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Interactive brains, social minds: Neural and physiological mechanisms of interpersonal action coordination

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Abstract

It is now widely accepted that inter-brain synchronization is an important and inevitable mechanism of interpersonal action coordination and social interaction behavior. This review of the current literature focuses first on the forward model for interpersonal action coordination and functional system theory for biological systems, two broadly similar concepts for adaptive system behavior. Further, we review interacting-brain and/or hyper-brain dynamics studies, to show the interplay between intra- and inter-brain connectivity resulting in hyper-brain network structure and network topology dynamics, and consider the functioning of interacting brains as a superordinate system. The concept of a superordinate system, or superorganism, is then evaluated with respect to neuronal and physiological systems group dynamics, which show further accompanying mechanisms of interpersonal interaction. We note that fundamental problems need to be resolved to better understand the neural mechanisms of interpersonal action coordination.

1. Introduction

Traditionally, studies on social cognition employed a single-person account, wherein individuals were tested without actual social interaction. The social contexts researched in those studies often referred to individuals processing social stimuli (Konvalinka and Roepstorff, 2012; Sebanz et al., 2006). Sebanz et al. (2006) criticized such studies investigating isolated minds; they argued that, in order to learn about social interaction, one needs to study actual social interaction (see also Babiloni and Astolfi, 2014; Czeszumski et al., 2020). Others also argued that social cognition might be different during real-time social interaction with another person, compared to when merely (passively) processing social stimuli (Schilbach, 2010), as it encompasses "much more than observing and imitating" (Konvalinka and Roepstorff, 2012). Pfeiffer et al. (2013) speak about "offline" and "online" social cognition or interaction and provide an experimental landscape of research in social neuroscience, where real-time social interaction remains largely illusive, representing the "dark matter" of social neuroscience (see also Schilbach et al., 2013).

The demands of social interaction, such as coordinating one's own actions with those of others (Sebanz et al., 2006), are described under the term of *joint action*, by research focusing on the social interaction between two or more people (Konvalinka and Roepstorff, 2012). Konvalinka and Roepstorff (2012) indicated that although there have been studies in line with this joint action account, the research focus was still mainly on effects within (and not between) the interacting individuals. The authors argued that by looking at the interaction partners separately, relevant aspects of the ongoing interaction might be overlooked (see also Montague et al., 2002). Consequently, modulations of processes within the brain during interaction are hard to capture by applying the single-person account – instead, different multi-person accounts are needed.

A relatively new technique in neuroscience – *hyperscanning* – enables researchers to record data from two or more brains simultaneously and thus to analyze not just within- but also between-brain synchronous activity (Babiloni and Astolfi, 2014; Dumas et al., 2011; Sänger et al., 2011). Furthermore, hyperscanning allows for applying statistical and mathematical methods in order to determine correlations and causalities in interaction partners' brains during joint action (Babiloni and Astolfi, 2014) and, therefore, for investigating the neural mechanisms underlying social interaction (Sänger et al., 2011).

The joint action account of social cognition research investigates mechanisms underlying social interaction that rely on processes within and between the interaction partners' brains (Czeszumski et al., 2020;

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Konvalinka and Roepstorff, 2012). Studies utilizing the hyperscanning approach revealed functional analogies between interaction partners' brains, which have been labeled differently in literature, ranging from functional connectivity to causality. Konvalinka and Roepstorff (2012) concluded that these findings imply either that the reported similarities are caused by shared sensory input and sensorimotor output of interaction partners or that there is something more that cannot entirely be explained on the level of the behavior investigated (cf. Lindenberger et al., 2009). Nevertheless, Babiloni and Astolfi (2014) stated that the interpretability of such connectivity between brains is limited. They also argued that correlations or different types of couplings identified between the signals of interaction partners' brains does not mean that a physical "communication channel" between them exists, but rather suggests the presence of an *indirect* connection or an "indirect chain of events" within the two brains or "a fine-grained temporal interplay between regions involved in motor planning and regions involved in thinking about the mental states of others" (Schippers et al., 2010, p. 9388).

The focus of the present review is on neural and physiological mechanisms of interpersonal action coordination. We provide an overview of hyperscanning studies with an emphasis on intra- and inter- brain synchronization and network topology dynamics, which have received relatively little attention. First, we will introduce an extended forward model for interpersonal action coordination (cf. Sänger et al., 2011) and substantiate it by means of biologically and physiologically valid functional system theory introduced by Petr K. Anokhin (Anokhin, 1974). Thereafter, we summarize representative studies and reviews concerning the interacting brains and hyper-brain network activity accompanied by hyper-brain network topology dynamics. We will then outline group interaction studies including both group brains and physiological systems dynamics and reconsider the earlier proposed view of group interaction as a superorganism or superordinate system (cf. Müller et al., 2018a, 2019). Finally, we summarize the three theoretical concepts (i.e., forward model, functional systems theory, and the superorganism concept) in terms of their commonalities and discrepancies, and show their usefulness for analyzing social interaction and revealing its mechanisms.

2. Forward model for interpersonal action coordination

Joint action requires coordination of interacting the people's individual actions in space and time (Vesper et al., 2013). This often needs to happen online and very fast – thus, reacting based on the *observation* of a partner's fulfilled action does not seem quite sufficient (Knoblich and Jordan, 2003; Vesper, 2014). Instead, it is proposed that individuals predict interaction partner's actions and the corresponding consequences (for a short overview, see Vesper et al., 2017). Hence, people can adapt their own actions in accordance to these predictions, which facilitates fast and accurate interpersonal coordination (Vesper, 2014; Vesper et al., 2017). Further, individuals are supposed to rely on their own motor system when predicting other's actions and its effects (see Vesper et al., 2017). This assumption is supported by evidence implying that, during the observation of other's actions, representations of the respective perceptual and motor programs are activated in the observer's brain (see also Wilson and Knoblich, 2005; Wolpert et al., 2003). These notions could be explained in the context of internal forward models (Sänger et al., 2011; Vesper et al., 2017), which are the subject of this section.

