerr et al., 2020)	Cortisol attunement (Di Lorenzo et al., 2022); Physiological attunement (Ostlund et al., 2017)	Affect attunement (Jonsson and Clinton, 2006)	Not Specified
Coherence	Brain coherence (Cui et al., 2012); dual-fNIRS wavelet transform coherence (Reindl et al., 2018); cerebral coherence (Stolk et al., 2014); dual-EEG partial directed coherence (Astolfi et al., 2011)	–	Physiological coherence (Murata et al., 2021)	–	Frequency, Time
Contingency	–	Social contingency (De Felice et al., 2021); behavioural contingency (Phillips et al., 2023)	–	Judgement contingency (Mutter et al., 2007)	Time, Direction
Coordination	Brain coordination (Basso et al., 2021)	Leader-follower behavioural coordination (H. Zhang et al., 2023); action (painting) coordination (Abraham et al., 2023)	Breathing coordination (Rochet-Capellan and Fuchs, 2014)	Joint action coordination (Cerullo et al., 2021)	Time
Co-regulation	–	Biological and behavioural co-regulation (Bornstein and Esposito, 2023)	Physiological co-regulation (Abney et al., 2021); parental co-regulation (Wass et al., 2019)	–	Time
Correlation	Dual-fNIRS inter-subject correlation (Piazza et al., 2020)	Lagged cross-correlation (Beebe et al., 2016)	–	–	Time, Similarity
(Dynamic) Coupling	Neural coupling (Stephens et al., 2010); inter-brain coupling (Dikker et al., 2021)	Sensorimotor coupling (Dumas and Fairhurst, 2021)	Autonomic coupling (Chatel-Goldman et al., 2014); cardiac and respiratory coupling (Müller and Lindenberger, 2011)	–	Time, Similarity
Convergence	–	Phonetic convergence (Mukherjee et al., 2018)		Semantic convergence (Salazar et al., 2021)	Not Specified
Covariation	–	–	Cortisol covariation (Engert et al., 2018; Meyer et al., 2019; Saxbe et al., 2015); physiological covariation (Waters et al., 2014)	–	Not Specified
Entrainment	Interpersonal neural entrainment (Wass et al., 2020)	Motor entrainment (Molinari et al., 2006)	–	–	Frequency
Homophily	Neural homophily (Parkinson et al., 2018)	–	–	Semantic homophily (Šćepanović et al., 2017);personality homophily (Noe et al., 2016); purchase homophily (Ma et al., 2015)	Not Specified
Mimicry	–	Motor mimicry (Hatfield et al., 2014); smile mimicry (Fasya et al., 2024)	Autonomic state matching (Wass et al., 2019)	Emotional mimicry (Hess and Fischer, 2014)	Direction, Order, Similarity
Mirroring	Neural mirroring (Endedijk et al., 2017; Hasson and Frith, 2016)	Behavioural mirroring (Ellingsen et al., 2020)	–-	–-	Similarity, Time, Frequency
Resonance	Neural resonance (Krautheim et al., 2019)	Motor resonance (Cracco et al., 2016)	Cortisol resonance (Engert et al., 2019)	–-	Similarity

(*continued on next page*)

Table 1 (*continued*)

Term	Level of measurements				Nature of the dynamic and informativeness
	Brain	Behaviour	Physiology & Endocrinology	Higher level cognition (beliefs, goals, intentions)	
(Social) allostasis	–	–	Allostasis dependence (Atzil et al., 2018)	—	Not Specified
Synchrony	Interpersonal neural synchrony (T. Nguyen et al., 2020); inter-brain synchronisation (Dumas et al., 2010); brain-to-brain synchrony (Azhari et al., 2019)	Biobehavioural synchrony (Feldman, 2017); sensorimotor synchronisation (Repp and Su, 2013)	Physiological synchrony (RSA) (Abney et al., 2021); synchronised arousal (heart rates) (Konvalinka et al., 2011); synchronised oxytocin release (Spengler et al., 2017)	Synchronised conceptual knowledge (Atzil and Gendron, 2017)	Not Specified

metronome-driven and cooperation (team-focused) condition (T. Liu et al., 2021). The authors found that IBS over fronto-temporal areas was highest during the cooperation drum beating condition, suggesting that shared mental representations with high efficiency of information exchange across the entire team may be a key component for IBS to emerge. Similar findings were reported in an EEG hyperscanning study by Reinero et al., (2020), where groups of four participants were asked to complete a series of problem-solving tasks either independently or as a team. Results showed that group IBS was stronger during team-based cooperation and correlated with collective group performance.

IBS in group settings can also be studied to investigate hierarchy, as it provides a neural correlate of different interpersonal dynamics between members of the same group. In fact, it is well known that most social groups are hierarchically structured (e.g., Sapolsky, 2005; Sidanius et al., 2001), and that the hierarchical structure and different status of within-group relationships shape interpersonal interactions among group members (e.g., Halevy et al., 2011; H. Zhang et al., 2023). Accordingly, some hyperscanning studies investigated the relationship between IBS, leader emergence and leader-follower interaction within hierarchical groups. For example, Jiang et al., (2015b) used fNIRS hyperscanning in groups of three participants while they were discussing a fictitious scenario. Data was analysed to reveal which of the three participants emerged as the leader and which remaining two participants as followers. The authors showed that IBS for the leader-follower pairs was higher than IBS for the follower-follower pairs in the left TPJ. In addition, leader-follower IBS was significantly higher during leader-initiated (compared to follower-initiated) communication, and this was significantly correlated with leaders' communication skills and competence. In another fNIRS hyperscanning study, groups of three participants were instructed to complete a creative problem-solving task in two conditions either involving externally appointed or spontaneously emerging leader and follower roles (He et al., 2023). Findings showed that, compared to the appointed leader-follower role condition, in the spontaneously emerging leader condition not only creative group outcomes were better, but also leader-follower IBS was higher over a number of brain regions, including the right angular gyrus (rAG), between the leader's rAG and the follower's right supramarginal gyrus, and between the leader's right middle temporal gyrus and the follower's right motor cortex. Importantly, IBS was associated with the degree of perspective-taking behaviours (e.g., ideas exchanges across group

Box 1
Glossary.