2.1. Extending the single forward model for interpersonal action coordination

The human brain uses sensory representations to determine future actions. Dependent on sensory feedback it can generate a new motor command or update the current one, thereby completing the sensorimotor loop (cyclic interaction between the somatosensory and motor systems). The central nervous system internally simulates aspects of the sensorimotor loop in order to enhance planning, control, and learning mechanisms. Neural circuits responsible for these simulations are termed *internal models* (Fanselow and Connors, 2005; Wolpert et al., 2003; Wolpert and Ghahramani, 2000). As suggested by Wolpert et al. (1995): "There are two varieties of the internal model: (i) forward models, which mimic the causal flow of a process by predicting its next state (for example, position and velocity) given the current state and the motor command; and (ii) inverse models, which invert the causal flow by estimating the motor command that caused a particular state transition" (p. 1880). Thus, forward models map the relation between an action and its sensory consequence (Adams et al., 2013; Miall, 2003; Wolpert and Ghahramani, 2000), which produces a temporary prediction (Vesper, 2014). For this reason, the terms "forward model" and "predictor" are often used interchangeably (e.g., Wolpert et al., 2003; Wolpert and Ghahramani, 2000).

It has been suggested that the actions of others can be decoded by activating one's own action system at a certain (subthreshold) level, and indeed there appears to be a specific neural mechanism (e.g., mirror neuron system) that decodes such information (Wolpert et al., 2003). The proposal that, during interpersonal action coordination, people use their own internal models to simulate other people's actions in order to make predictions is in line with this notion (Vesper, 2014; Vesper et al., 2013; Wolpert et al., 2003). Vesper et al. (2013) refer to a line of empirical evidence showing that activity in one's own motor system can be found during observation and imitation of others' actions (see also Wolpert et al., 2003). Using one's own motor system to infer predictions for others' actions facilitates fast interpersonal action coordination, as interaction partners can predict what the others will do instead of simply reacting based on what the others have already done (Knoblich and Jordan, 2003; Sebanz et al., 2006).

Neurophysiologically, this process could be implemented in the mirror neuron system (Sänger et al., 2011; Vesper et al., 2017). When we see someone about to act, our own motor system is activated (Gallese, 2003; Rizzolatti et al., 2001). The mirror neuron system consists of neurons, coding for perception and execution of actions, and, therefore, links the perceptual and motor systems (Gallagher, 2009; Gallese, 2003; Hasson and Frith, 2016; Miall, 2003; Rizzolatti et al., 2001).

2.2. Forward model in joint action

In order to reach a common action goal, joint action usually requires people to actively modify their own actions (Vesper, 2014; Vesper et al., 2010). Accordingly, joint action demands not only the integration of one's own and other's actions (Novembre et al., 2014), but also the anticipation of what others are going to do (Knoblich and Jordan, 2003). Such anticipatory processes facilitate joint action, as they enable individuals to plan and execute their own actions in accordance to predictions about the other's next actions (Keller et al., 2014; Sebanz et al., 2006). In line with this, Sebanz et al. (2006) assume that joint action relies "on the abilities (i) to share representations, (ii) to predict actions, and (iii) to integrate predicted effects of own and others' actions" (p. 70). Therefore, during joint actions, people need to comprehend what others are doing and to predict what others are going to do (Sebanz and Knoblich, 2009).

In order to adjust their own actions to those of action partners, individuals not only hold representations of their own task, but of their interaction partners' task as well (Loehr and Palmer, 2011; McEllin et al., 2018; Sebanz et al., 2006). This implies that, during joint action, each interaction partner knows what the others will do. The shared representation of tasks advances the individual's own anticipatory action planning, since they do not have to respond to observed actions (Sebanz et al., 2006). Nevertheless, Vesper et al. (2010) argued that, during joint actions, people have to represent the (common) action goal and their own task at least – representing the interaction partners' task as well may be beneficial but is not necessary for successful joint action.

Fig. 1 shows an extension of the forward model in interpersonal action coordination proposed earlier by Sänger et al. (2011). Like Sänger et al. (2011), we assume the forward model of joint actions to be three-layered. Based on a joint goal, each individual holds an own forward model, a representation of the interaction partner's forward model, and a representation of the shared or joint forward model. Some of the assumptions depicted in the joint action forward model in Fig. 1 are supported by literature reviewed above, but other assumptions remain tentative.

Let us first have a look at the *individual forward model* (cf. Sänger et al., 2011; Wolpert et al., 2003). Based on the joint goal and by considering external influences, an individual action intention and an according action prediction are formed. These information flows are integrated by the sensorimotor system, which applies motor commands for action execution and an efference copy of motor commands to compare sensory consequences of action execution. Subsequently, the actual and predicted action effects are compared in the sensory system in order to adapt further actions.

In the second layer, the individual holds a *representation of the other's forward model*. Based on motor simulation, the individual is capable of predicting consequences of the interaction partner's task (cf. Vesper et al., 2013; Wolpert et al., 2003). The other's action intention and prediction are considered and integrated in order to provide information about the sensory consequences of both the expected and the real effect of the other's action. The comparison between the interaction partner's predicted and actual action could help individuals to adapt their own actions to their interaction partner's (cf. Sänger et al., 2011).