A selection of key terms most commonly used in Relational Neuroscience research

Alignment: The degree of similarity between different time series.
Attunement: The process of becoming aware and considering someone else's mental and emotional state.
Coherence: Mainly used by the fNIRS community to indicate the results of wavelet transform coherence (WTC) analysis, providing information on the extent to which two signals are related in both temporal and frequency domains.
Contingency: The extent to which knowledge of one event reduces uncertainty about another.
Coordination: Level of organisation of different elements of a system.
Co-regulation: The continuous process of modifying an interaction partner's behaviours and neural and physiological activity patterns.
Correlation/ covariation: Measure of the extent to which two variables or time series are linearly related.
Convergence: The process of converging to a similar state.
Dynamic coupling: The dynamic relationship between two signals – i.e., when one signal goes up, the other may go down at the same time or after a certain time lag. This is in opposition to mirroring.
Entrainment: A process whereby two interacting oscillating systems assume the same period.
Homophily: The tendency for people to seek out, or be attracted to those who are similar to them.
Mimicry: The unconscious or automatic imitation of gestures, behaviours, facial expressions, speech, posture and movements.
Mirroring: When two signals are identical in their temporal and frequency patterns. This is in opposition to dynamic coupling.
Resonance: The reinforcement or prolongation of an oscillation through reflection by another object (or agent).
Social allostasis: The process through which an individual's neurophysiology is actively co-regulated through social interaction with another individual.
Synchrony: The extent to which two or more signals are temporally related. This is often used as an umbrella term to define interdependence of multiple signals, but it does not refer to specific properties of the signal-to-signal relationship.

members).

Besides assessing IBS during within-group interaction as illustrated above, IBS can also be looked at when two (or more) groups interact with one another either cooperatively or whilst being exposed to a between-group conflict scenario. For example, a fNIRS hyperscanning study by Yang et al. (2020) looked at IBS during three-versus-three-person intergroup competitions. Participants within each group were asked to donate money from a personal financial endowment to their in-group fighting capacity. The group with the highest fighting capacity (cumulative donation) would beat the other group and eventually earn all the invested money from the personal financial endowments of the defeated group. The amount of money donated to the in-group was taken as a measure of inter-group hostility. Results showed that within-group IBS over the right dlPFC correlated with the degree of intergroup hostility applied to outcompete rival outgroups. Similarly, Zhang and colleagues (2023) examined IBS using fNIRS hyperscanning in two groups of three participants each that were either part of an "attacker" and a "defender" group and each had one self-elected leader. They discovered that the higher IBS was in the dlPFC of leader-follower pairs, the more followers reciprocated their leader's initiatives. This, in turn, resulted in the entire group being more successful to shield themselves against the out-group attacks.

Taken together, hyperscanning research in dyads and in larger groups has revealed that IBS emerges during interpersonal communication and cooperation in a range of different tasks and settings. Interactivity seems to be a driving factor, above and beyond shared sensory input, as IBS typically rises with increasing levels of mutual engagement (e.g., compared to rest and individual engagement) and significantly correlates with behaviours and interaction outcomes. This may be explained by the fact that IBS may reflect mechanisms of mutual attention and prediction. As illustrated by the studies discussed in this section, hyperscanning thus enables us to address interesting research questions pertaining to dyadic and group dynamics, including leader-follower relationships and inter-group processes. As such, it can reveal new pathways for modelling and potentially promoting interpersonal communication and cooperation within and across social group divides, including both neurotypical and neurodiverse individuals (see e.g., Zhou and Wong, 2024). In the next section we consider how this extends from shared motor coordination and communication tasks to shared emotional experiences.

3.2. Empathy for pain

As part of interpersonal exchanges, individuals often engage in the mutual sharing of affective and emotional states. In hyperscanning research, the scenario that has been most extensively examined to date involves the emergence of IBS associated with empathy for pain. With regards to the Relational Neuroscience dimensions (see Section 2.1*), of particular interest for research on empathy is the interpersonal closeness dimension.*

Empathy – the capacity to emotionally immerse oneself in someone else's affective and emotional experience – plays a pivotal role in nurturing interpersonal connections and societal harmony by facilitating the exchange of experiences, needs, and desires among individuals (see e.g., Hardee, 2003; Heath and Gray, 2022; Moudatsou et al., 2020; Riess, 2017; Singer and Klimecki, 2014; Zaki and Ochsner, 2012). The neural mechanisms underlying empathic processing have been extensively studied using single-person neuroimaging paradigms, most of which looked at empathic responses towards the suffering of others associated with pain experiences (for reviews see e.g., Fan et al., 2011; Lamm et al., 2011; Schurz et al., 2021). Several lines of research highlight an important role of a number of shared neural networks that activate both during first-hand experience of pain and the perception of a corresponding emotional or somatosensory state when observing pain in other people (see e.g., Corradi-Dell'Acqua et al., 2016; Gallese, 2003; Preston and de Waal, 2002; Rizzolatti and Craighero, 2004).

Building upon such first- and third-person neuroimaging evidence, initial hyperscanning studies have been conducted to better understand the interpersonal brain dynamics underlying empathy for pain. For example, Ellingsen et al., (2023) used fMRI hyperscanning in patients who were administered painful (versus non-painful) pressure either with a clinician present or in isolation. Findings showed that patients reported lower pain ratings of painful pressure when a clinician was present. Furthermore, they revealed that clinicians showed increased dynamic dlPFC IBS with patients' somatosensory (S2) activity during painful pressure, and that the strength of patient-clinician S2-dlPFC IBS was positively correlated with patient self-reported therapeutic alliance (i.e., the patient self-reported quality of clinical consultation prior to the scanning procedure). Another study by Peng et al., (2021) used EEG hyperscanning during a pain-sharing task in which high- or low-intensity pain stimulation was randomly delivered to one participant of a dyad on different experimental trials. The authors reported that expecting high- (versus low-) intensity pain was associated with increased IBS of sensorimotor α-oscillations. Furthermore, IBS of sensorimotor α-oscillations was related to mutual affective empathy because it mediated the effects of pain-stimulation intensity on mutual affective sharing for partner-directed pain. Together, these findings suggest that mutually sharing affective states – here indexed by empathy for pain – yields increased IBS, which may also relate to prosocial behaviour and dyadic emotion regulation.

In summary, IBS emerges during shared emotional experiences, such as when one person witnesses another experiencing pain. The degree of IBS in these situations varies depending on the degree of empathy experienced and the interpersonal closeness of the interactants. As such, this research has important implications in the context of clinical work and for understanding how relationships are formed and maintained (see next section).

3.3. Attachment and bonding

Attachment and bonding constitute vital functions for human survival, development, and mental and physical health across the lifespan. Below we summarise the emerging hyperscanning literature which has been interested in establishing links between IBS and attachment and bonding in child-parent and romantic partner dyads. With regards to the Relational Neuroscience dimensions (see Section 2.1*), of particular interest for the study of attachment and bonding is the interpersonal closeness dimension, and how it develops through interactivity.*

According to the most recent conceptualisations – which mainly draw upon social baseline theory and an evolutionary theory of social regulation (Atzil et al., 2018; Coan and Sbarra, 2015) –, the principal role of attachment and bonding is linked to energy conservation and co-regulation through social allostasis during significant environmental challenges (e.g., threat, illness, etc.). Attachment is thus thought to represent an innate social survival strategy that is triggered under distress, because being close to others allows a "care seeker" to draw upon a caregiver's resources for co-regulation (White et al., 2023). Bonding, in turn, ensures that complementary caregiving behaviours from a caregiver emerge and are efficiently directed towards the "care seeker" (Mikulincer and Shaver, 2019). Bio-behavioural synchrony (BBS) – the alignment of behaviour, physiology and brain activity during and shortly after social interaction – is regarded as a key interpersonal process - not only in the establishment and maintenance of close emotional bonds related to attachment and bonding, but also for efficient co-regulation and social allostasis (Feldman, 2017). With the emergence of hyperscanning, there has thus naturally been great interest in establishing links between attachment and bonding in child-parent and romantic partner dyads as well as BBS, and particularly IBS.