Sänger et al. (2011) assumed a third layer, expressing an individual's *representation of the joint forward model*. Here, joint action intention and prediction are considered and integrated to provide information about the sensory consequences of the expected and also the real effect of joint action. A comparison of predicted and actual joint action outcome could help individuals to improve coordination. Finally, the result of this comparison (sensory congruency or discrepancy) taking place on all three layers will terminate the forward model if the goal is achieved or the forward model is corrected in an appropriate way to achieve the intended result or the joint goal.

Nevertheless, it is justified to ask here: Why is a joint forward model needed if participants are already tracking and predicting their own and their interaction partner's actions? In our view, the third layer, i.e., *the joint forward model*, is not a simple combination of the two lower levels, but a representation of a common goal and actions that exceed the

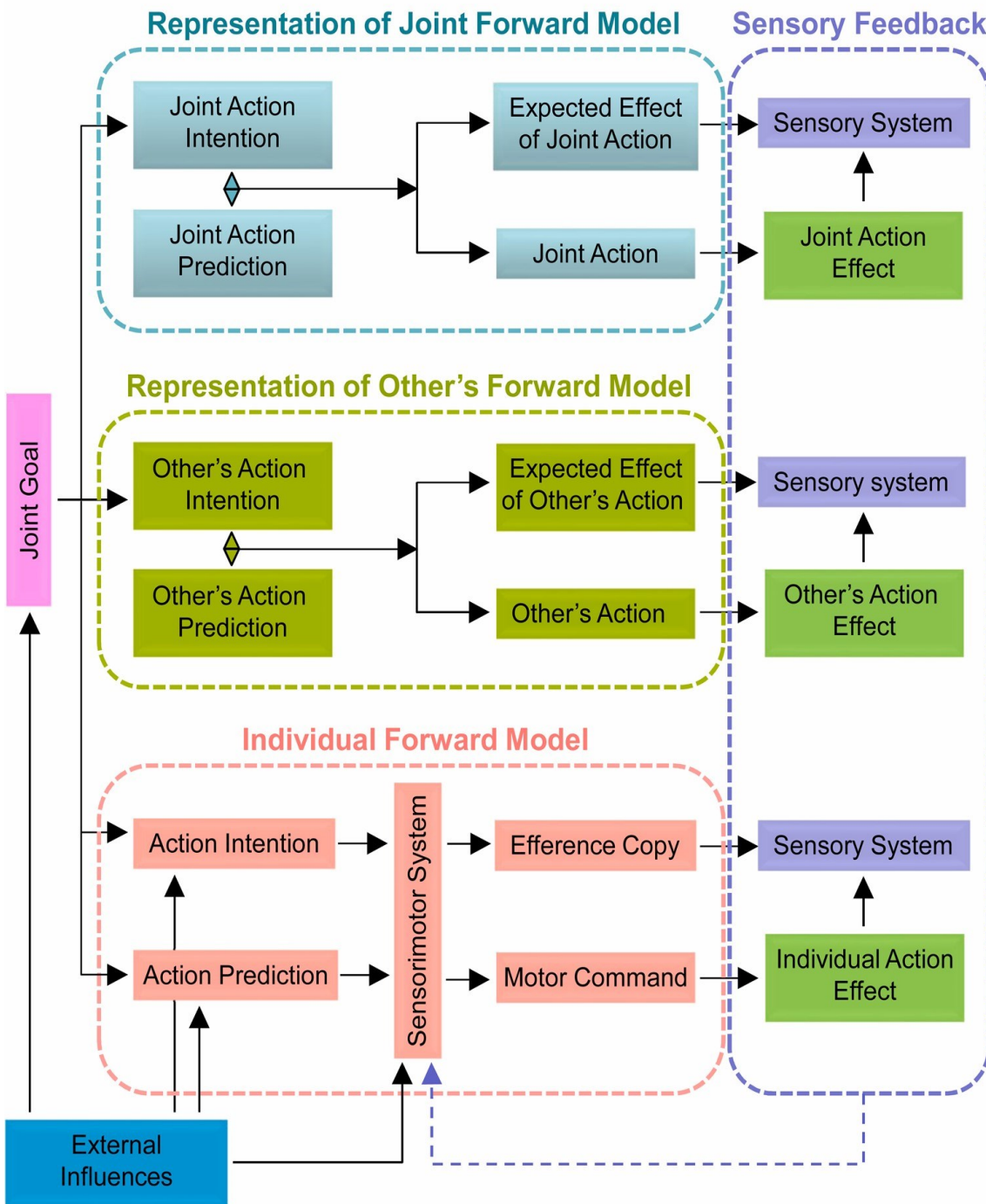## Forward Model of Interpersonal Action Coordination

Fig. 1. Forward model for interpersonal action coordination. On a first layer (Individual Forward Model), one's own action intention and prediction, as derived from the joint goal and considering external influences, is represented. The sensorimotor system thereupon builds a motor command and an according efference copy. The action effect caused by the execution of the motor command is compared with the efference copy in the sensory system. The result of this comparison (sensory congruency or discrepancy) influences the following actions such that the joint goal is approached and finally reached. On a second layer (Representation of Other's Forward Model), the other's action intention and prediction as well as the corresponding implementation with its assumed sensory consequences are represented. With regard to the interaction partner, one's own sensory system thus compares the expected and the actual action effects of the other. Especially when the involved individuals are highly skilled in their interactive tasks, an additional third layer (Representation of Joint Forward Model) is assumed in which the joint intention and prediction are represented. Again, a comparison of predicted effect and outcome of joint action takes place in the individual sensory system, thereby determining the progress of coordinated action. The various representational layers of the actors are intertwined by sensorimotor feedback loops (adapted from Sänger et al., 2011).

individual representations. Depending on how many interaction partners are involved in the joint action, the third layer will dominate over the second layer, because it will be easier to evaluate and predict the joint action than that of each of many individuals. Moreover, we assume that this third layer may especially evolve in the course of acquiring expertise in activities that require very high and precise levels of interpersonal action coordination, such as professional dancing and acrobatics, but also competitive sports such as judo or boxing.

Let us imagine a couple dancing a tango in a ballroom. In order to perform tango or any other dance correctly and effectively, each dancer must not only be able to *react* to the other's movement, he/she must also *predict* the movement of his/her partner, otherwise his/her movements will be too slow (cf. Pickering and Garrod, 2013). In addition, both dance partners must have a common goal and intention, as well as a common conception of how to dance tango. These common intentions, imaginations, and thoughts should also be predicted in order to effectively accomplish the joint action. All these information flows representing the individual's, other's, and joint forward models must be integrated and fed back to the sensorimotor system(s) after conducting the actions to correct or update all these forward models if necessary. Moreover, these representations of the forward models permanently include and integrate external influences, such as music, other dancers, or spectators in the ballroom, etc. In fact, dancing is a complex form of human activity and "… incorporates many aspects of interpersonal coordination, including touch, eye gaze, sensory-motor interactions, rhythmic or in tandem movement, physical movement coordination, facial expressions, or emotional qualities, and even synchronization with other physiological parameters, such as breathing, heartbeat, and sympathetic tone" (Basso et al., 2021). All this indicates that the suggested forward model of interpersonal action coordination is a multivariate construct integrating and reflecting a variety of influences and interactions of human social behavior.

3. Functional system theory

Since human goal-directed behavior is regulated by various factors that work together as a system, the systems approach can be very useful for the better understanding of human social behavior and social interaction (Coey et al., 2012; Luhmann, 1995; Maturana and Varela, 1980; von Bertalanffy, 1968). In the early 1940s, the Russian neurophysiologist Petr K. Anokhin proposed a new conditioning concept – the theory of functional systems – wherein he suggested a concrete and uniform mechanism for the formation and operation of a functional system (Anokhin, 1974). Within the framework of this theory, elements of a system are not arbitrarily put together, but there is a system-forming factor that combines certain (not all) elements into a system that has a specific functional meaning. In the theory of functional systems, a *valuable* (beneficial for an organism and the system itself) *result* that the system strives for survival and that integrates all functional elements into a uniform coherent system is considered to be the *system-building factor*. This result dominates the system and determines its formation by choosing the degrees of freedom necessary to achieve the result. An organization, no matter how large it may be and how many elements it comprises, can be regarded as a self-organizing or self-controlling system if its functioning, i.e., interaction of system components, leads to a certain valuable result and if there is feedback on the degree of usefulness or value of this result for the system (Anochin, 1978; Anokhin, 1974).

One further peculiarity of functional system theory is that the system always has certain *architectonics* (the unifying structural design or organization principle), which is similar or practically the same for all types of systems. Thus, every functional system is built according to the *isomorphism principle*, i.e., a functional system of any level of complexity has a basically identical organization (Sudakov, 2015, 1997). The components or blocks of any system are: (a) afference synthesis, (b) decision making, (c) acceptor of action result with an action program, (d) evaluation of the action result, and (e) reafference. These system blocks represent stages of information processing of any behavioral act. Thus, the useful adaptive result, which is the system-forming factor, and dynamic operational architectonics are two principally important features of Anokhin's theory of the functional system (cf. Sudakov, 2015).

The operational architectonics of the functional system is shown in Fig. 2. It is evident that the functioning of the system begins with an *afferent synthesis,* the initial stage of the central architectonics of functional system involving integration of neural afferentation and information flows from internal and external circumstances. At this stage, four different information flows are processed simultaneously: *motivation* (leading internal need dominating at this point), *contextual afferentation* (entirety of external influences or situation conditions prevailing at this point), *starting afferentation* (starting or trigger stimulation), and, finally, *memory* or memory content from previous experiences regarding the aforementioned conditions. Integration of all these information flows leads to *decision making*. The decision-making process completing the afferent synthesis results in important moments: It reduces unnecessary degrees of freedom, as already at this point, the result to be achieved is chosen and hence corresponding parameters are set. These parameters of the result are passed on and integrated into the *acceptor of action results* and *action program*. This stage of forming the action acceptor and the action program is crucial for the system. These two blocks receive information about the planned result, on the basis of which an action program is created with the corresponding efferences that should lead to the achievement of the result. When the result is achieved, its parameters are fed back to the acceptor of action results through *reafference* or *backward afferentation* to be compared with previously planned parameters and features of the action program in form of efferences. Once this comparison detects a match, the behavioral act is terminated and the system is dissolved or replaced by another. If the parameters compared in the action acceptor do not match, the action program and further actions are corrected until there is a full match of the planned and achieved parameters of the result. Alternatively, a mismatch can also lead to an *orientation reflex* that reactivates or switches components of the afferent synthesis and prompts an extended condition analysis of afferent information involving new internal and external factors. This elicits renewed decision making and the formation of a corrected action acceptor and action program, which are more likely to achieve the result by the improved or extended analysis of afferent information (cf. Anochin, 1978; Anokhin, 1974).

Some important organizational principles of functional systems (besides the isomorphism principle mentioned above) merit being emphasized: namely *hierarchical* and *holographic* principles of organization. When forming the system hierarchy, each lower level of the system hierarchy with a corresponding set of results forms a basis for the next higher level of the system hierarchy, and so on (see Fig. 3A for details). It is obvious that in this case the *system hierarchy* is transformed into a *hierarchy of subsystems' results* that need to be achieved at each of the previous levels of the system's organization (cf. Anokhin, 1974; Vitjaev, 2015). Apparently, the organism forms its systems in this exact way, which is the only way in which systems with a wide range of components can be organized. In our view, this also applies to society. According to the *holographic* principle of organization (see Fig. 3B for details), each element of a functional system reflects the activity of the entire functional system in its properties (cf. Sudakov, 2015), where the backward causation should also be true. That is, the entire functional system imposes boundary conditions for its constituents or subsystems (cf. Noble, 2012). The holographic principle was originally discovered in optics by Dennis Gabor (1951, 1949, 1948) and was used by Karl Pribram (1999, 1971, 1969) to explain the neural mechanisms of memory and other brain functions. At the same time, Gabor (1969, 1968a, 1968b) and Longuet-Higgins (1968) developed a mathematical model to demonstrate holographic temporal recall and associative memory functions (cf. Kelly et al., 2013).