Regarding child-parent attachment and parent-child bonding, several recent investigations reported increased IBS during different interactive tasks in dyads of biologically related children and their mothers as opposed to pairings of children with stranger females (e.g., Reindl et al., 2018, 2022). Recent data showed that IBS during cooperation correlates with dyadic interaction quality in mother-child dyads (T. Nguyen et al., 2020), caregiving beliefs in father-child dyads (T. Nguyen et al., 2021) and self-reported child-mother attachment (Miller et al., 2019). Furthermore, in a first study linking IBS during collaboration in a large sample of mother- and father-child dyads with narrative attachment representation measures obtained from both parents and children, individual differences in maternal attachment representations coincided with IBS within frontal regions among mother-child dyads (Nguyen, Kungl et al., 2024).

There is also accumulating evidence that BBS may be involved in attachment and bonding within romantic relationships (e.g., Djalovski et al., 2021; Kinreich et al., 2017; Shao et al., 2023). For instance, naturally occurring patterns of electrodermal activity and behavioural motion in men and women were associated with the outcome of a first date (Zeevi et al., 2022). Furthermore, participants who showed a high consensus with their romantic partner in the evaluation of relationship quality exhibited increased responses to affective touch of the romantic partner in reward-associated brain areas (Kreuder et al., 2017). More specifically pertaining to co-regulation and social allostasis under distress, one study found that hand holding in romantic partners during pain administration correlated with increased IBS in a network that mainly involved the central regions of the pain target and the right hemisphere of the pain observer, and further correlated with analgesia magnitude and observer's empathic accuracy (Goldstein et al., 2018). Further supporting evidence comes from a study combining synchrony in skin conductance responses (SCR), subjective pain ratings and brain activity obtained through fMRI, probing the effects of social support on pain processing (Reddan et al., 2020). The study found that synchrony in couples' SCR was correlated with reductions in self-reported pain, and individual differences in synchrony were correlated with the partners' trait empathy. Increased IBS when one interaction partner is in distress and the other partner offers co-regulation may thus reflect the efficiency of social allostasis.

Variation in IBS as a function of individual differences in relationship quality and attachment has not yet been directly evidenced. However, previous data from single-person fMRI and EEG studies suggest that a secure-like attachment relationship may support, whereas an insecure and particularly avoidant attachment may hinder underlying neuropsychological processes, and that affective touch transmitted by unmyelinated C-tactile (CT) fibers may be one of the underlying mechanisms (e.g., Coan et al., 2006; Krahé et al., 2016, 2018). Likewise, it has been shown that traumatic experiences are linked to altered behavioural evaluation and neural processing of social touch (e.g., Maier et al., 2020; Strauss et al., 2019) and it has been suggested that disrupted touch processing after trauma exposure may impair social interactions and confer elevated risk for future stress-related disorders (e.g., Stevens et al., 2024).

Despite emerging links between IBS and attachment and bonding, more work is still needed to fully understand this relationship. For example, recent evidence suggests that more IBS may not always be better for interaction and relationship functioning and even linked to insecure attachment (e.g., Nguyen, Kungl et al., 2024). Along these lines, co-regulatory social interactions are unlikely to be characterised by constant and indiscriminately high BBS and IBS. Instead, there are dynamic sequences of increased and decreased BBS and IBS that likely reflect rupture and repair processes (e.g., Mayo and Gordon, 2020). It is exactly this dynamic nature of BBS and IBS that, in association with attachment and bonding, is thought to contribute most importantly to child brain development via social allostasis (e.g., Atzil et al., 2018; Atzil and Barrett, 2017).

3.4. Developmental neuroscience

Developmental researchers are increasingly embracing the opportunity to study interpersonal brain dynamics by means of hyperscanning within and across different age groups. This work has yielded new insights into the interpersonal mechanisms of social and emotional development from infancy to adolescence. With regards to the Relational Neuroscience dimensions (see Section 2.1*), of particular interest for developmental neuroscience is the interactivity dimension and how it shapes the interpersonal closeness dimension long-term.*

A growing body of empirical evidence shows that IBS emerges early in human development and can already be observed in the early interactions between infants and their caregivers. According to the BBS framework (Feldman, 2017; see Section 3.3), the coordination of behavioural and biological (including IBS) dynamics during social contact is a fundamental characteristic of human attachment relationships with deep ontogenetic roots in the infant-caregiver bond.

The youngest age at which IBS has been documented in infant-caregiver dyads to date is at 4–6 months (Nguyen et al., 2021, 2023). Using fNIRS hyperscanning Nguyen et al. (2021) found that caregivers and infants showed more synchronised brain activities when the caregiver held the baby compared to when both were seated apart. During a face-to-face free play interaction, longer durations of affectionate touch (e.g., soft stroking) were also positively associated with IBS. These findings underline the crucial role of social touch as a communication channel at this young age. Yet, infants and caregivers also already exchange vocalisations in so-called proto-conversations at this age. An in-depth analysis of the vocal turn-taking patterns in the same dyads during free play revealed that higher turn-taking frequency was associated with enhanced IBS (Nguyen et al., 2023). In slightly older infants, at 9–15 months, fNIRS hyperscanning further showed that caregiver-infant IBS was higher when infants and caregivers were engaged in a face-to-face interaction with each other, compared to when each was interacting with another person in the same room (Piazza et al., 2020). Moreover, higher levels of IBS were observed around moments of mutual gaze and infant smiling, confirming the role of gaze and emotional expressions as further early emerging modes of communication. Taken together, like in adult dyads, IBS between infants and caregivers seems to be linked to mutual engagement and the exchange of communicative signals in face-to-face interactions.

Evidence from EEG hyperscanning studies with infants also hints towards mutual engagement as a facilitator of IBS. Leong et al. (2017) report higher levels of mutual influence between 8-month-old infant and adult EEG time series during eye contact compared to averted gaze. Yet, another study did not confirm the proposed role of mutual gaze onsets for simultaneous phase-resetting of neural oscillatory activity in infants and adults (Marriott Haresign et al., 2023). Thus, the mechanistic role of mutual gaze for interpersonal alignment of brain rhythms between infants and adults remains disputed. Supporting a general link between mutual engagement and IBS in infant-adult pairs, Endevelt-Shapira et al., (2021) report higher levels of connectivity between caregiver-infant EEG time series compared to caregiver-stranger dyads. Interestingly, this difference was attenuated in the presence of maternal body odour, which also induced greater behavioural social engagement in infants, hinting at a role of chemo-signals in facilitating allo-parenting - i.e., care provided by individuals other than the parents.