Human functional systems are primarily caused by an individual's
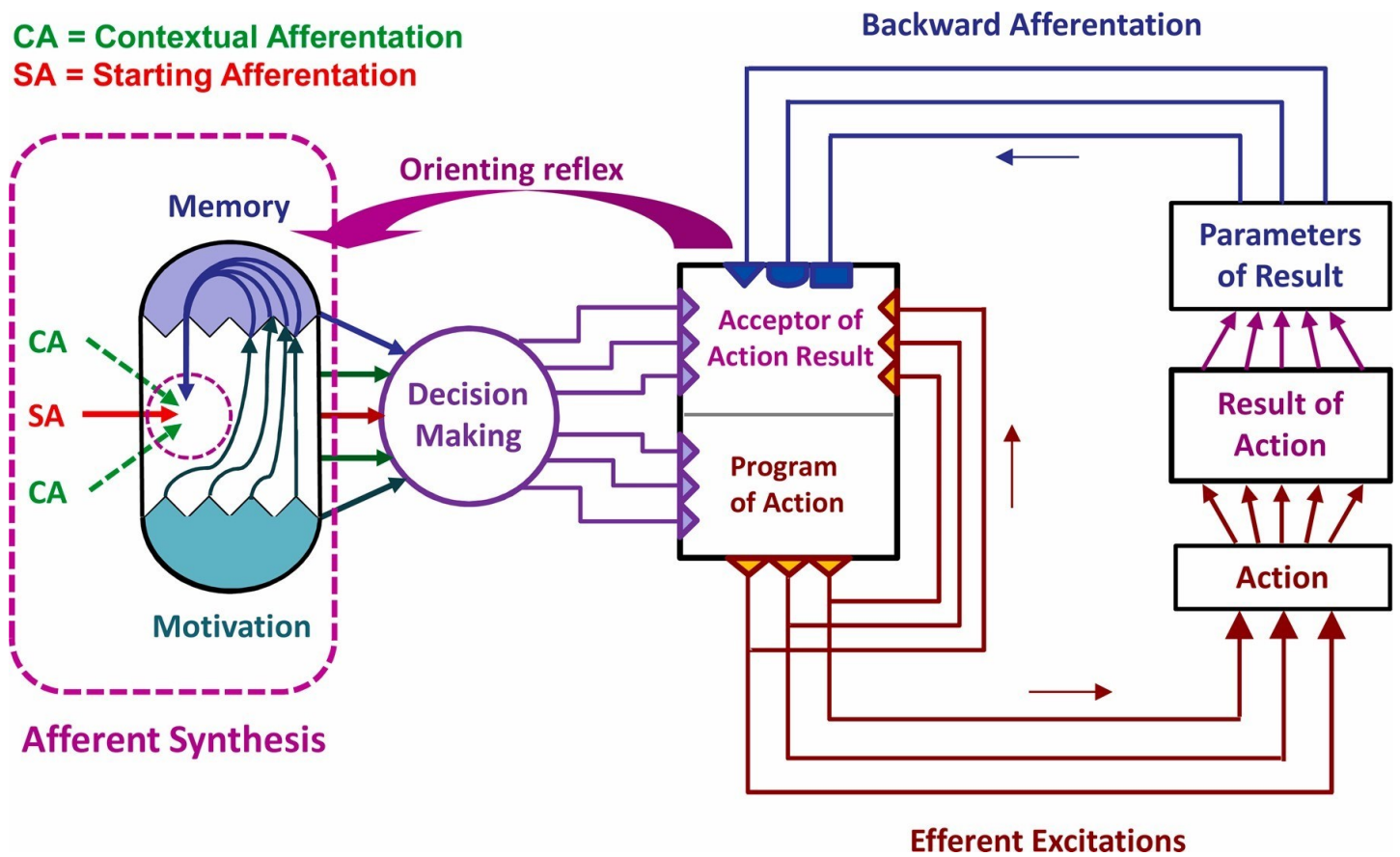
Fig. 2. The operational architectonics of the functional system. The components or blocks of the functional system are represented: (a) afferent synthesis including four different information flows: memory, motivation, contextual, and signaling afferentations, (b) decision making, (c) acceptor of an action result with a program of action, (d) action and the following evaluation of the action result, and (e) backward afferentation or reafference. Depending on the effectiveness of action and achieved action result, an orienting reflex can be activated if an additional situation analysis and extended afferent synthesis should be necessary. These system blocks represent stages of information processing of any act of behavior driven by a useful adaptive result, which should be achieved during action. This result is the system-forming factor of any functional system and is responsible for the selection of its constituents (adapted from Anokhin, 1974).

current needs and are formed by metabolic, homeostatic, and behavioral processes that are specific to humans and are important to organize various facets of life and to achieve socially significant results. "The subject constantly interacts with the results in order to improve them. Human social activity is mainly organized by special functional systems that determine the subject's intellectual activity. The results of human mental functional systems are reflections of vitally important concepts and abstract ideas about external objects and their relationships, instruction, knowledge, etc., in the subject's mind." (Sudakov, 1997, p. 395)

If we returned to our example with the dancing couple to explain the functional system approach, we could imagine the following. Let us consider the dancing couple as a supersystem with two subsystems that want to achieve a common result – dancing tango together. Each subsystem would go through all the stages of the functional system to achieve each own individual result underlying the common one. At the stage of afferent synthesis, the following information then flows together: the *motivation* to dance tango together, the *contextual afferentation* in form of musical accompaniment, the partner's behavior and movements, the size and other parameters of the ballroom, other dancers or spectators in the ballroom, etc., the *starting afferentation* in form of a music passage or the partner's cue, or both, and *memory* of previous experiences of tango dancing and other learned skills. The integration of all these information flows leads to *decision making* that reduces unnecessary degrees of freedom (e.g., several movement patterns, including eye movements, that might be counterproductive for tango dancing) and crystallizing out the parameters of the result. These parameters of the result are, or will be, integrated into the *acceptor of action results* and *action program* as a sequence of dance steps that must be performed, specific activation patterns of nerves and muscles that are necessary to execute the planned actions (which can serve here as necessary degrees of freedom), etc. When the result is achieved (e.g., a specific dance step in the sequence of steps), its parameters are fed back to the acceptor of action results through *reafference* or *backward afferentation* to be compared with previously planned parameters and features of the action program. This loop, which is under the control of the *acceptor of action results*, is active throughout of the dance and permanently performs this comparison between planned and achieved parameters of the result. If necessary, corrections are initiated or the afferent synthesis is even activated again (*orientation reflex*) if an extended analysis of the situation is required (e.g., changed conditions in the ballroom).

As mentioned above, dancing is a complex form of human activity with many aspects of interpersonal coordination. To satisfy all these aspects of the action, several subsystems are required, which are then designed according to hierarchical and holographic principles of organization. We would like to point out here that the functional system is not a rigid, but rather a constantly changing dynamic structure. Only the elements that lead to the desired result are selected, and this selection is in a constant flux and evolution. We would also like to stress the corresponding similarity between the concept of the forward model described above and that of the functional system, which complement each other and allow a better understanding of human behavior, even at the molecular, neural, and/or physiological levels that are embedded into social and peoples' interaction context.

4. Interacting brains
4.1. Intra- and inter-brain synchrony as an interactional entity

As indicated by the forward model as well as by the functional system approach, social interaction requires neural representation of others' mental states with corresponding beliefs, intentions, and expectations, or predictions. This constitutes a continuum of actions and interactions that have a systemic character, i.e., function as a whole. Moreover, each agent of an interaction has an own forward model and a corresponding

A Hierarchical principle
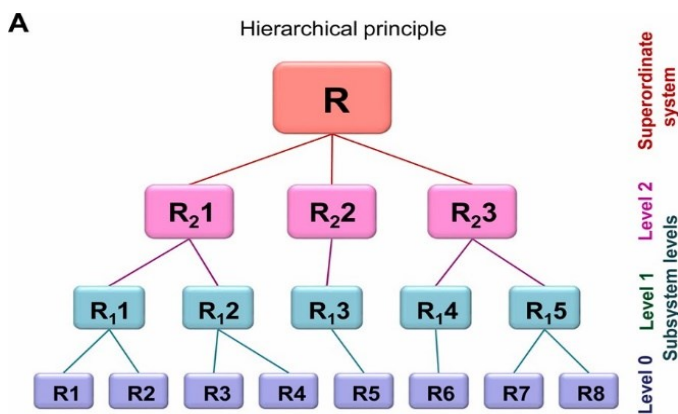
Fig. 3. Hierarchical and holographic principles of the functional system. (A) Hierarchical organization of the functional system. It is shown that the system hierarchy is transformed into a hierarchy of results of subsystems. Three different subsystem levels and a superordinate system level are presented. To achieve the result R of the superordinate system, the results on the three subsystem levels should be achieved first. Each result at each hierarchical level forms a corresponding functional system to be achieved (cf. Anokhin, 1974). (B) The holographic organization of a functional system. According to the holographic principle, the properties of each element of a functional system reflect the activity of the entire functional system as well as the activity of the corresponding subsystem level. At the same time, the entire functional system as well as the subsystem modules on different subsystem levels imposes boundary conditions for its constituents (cf. Sudakov, 2015).