While longitudinal research on IBS is still lacking, evidence from cross-sectional studies suggests that it continues to play a vital role in caregiver-child interactions in preschool and early school age. Beyond infancy, the first study providing evidence that caregivers establish IBS with their 5- to 9-year-old children applied an fNIRS hyperscanning paradigm (Reindl et al., 2018). The study revealed that children synchronise PFC activation specifically with their caregiver, as opposed to a stranger, during a computerised collaboration task, but not during competition. Moreover, the relation between parents' and children's emotion regulation skills (as assessed through questionnaires) was mediated by the neural synchrony the dyads established during cooperation. Though correlational in nature, this finding speaks to a potential link between parent-child IBS and children's acquisition of adaptive emotion regulation skills from their parents. This proposed link between parent-child emotion co-regulation and IBS was further corroborated by a study showing that higher self-reported parental stress (a challenge to adaptive co-regulation) was related to reduced levels of mother-child neural synchrony during movie-watching in preschoolers (Azhari et al., 2019).

Using a less controlled, more naturalistic task than Reindl and colleagues, Nguyen et al. (2020) confirmed that preschoolers and their caregivers synchronise frontal and temporoparietal brain activities during cooperation. Higher levels of IBS were observed when children solved a tangram puzzle task together with their mothers compared to solving the same task alone. While this general pattern was later replicated for fathers (Nguyen et al., 2021), the behavioural correlates of IBS differed relative to biological parent sex. In mother-child pairs behavioural reciprocity and child agency were found to be positively related to IBS during cooperation (Nguyen et al., 2020). Similarly, a high frequency of vocal turn-taking, which is indicative of a high degree of mutual engagement in a conversation, was related to higher IBS in the same mother-child pairs (Nguyen et al., 2020). Overall, this suggests a rather active role of the child in establishing IBS with the mother by preschool age. In father-child pairs, however, the same correlational patterns were not observed. Instead, fathers who self-reported a higher degree of involvement in caregiving and a strong appreciation of their role as a father displayed the highest levels of IBS with their children. This result leaves open what exact behavioural interactional patterns support father-child synchrony during an ongoing social exchange for further investigation. Yet, it clearly points to the importance of fathers' self-reported attitude toward their role as a parent when connecting with their child (Nguyen et al., 2021).

Apart from its established links to communication and collaboration, IBS has been repeatedly shown to facilitate social learning among adults (Pan et al., 2018, 2021). An fNIRS hyperscanning study by Piazza and colleagues (2020) offered evidence that it relates to learning in children as well. Preschoolers in this study engaged in joint book reading with an adult experimenter. The picture book contained novel words and objects. IBS in the parietal cortex between child and experimenter during joint reading related to children's later recollection of the novel object labels. This suggests that similarly to what has been observed in adults, neural synchrony is linked to learning in children.

Relatively few studies so far have addressed IBS in adolescents, although this developmental phase is highly interesting in the context of Relational Neuroscience. This is because adolescence is marked by both a high degree of anatomical and functional brain maturation and restructuring (Fuhrmann et al., 2015) and by profound changes in social relations, including heightened importance of peer-relations and the establishment of first romantic partnerships (Steinberg and Morris, 2001). An fNIRS hyperscanning study with children and adolescents aged 10–18 years replicated previous findings of increased IBS during a computer-based cooperation task with the parent compared to a stranger (Reindl et al., 2022). Using the same task, no differences in neural synchrony in adolescents with and without an autism diagnosis were observed during cooperation with their parent (Kruppa et al., 2021). The latter study pointed to a potential age-effect in the non-autistic participants in the sense that IBS with the parent seemed to decrease during cooperation but increase during competition with increasing age. While pointing to potentially interesting age-related changes of neural synchrony patterns in this age range, replication across different samples and tasks, ideally including longitudinal investigations, seem warranted before drawing firm conclusions on developmental changes in the role of IBS.

From a Relational Neuroscience perspective, peer-interactions in adolescence are an especially interesting field of research that has barely been tapped by existing hyperscanning studies to date. Dikker and colleagues (2017) assessed a group of high-school students aged 17–18 years with EEG hyperscanning during regular classroom interactions. Higher levels of engagement during class were reflected in higher degrees of IBS. IBS was further related to social dynamics in class, especially how much students liked the teacher and each other. The study offers an important proof-of-concept for hyperscanning in ecological contexts and points to IBS as a highly interesting marker for peer-relations and interactional dynamics in real-life contexts that hopefully inspires further hyperscanning research in this age group. More recently, M. Yang et al., (2023) showed that adolescent dyads exhibited greater IBS compared to adult dyads during a cooperative game over frontal and parietal regions. In line with evidence showing the importance of peer-influence and peer-cooperation in adolescence (Laursen and Veenstra, 2021), these findings point at the importance of investigating interpersonal neural (and behavioural) dynamics across the life-span and at different stages of development.

Taken together, developmental Relational Neuroscience research has revealed that the two core dimensions of interactivity and closeness relate to IBS in dyads across human development, from early infancy through to adulthood. While research into caregiver-infant and caregiver-child dyads has enhanced our understanding of early communication and emerging social bonds (see also Section 3.3), the field has barely tapped the potential of hyperscanning to promote our understanding of child-peer relationships. Furthermore, while first efforts into multimodal scanning of brain, behaviour, physiology, and endocrine processes have been put forward, including in developmental research (see next section), longitudinal research into the development of intra- and interpersonal brain-body and brain-brain dynamics is still lacking.

4. Beyond hyperscanning

In the previous section, we have presented evidence for the 'hyperscanning effect', where synchronisation patterns emerge across brain signals of interacting minds. Yet, the most commonly used hyperscanning methods suffer from a number of limitations, including constraints in temporal (fNIRS) and spatial (EEG) resolution and impose certain restrictions on the research participants, such as requiring them to wear sensors. Furthermore, interpersonal synchronisation is not limited to brain signals. It extends to at least three other modalities, namely behaviour, physiology and endocrinology, which are together with brain activity summarised as BBS (Feldman, 2017). In what follows, some examples of synchronisation in behaviour, physiology and endocrinology will be provided, without the aim of these examples being exhaustive. Note that, besides the domains included in BBS research, additional measures can include self-report questionnaires, semi-structured interviews, etc., but we will not review these here as these typically target trait-like variables, higher-order beliefs and concepts (see Fig. 3), and not real-time interactional dynamics.