B Holographic principle
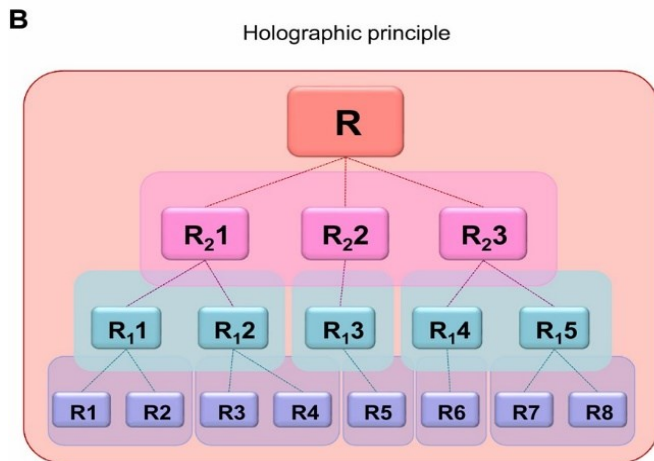
neural representation of it, and these representations are adjusted in time. The agents' interaction can also be regarded as a superordinate system, or superorganism, that imposes boundary conditions on the dynamic features of the individual agents (cf. Müller et al., 2018a). Adjustments of neural representations of single forward models (or functional systems) and superordinate system behavior can only emerge if the neural processes of the agents are in sync (De Jaegher et al., 2010; Keller et al., 2014; Sänger et al., 2011). Synchronization both within and between brains seems to be crucial for interpersonal action coordination and is an inevitable element of neuronal communication systems within and between agents. Interestingly, most hyperscanning studies are focused on inter-brain synchronization, whereas intra-brain synchrony remains disregarded (Dumas et al., 2010; Goldstein et al., 2018; Hu et al., 2017; Lu and Hao, 2019; Mu et al., 2016; Nozawa et al., 2019; P´erez et al., 2017). Still other authors focus on the processes within the brains and neglect the interaction between the brains (Babiloni et al., 2011, 2012; Bhat et al., 2017; Sebanz et al., 2006; Tognoli et al., 2007; Tsai et al., 2008; Vanzella et al., 2019). However, ever more studies are examining the processes from both sides or in a uniform context, i.e., they consider both intra- and inter-brain synchrony as an interactional entity (Ahn et al., 2018; Astolfi et al., 2020; Dumas et al., 2012; Hu et al., 2018; Müller et al., 2013, 2018b; Müller and Lindenberger, 2014, 2019; Sänger et al., 2012, 2013; Stone et al., 2019; Szymanski et al., 2017; Yun et al., 2012). In our view, both these synchronization activities, reflecting the common integrated state known as *hyper-brain* activity, are of paramount importance. Presumably, the forward model representations (e.g., information on direction of movement, force, timing, movement velocity, muscle activity, etc.) are rather reflected in within-brain connectivity or other activity patterns (e.g., spectral power, event-related potentials, etc.) within single brains. However, the adjustment of these activity states can only be facilitated by inter-brain connectivity or synchrony. Thus, interpersonal interaction is committed to steady communication between the cell assemblies within the interacting brains and steady adjustment of these neuronal states or dynamics between the brains (cf. Shamay-Tsoory, 2021).

Interestingly, in a recent hyperscanning neurofeedback study, it has been shown that participants can learn to adjust their brain activity by using inter-brain synchrony as a neurofeedback feature (Müller et al., 2021). The authors used two different designs where the subjects were able to control (a) their common state without any feedback about their own contribution to this state (so-called *ball task*) and (b) the common state with feedback about their own contribution to this state (so-called *pendulum task*). The feedback was computed and provided in form of approaching balls or pendula at delta and theta frequencies (2.5 and 5 Hz, respectively). Results of the study showed higher inter-brain coupling strengths during the neurofeedback tasks as compared to resting state. Moreover, inter-brain synchrony as well as other oscillatory measures (e.g., power spectral density and peak frequency) revealed significant correlations with the subjective post-survey item scores, reflecting subjective feeling, test partner's likability, and estimated capability to influence the task using different strategies, such as concentration, relaxation, generation of thoughts, and mental calculation. Thus, the results of the study showed that inter-brain synchrony can be enhanced if corresponding feedback about it is provided.