Synchronisation in *behaviour* can be observed in a variety of measures and – similarly to what was discussed for IBS (see Section 3) – it has been found to correlate with interaction quality. Interaction partners are known to typically synchronise their facial expressions and gesturing during social interactions (e.g., (Shadaydeh et al., 2021). Similar patterns have been found to spontaneously emerge for mutual gaze (e.g., Koul et al., 2023; Leong et al., 2017), verbal turn-taking (e.g., Nguyen et al., 2021) and body movements in dance (e.g., Bigand et al., 2024). Furthermore, an important component of social relationships is the development of shared mental representations of meanings between individuals, that is, a common language, which develops through mutual adaptation to one another's linguistic behaviours (including syntactic, phonological and semantic factors) – a process also known as linguistic alignment (Pickering and Garrod, 2006). As such, linguistic alignment constitutes reflections of social communication. For example, it has been shown that clinician-patient pitch synchrony and linguistic prosody correlate with the quality of the therapeutic relationship, improving psychotherapy outcomes (e.g., Reich et al., 2014). Moreover, evidence suggests that therapist-client movement synchrony can be positively related to therapeutic success, especially when therapists appear to lead movement synchronisation (e.g., Altmann et al., 2020; Ramseyer and Tschacher, 2016).

In the *physiology* domain, synchronisation has been observed, for example, at the level of the autonomic nervous system by means of heart rate variability (Suga et al., 2019) and respiration (Goldstein et al., 2018). Nguyen et al. (2021) furthermore measured mother-infant brain activities (fNIRS), physiological arousal (respiratory sinus arrhythmia) and behaviour (social touch and affect) in different conditions. Findings revealed that both neural and physiological synchrony between caregiver and infant were elevated during a face-to-face free play interaction compared to a condition with no direct contact. During the free play interaction, divergent behavioural correlates were observed: While neural synchrony was related to duration of affectionate touch, physiological synchrony was related to infant negative affect. These results hint at different mechanisms and potential functions of neural versus physiological synchrony. Whereas neural synchrony seems to be related to communication across different signal modalities, physiological synchrony may allow for early co-regulation in caregiver-infant dyads (see e.g., Feldman, 2011; Wass et al., 2019). In fact, infant expressions of negative affect induce arousal in the caregiver and ideally elicit comforting behaviours to calm the dyad down again. Supporting this view, using whole-day electrocardiographic recordings, Wass et al. (2018) showed that caregivers tend to mimic their babies' autonomic state preferentially when babies' arousal is high and requires the caregivers' co-regulation. This converging evidence is another important reminder that "more synchrony" is not always better for the interaction or the participating individuals. Instead, flexibly switching between more and less synchronised states may be optimal (Mayo and Gordon, 2020). Furthermore, these findings help to illustrate that synchrony on different levels of observation (e.g., neural, physiological) can have very different mechanisms of emergence and functions. For a more extensive overview of the physiological synchrony literature, please refer to recent systematic reviews and/or meta-analyses by e.g., Mayo et al. (2021), DePasquale (2020), and Miller et al. (2023).

With regards to *endocrinology*, synchronisation has been reported in stress hormones (e.g., salivary cortisol; Doerr et al., 2018) over durations of one to five days, as well as in single laboratory sessions (for a review see Engert et al., 2019). In this context, numerous studies have shown that psychosocial stress can be resonated with (e.g., Engert et al., 2019; Erkens et al., 2019; Schury et al., 2020). The primary focus in empathic stress studies is usually directed towards synchronisation in physiological variables such as measures of autonomic and particularly sympathetic activity (i.e., facial thermal imprints, heart rate, inter-beat interval, pre-ejection period, respiratory sinus arrhythmia) as well as salivary cortisol. Across studies, findings generally show that stress resonance as indexed by physiological synchronisation has a higher likelihood to arise in emotionally close relationships (e.g., romantic partners, mother-child pairs, Blasberg et al., 2023; Waters et al., 2017) and with spatial proximity (i.e., in real-presence), but can also occur in strangers and from simple exposure to videos (e.g., Engert et al., 2014). Granting further ecological validity to such physiological stress resonance shown in the laboratory, one study found that the extent to which women resonated with their partner's stress in the lab was linked to their extent of cortisol covariance in every-day life (Engert et al., 2018).

Given these promising physiological stress resonance findings, research is currently underway to also investigate the underlying brain processes within relational dynamics to elucidate how synchrony in physiology may be associated with synchrony in brain activity. To date, we are only aware of one published fNIRS hyperscanning study that looked at dyadic IBS during acute stress induced in the laboratory and revealed increased IBS over the right TPJ in the stress (versus a control) condition (Lin et al., 2023). However, this study did not collect any physiological stress measures. Obtaining more insights into the association between IBS and physiological stress resonance will build the groundwork for the development of future intervention strategies to reduce empathic stress load in vulnerable settings (e.g., social care work) and individuals (e.g., children or partners in chronically stressed families).

Beyond stress-related hormones, the role of other hormones and neurotransmitters requires further attention in hyperscanning research. For instance, correlations between parental and child salivary oxytocin have been observed and linked to parental caregiving behaviours and child social reciprocity (Feldman et al., 2013). Furthermore, intranasal application of oxytocin was shown to increase behavioural coordination and neural synchrony between interacting men (Mu, Guo, and Han, 2016). Neuropharmacological work can thus reveal processes of physiological synchronisation as well as its links to IBS.

Taken together, such multifaceted evidence of BBS is consistent with an embodiment perspective that implies reciprocal relationships between bodily-motor and cognitive-emotional processes (see e.g., Hamilton, 2021; Ramseyer and Tschacher, 2011). Recently, there has been a notable trend towards more multidisciplinary approaches to scientific investigations (see e.g., Arredondo, 2023; Crum, 2021; Disis and Slattery, 2010; Shamay-Tsoory and Mendelsohn, 2019; Stangl et al., 2023). In line with this trend, Relational Neuroscience research advocates for the combination of neuroscientific techniques, such as neuroimaging hyperscanning, alongside other multi-modal approaches. One example of such a multi-modal approach within the realm of Relational Neuroscience has been suggested as part of an integrative theoretical and methodological framework called the "5E approach". In this approach, the "E"s stand for embodied, embedded, enacted, emotional, and extended perspectives of empathy, highlighting the relevance of studying empathy as an active interaction between embodied agents, embedded in a shared real-world environment (Troncoso et al., 2023). Overall, such a holistic approach is required to mechanistically understand the dynamics governing interacting minds and to accurately model human sociality.

5. General discussion

5.1. Overarching theories that can be developed and tested through hyperscanning research

In the previous sections, we have summarised the surging empirical evidence for the 'hyperscanning effect', showing the variety of social contexts where synchronisation between brain signals of interacting individuals emerges. However, the question remains of what this phenomenon means. Several theories on the potential mechanisms that may underlie the emergence of IBS during social exchange, as well as its potential functions, have been put forward. These theoretical proposals can be roughly clustered around four major points of focus, which we briefly review in turn: communication, social learning, mutual prediction, and co-regulation.

Several early theoretical proposals focused on the role of *communication* in explaining the 'hyperscanning effect' itself as well as its conduciveness in social interactions (e.g., Dumas, 2011; Hasson et al., 2012). For example, based on the well-established role of neural tracking for speech perception (Giraud and Poeppel, 2012), Hasson and colleagues (2012) propose that IBS may arise from the mutual exchange of rhythmic communicative signals, such as speech. In a verbal conversation, auditory brain regions of the listener will entrain to the speech signal – and thus the motor system – of the speaker. As neural speech tracking is enhanced by attention, mutual attentiveness during a conversation facilitates the resulting synchronisation of brain activities. Consequently, speech signals will be amplified in the respective listener's auditory system promoting shared understanding. Extending beyond speech signals to apply a similar logic to non-verbal signals, Dumas (2011) suggests that interpersonal perception-action loops emerge during a social interaction, including non-verbal exchanges, such as gestural imitation. He proposes that the resultant neural synchronisation facilitates information transmission between interlocutors. This account is supported by evidence reviewed above, showing that IBS is greater in 'successful' communicative interactions, and can be further tested by modelling IBS with reference to a large range of behavioural communicative signals (both verbal and non-verbal). As IBS is mainly conceptualised in directly communicative contexts here, the focus in this area of research has been on the interactivity dimension (see Section 2.1). Although these theories first and foremost address how IBS emerges within social interaction through mutual entrainment, they also suggest a potential function, namely facilitated communication.

Building on these proposals of momentary communicative benefits of IBS, other authors have argued for its role in promoting long-term *social learning* (see e.g., Pan et al., 2020; Shamay-Tsoory, 2022). In her interbrain plasticity model, Shamay-Tsoory proposes that social learning exchanges induce both short- and long-term experience-dependent changes in intra-brain and inter-brain functional connectivity patterns. Specifically, during social learning, reciprocal interpersonal feedback loops (e.g. back-channelling) between teacher and learner are suggested to induce neural synchrony. Over repeated learning sessions, IBS is predicted to relate to both skill acquisition and an improvement in the ability of learner and teacher to synchronise in future exchanges. This account can be tested via paradigms where teacher-learner dynamics are tracked over multiple sessions and are considered both at the dyadic and individual levels. While the interactivity dimension has so far been stressed in social learning accounts, changes in long-term connectivity patterns may well be bidirectionally related to interpersonal closeness too. Future studies should explore this dimension and how it modulates interpersonal dynamics in relation to IBS and learning benefits.

Complementing these theories focusing on information exchange, several accounts have pointed to the role of *mutual prediction*, explaining how and why IBS emerges (see e.g., Hamilton, 2021), including its consistent association with improved cooperation performance (see Czeszumski et al., 2022). Koban and colleagues put forward the view that continuous mutual prediction and behavioural alignment during social interactions may reduce computational costs by way of reducing prediction error, in line with predictive processing accounts (Koban et al., 2019). Spontaneous synchronisation of behaviour (and associated neural activity) may thus arise in social interactions as a reflection of neural computational efficiency. Increased predictability in synchronised interactions will in turn facilitate communication due to freed-up computational resources (interactivity dimension). This may also promote affiliative bonding and group cohesion (interpersonal closeness dimension) through engagement of the reward circuitry (Hoehl et al., 2021). In the long run, increasing efficiency in mutual prediction and associated changes in inter-brain functional connectivity may underlie social learning and support mutual understanding (see Mayo and Shamay-Tsoory, 2024). Multi-modal cross general-linear model analysis, where behaviour, physiology and brain signals from all interactants are modelled together, represents a key approach to test this account. Notably, in mutual prediction accounts, IBS has alternately been identified as the outcome of predictive processing (Hamilton, 2021) or its facilitator (Koban et al., 2019), so the question whether mutual prediction explains the emergence of IBS or should be considered as its function, or both, has not been settled yet.

The attachment- and bonding-related function of IBS has also prominently been addressed in theoretical accounts focusing on its co-regulatory aspects (e.g., Gvirts & Perlmutter, 2020; Feldman, 2017; Atzil and Gendron, 2017). These accounts point to the role of interpersonal BBS in the early *co-regulation* of the child's physiological and emotional needs through the caregiver. Based on early experiences of sensitive caregivers responding to the child's signals and needs, children learn how to co-regulate and 'tune-in' their internal bodily processes to those of the people interacting with them (see e.g., Atzil et al., 2018). Long-term, this co-regulation process supports the development of adequate representations and predictions about positive social interactions and relationships. This enables one to competently engage in social exchanges and learn how to form and maintain social bonds with others throughout the lifespan, including with peers and later with romantic partners (interpersonal closeness dimension). Thus, the focus is here on the proposed function of IBS in promoting long-term attachment and bonding. This account would benefit from longitudinal and developmental experimental paradigms, with studies looking at child-caregiver interaction and how this shapes future adult interactions, across physiological, endocrinological and neural levels (see e.g., Ulmer Yaniv et al., 2021).

Notably, the above theoretical accounts are not necessarily competing or mutually exclusive. In fact, the 'hyperscanning effect' seems to be such a ubiquitous phenomenon, arising in different contexts and between various types of interaction partners, that various pathways and functions are conceivable. Several theoretical accounts address this complexity. For instance, it is often pointed out that IBS seems to operate at different hierarchy levels, from spurious coupling due to similar perceptual input to interpersonal alignment of goals and semantic representations (e.g., Dumas and Fairhurst, 2021; Jiang et al., 2021), often operating on different time scales (e.g., Hoehl and Bertenthal, 2021; Piazza et al., 2021). Similarly, it is acknowledged in many theoretical approaches that "more synchrony" is not always better and that there probably is such a thing as "too much synchrony". Specifically, Mayo and Gordon (2020) put forth a model of flexible synchrony pointing to the dynamic nature of social interactions that involve changes in the degree of interpersonal synchrony over time depending on contextual and individual factors. The interplay of endogenous and exogenous factors in modulating synchrony has further been supported by empirical evidence (Dikker et al., 2020). In their model, Dikker and colleagues (2020) describe external synchronisers, individual momentary states (e.g., motivations) and traits (e.g., personality) as well as dyadic factors such as social closeness that play into dynamic changes in mutual engagement and synchrony over time. Therefore, scholars agree on the complexity and the myriad of factors that play a role in the emergence of the 'hyperscanning effect'. Yet, mutual attentiveness to each other and shared attention toward exogenous stimulation seem to be major determinants of the degree to which IBS arises and wanes during social interactions (see e.g., Dikker et al., 2020; Hasson et al., 2012; Hoehl et al., 2021).

Finally, the question of whether IBS constitutes a mechanism underlying social communication and cooperation, or merely a neural correlate of these mechanisms remains a topic of debate (see e.g., Gvirts Provolovski and Perlmutter, 2021; Holroyd, 2022; Moreau and Dumas, 2021; Novembre and Iannetti, 2021). While this is not a critical question in light of the different accounts reviewed here, which usually discuss the 'hyperscanning effect' as a result or biomarker of several underlying processes, e.g., neural entrainment to communicative signals, mutual prediction, and shared attention, it is certainly a question of theoretical interest. Discriminating between the correlational versus the causational role of IBS in social interaction poses a major challenge for future research in Relational Neuroscience. We discuss this in the section below.

5.2. Outstanding theoretical challenges

One of the latest debates in the field revolves around clarifying the origin and meaning of interpersonal dynamics (see e.g., Novembre et al., 2023; Verga et al., 2023), especially IBS (see e.g., Hamilton, 2021; Holroyd, 2022; Novembre and Iannetti, 2021). Hyperscanning studies yield insights into social phenomena beyond what single-scanner studies provide. We have called this the 'hyperscanning effect'. Yet, the exact nature of this effect (or bonus) is often difficult to assess (see e.g., Holroyd, 2022). If the objective was to record neural data in a social context that was ecologically valid, then it would suffice to collect those data from only a single individual as they interacted with a partner. Alternatively, if one wanted to relate neural data between two (or more) individuals, then one could do so from multiple participants exposed to the same stimuli (like a movie) even if they never actually interacted with one another (see e.g., Nastase et al., 2019; Yeshurun et al., 2021). However, the 'hyperscanning bonus' derives its value from *simultaneously* recording the brain activity of two (or more) *interacting* individuals. Thus, for example, hyperscanning could be used to demonstrate that the relationship between the brain states of two people differ depending on whether they watched the same movie together or alone (see e.g., De Felice et al., 2024), which requires recording the brains of *both* members of the dyad *while* they interact.

However, the *mechanistic* meaning of the bonus can still be difficult to infer. In principle, the bonus indicates a state of shared social experience. Consider a hypothetical hyperscanning experiment involving participants diagnosed with autism, which has been associated with atypical behavioural and IBS (see e.g., Key et al., 2022; McNaughton and Redcay, 2020; Wang et al., 2020; Zhou et al., 2022). If an autistic person and a neurotypical person exhibited less IBS while watching a movie together, compared to an individual watching condition, than did two neurotypicals, then one could conclude (given sufficient statistical power) that at least one of the two individuals in the first dyad were relatively insensitive to the presence of their partner during the movie. In this case, the 'hyperscanning bonus' would reveal something about the social dynamics associated with autism. Furthermore, follow-up analyses could identify the specific neural systems underlying this diminished response, which is an opportunity made possible only because of the bonus.

Still, the 'hyperscanning bonus' cannot on its own tell us whether IBS *causally* modulates social interactions or whether it is a byproduct of those interactions. In other words, does reduced IBS in autism reveal the pre-existing fact of atypical social dynamics or does the phenomenon give rise to the atypicality? This question is not just of academic interest as the latter possibility holds out the potential for the development of novel therapeutics. Causal evidence for IBS requires an exceptionally high standard of proof (see e.g., Holroyd, 2022). Techniques for doing so are only starting to be developed, including methods involving non-invasive brain stimulation (e.g., Novembre and Iannetti, 2021) and neurofeedback (e.g., Gvirts Provolovski and Perlmutter, 2021; Kostorz et al., 2023) in humans, direct interventions in animal models (e.g., Kingsbury et al., 2019; Rose et al., 2021; Zhang and Yartsev, 2019), and statistical efforts to infer causal mechanisms from correlational data (e.g., Bilek et al., 2022). In particular, multi-brain stimulation reverts the logic of hyperscanning – which can only measure IBS as a function of other variables (e.g., behaviour) - and considers IBS an independent variable, which can be modulated in order to study the effects of such modulation on different aspects of behaviour. Recently, this approach has been implemented and proved feasible among diverse research groups (see e.g., L. Chen et al., 2023; Lapate et al., 2024; Lu et al., 2023; Pan et al., 2021).

This tension between the epiphenomenal and causal interpretations of the 'hyperscanning effect' highlights one of the most pressing issues within the field: a lack of widely-accepted theory about the origin and role of IBS (Holroyd, 2022). Fortunately, current efforts are rising to this challenge. For example, computational simulations have explored whether low-frequency (theta band) coupling between dynamically interacting agents can support IBS at higher frequencies (gamma band) (Moreau et al., 2022). Principles of active inference and predictive coding have also been applied to simulate generalized synchrony between singing birds (see e.g., Friston and Frith, 2015; see also Bilek et al., 2022). In addition, multi-brain stimulation has been used to induce IBS between interacting agents and test the causal role of IBS on specific cognitive processes such as music learning (see e.g., Pan et al., 2021). These examples, despite the need to be replicated, illustrate how the 'hyperscanning bonus' may indicate a causal mechanism rather than just an epiphenomenon. Future work should develop such theoretical and modelling approaches further and, ideally, instantiate the predictions in physical systems (i.e., in robots). Doing so would provide proof of principle that the bonus can be sustained despite physical limitations on the communication channels between real agents.

5.3. Implications and future directions

Research in Relational Neuroscience may have substantial implications for many aspects of society, virtually any context involving social dynamics. Despite still being far from closing the gap between research and implementation, an area of society where Relational Neuroscience research is growing in popularity is *education*: modelling the interpersonal dynamics arising within the classroom and between learners and teachers may advance current training strategies and develop new educational interventions (see e.g., Tan et al., 2023). In addition, given the importance of social interaction in learning (see e.g., De Felice et al., 2022), the Relational Neuroscience approach has the advantage of moving beyond considering the teacher and the learner as separate entities and instead pushes researchers to look at the dynamics arising within social interlocutors (e.g., teacher and learner(s)), getting closer to how humans learn in the real-world.

Relational neuroscience research could also provide a broader perspective on interpersonal and *intergenerational relationship dynamics* across different generations of parents, grandparents, and grandchildren, and thereby inform potential future psychological and/or social interventions (see e.g., Moffat et al.,. 2024; Dikker et al., 2024).

Mental health is another important area where Relational Neuroscience research can have large impact: neural and behavioural synchrony have been identified as biomarkers for patient-therapist relationships as well as for some patients' pathological traits (see e.g., L. Chen et al., 2023; Dandan et al., 2020; Guo et al., 2023; Saporta et al., 2022). This research has also unravelled how in certain contexts, such as stressful situations, more synchrony may not always be better (e.g., stress resonance studies; Engert et al., 2019), making this research field an extremely useful tool not only to model (dys-)functional human sociality per se, but also to better understand and potentially tackle mental health problems – one of the biggest challenges of our times. Studying the interpersonal dynamics between patients and practitioners may be helpful also beyond mental health to extend more generally to the medical field, and used to understand the quality of the clinical interaction, guide the course of treatment, and potentially even affect treatment outcomes.

Relational Neuroscience research can also provide important insights into the assessment of IBS differences in various *neurodevelopmental and psychiatric disorders*. As Schilbach (2016) has argued, psychiatric disorders may be construed as disorders of social interaction. As such, a psychiatrically motivated focus on the dynamics of social interaction may yield crucial insights into the potential underlying neurobiological and interpersonal mechanisms. Within this context, we would like to emphasise the concept of interpersonal (Dumas, 2022) or inter-personalized (Bolis et al., 2023) psychiatry, which moves away from a static spectrum of disorders to a more dynamic relational space. The concept furthermore describes how IBS can provide both a neurobiological means to assess core clinical features of mental disorders, and more objective data of interpersonal phenomena. The latter are an integral part of the psychotherapeutic process that otherwise remains hard to capture at the biological level. Although data on interpersonal synchrony – and particularly IBS - within this context is still sparse, some data have started to emerge in autism research. A recent combined systematic review and meta-analysis summarised the findings stemming from thirteen studies assessing interpersonal motor synchrony (i.e., the spontaneous, voluntary, or instructed coordination of movements between interacting partners), revealing reduced interpersonal motor synchrony in dyads composed of autistic and neurotypical individuals (Carnevali et al., 2024). Data on IBS, however, remains inconclusive. Kruppa et al., (2021) examined parent-child IBS by comparing dyads either comprising autistic children or neurotypicals (child age 8–18 years). While confirming differences in motor synchrony, they did not observe any group-differences in IBS. Similarly, Minagawa et al., (2023) did not find any differences in IBS during mother–infant interactive parenting in 3–4-month-old infants with and without an elevated likelihood of autism. Conversely, another study by Hasegawa and colleagues (2016) using magnetoencephalography (MEG) hyperscanning reported significant correlations between the index of mu suppression in the right precentral area and the traits (or severity) of autism in a small sample of 13 mothers and 8 children. Therefore, more research on interpersonal synchrony in autism is needed, ideally combining measures of IBS with measures of synchrony in behaviour (e.g., Branigan et al., 2016; Koehne et al., 2016), physiology (e.g., Baker et al., 2015) and endocrinology (e.g., Saxbe et al., 2017).

Considering the fast-growing presence of artificial agents (e.g., social robots, AI-based assistants) in society, Relational Neuroscience's findings may also have significant impact in current models of *human-robot interaction* (see e.g., Harris, 2024) and inform the way engineers design and program the behaviour and appearance of robots (see e.g., Obaigbena et al., 2024; Qi et al., 2024). Relational Neuroscience findings may drive the development of artificial agents that fit seamlessly into human life and promote a future where human-robot collaboration is more intuitive, smooth and widely integrated across many aspects of life-routine. However, it is important to say that applying insights from Relational Neuroscience to facilitate the design of smooth human-machine-interactions also comes with some ethical implications. For instance, there is a potential for inducing an undue amount of trust in the technology with possibly detrimental effects. Ideally, the design of human-machine-interaction should therefore strive for a balance between human need for sociality on the one hand, and system transparency and trustworthiness on the other (see e.g., Hoehl et al., 2024). A very promising paradigm within this context is the human dynamic clamp (HDC) that has been proposed as a general paradigm for studies of elementary forms of social behaviour in complex biological systems (Dumas et al., 2014). Not only has research applying the HCD paradigm shown that emotional responses are strongly influenced by dynamic features of virtual agents' behaviour (Zhang et al., 2016), but also that judgements of humanness and cooperation of others can modulate the functional connectivity between a right parietal and a prefrontal cortex neural hub as evidenced with high-resolution EEG (Dumas et al., 2020).

More generally speaking, while retaining the potential for many exciting applications, we urge caution in the use of hyperscanning methods as *diagnostic and/or intervention tools*. For example, in the context of neurodevelopmental and psychiatric disorders, while there are emerging findings on potential differences in motor and neural synchrony in certain interaction settings comprising neurodivergent individuals and/or dyads (see e.g., Kruppa et al., 2021; Minagawa et al., 2023), these findings are not consistent and extensive enough to reliably inform potential future interventions. An inherent challenge to any clinical and non-clinical applications of hyperscanning – and neuroimaging methods more generally – furthermore is its relatively low reliability within single-individual or -dyad settings. Neuroscience (and Relational Neuroscience more specifically) is quite far from using hyperscanning as a potential diagnostic and intervention tool in several everyday life contexts.

In the present review, we have described studies across a range of fields that mainly pertain to physical (as opposed to virtual) interactions. However, there is now accumulating evidence that in-person interactions may be substantially different from *virtual interactions* (see e.g., Balters et al., 2020; Barde et al., 2020; Schwartz et al., 2022). Future studies should therefore also consider how interpersonal dynamics change as a function of physical presence, compared to virtual presence. This is particularly important in a world that is becoming more digital by the day.

Finally, future Relational Neuroscience studies employing hyperscanning should consider *new experimental designs* and technologies, and be aware of the *ethical considerations* that come with them. For example, with the emergence of fully portable (i.e., wireless) EEG and fNIRS measurement devices and wearable magnetoencephalography (MEG) based on optically pumped magnetometers (OPMs) (see e.g., Holmes et al., 2023), experimental paradigms become increasingly naturalistic, both regarding their task design and measurement environment. While such a development offers promise in terms of ecological validity overall, researchers need to carefully plan the inclusion of active control conditions or other procedures, such as random permutation or phase scrambling, to account for spurious correlations (see e.g., Nguyen et al., 2021 and Vigliocco et al., 2024 for a deeper discussion on this). Furthermore, increased efforts are necessary to ensure full transparency in the reporting about, and inclusion of diverse demographic and phenotypic samples based on, for example, skin tones and hair types (see e.g., Kwasa et al., 2023).

6. Conclusions

We have proposed Relational Neuroscience as a novel integrative framework for the thriving field of research tackling the neural dynamics of social interactions and relationships. As opposed to broader frameworks, such as second-person neuroscience, Relational Neuroscience is specifically interested in the intricate and reciprocal relations that emerge both short- and long-term between the brain activity patterns of people engaged in various social relations, from spurious social encounters to lasting bonds. We argued that hyperscanning is the prime methodology to inform this field due to its unique ability to track mutual influences between interactants' brains in real-time. In contrast to sequential scanning, this technique can uniquely measure inter-brain patterns emerging beyond common-input processing. We have reviewed this 'hyperscanning effect', showing how this has now been well-documented in a range of social contexts, varying in the degree of interactivity and social closeness of interactants. By combining hyperscanning of brain activities with measures of bodily processes and behaviour, our understanding of mutual interpersonal patterns can be substantially enriched, from communication and cooperation, to empathy, attachment and bonding, social development and possibly more. Though methodologically and computationally challenging, multimodal and dynamic approaches are essential to address key outstanding questions pertaining to human sociality at the level of dyads and larger groups. Eventually, this will help reduce the gap between lab-based theoretical knowledge and real-world implications. Given the great practical relevance of Relational Neuroscience insights, including in therapy, education, and technology development, modelling naturalistic interactions will ultimately strengthen the potential for translating research findings into practical applications. The aim of this work is to support such an effort by offering clear definitions of key concepts and a straightforward theoretical framework with the potential to structure and guide further research into human sociality.

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