4.2. Topological distribution and communication frequencies of intra- and inter-brain synchrony

As shown in most interacting brain studies, the topological distribution of intra- and inter-brain synchronous activity is divergent or only partly overlapping (Dumas et al., 2020; Müller et al., 2013, 2018b; Müller and Lindenberger, 2019; Sänger et al., 2012). This indicates that the adjustment of synchronous single brains' activity states during interaction does not happen (or not always) on the same brain regions that reflect internal activity of the agents, but can involve other brain regions that are focused toward cooperation and/or synchronization. Presumably, there are specific relay stations in the brain that are designed to ensure communication between brains, whereby these stations can differ depending on the interaction type and situation. Fig. 4 represents an example of intra- and inter-brain connectivity and topological distribution of connectivity strengths within and between four guitarists' brains when playing the guitar in quartet (Müller et al., 2018b). These synchronization patterns refer to a music sequence of 5 s where the guitarists are starting to play Libertango by Astor Piazzolla. Guitarist D starts first, and the other three join in about one second later. Moreover, guitarist A is drumming on the deck of the guitar and setting the rhythm (cf. Müller et al., 2018b). It can be seen that each guitarist's brain possesses its own synchrony pattern both within and between the brains and that the topological distribution of coupling strengths within and between the brains are different, although with partly overlapping brain topology. Fig. 4 represents accumulated synchronous brain activity across the entire time sequence of 5 s but more detailed analysis representing 500-ms synchronization patterns (Figs. 3 and 4 in Müller et al., 2018b) shows that these patterns also have different dynamics. Thus, these different synchronization patterns, both within and between the brains, play a specific role in the regulation and coordination of activity among cortical circuits rather than being driven by the same
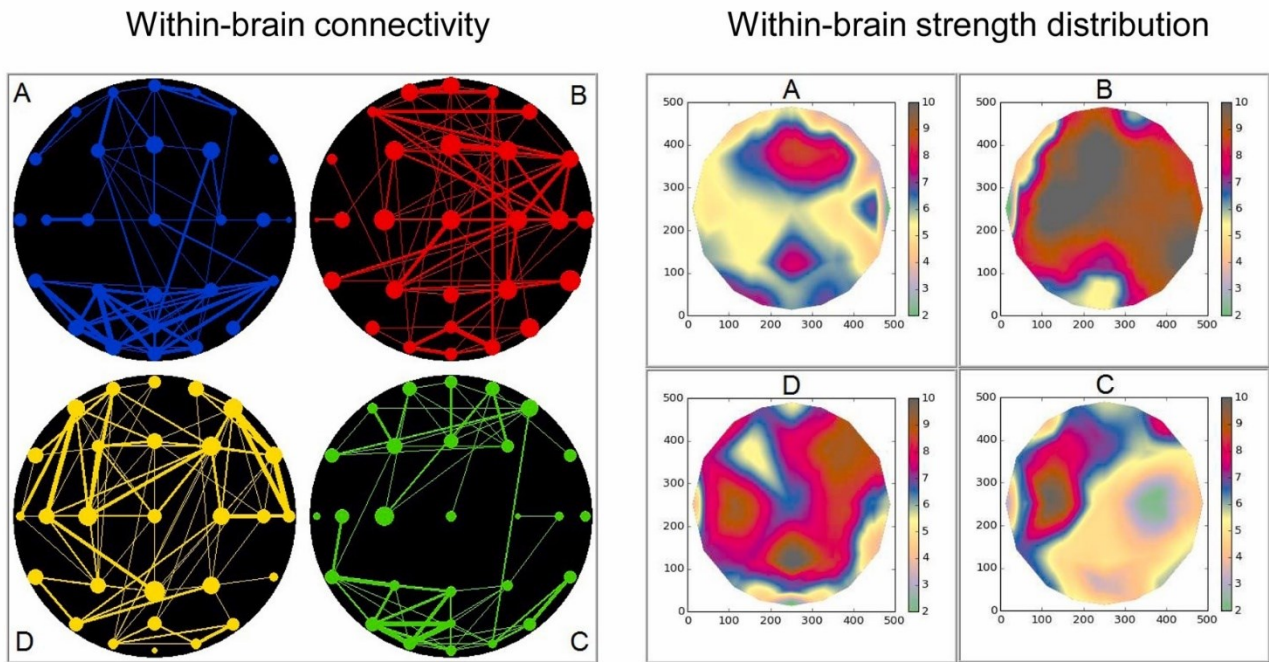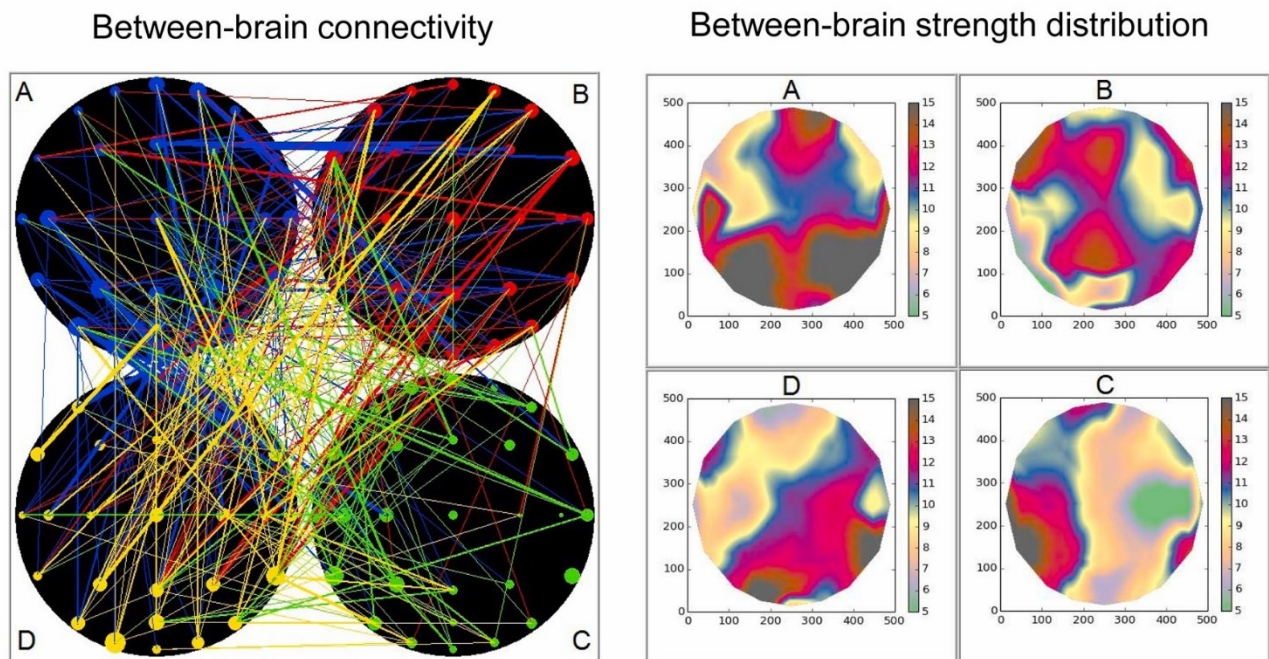
Fig. 4. Within- and between-brain connectivity, and topological distribution of connectivity strengths within and between four brains when playing the guitar in quartet. (A) Within-brain connectivity maps and topological distribution of strengths within four brains. (B) Between-brain connectivity maps and topological distribution of strengths for between-brain connections. The size of the circles in the brain connectivity maps represents the strength of the nodes (electrodes) and color codes the corresponding guitarist. Please note that only the within- and between-brain strongest connections are displayed. In the strength distribution maps, a high intensity of out-strength (accumulation of the big circles) is indicated by the dark red or brown color. Clearly, each guitarist's brain possesses its own synchrony pattern both within and between the brains, and the topological distributions of coupling strength within and between the brains are different, although with partly overlapping brain topology. The guitarists played different parts of Libertango by Astor Piazzolla (adapted from Müller et al., 2018).

shared sensory or sensorimotor experiences. For a different topology of inter-brain connectivity, see also the study on spontaneous imitation of hand movements that is reviewed below (Dumas et al., 2010).

A further important issue, especially concerning electroencephalographic (EEG) hyperscanning studies, is the fact that cell assemblies both within and between brains communicate with each other or coordinate their activity at different frequencies. It has been shown that hyper-brain networks occurring when playing the guitar in duet (Müller et al., 2013) or quartet (Müller et al., 2018b) are designated by a complex interplay of different frequencies, whereby the intra-brain connections primarily involved higher frequencies (e.g., beta) and inter-brain connections primarily operated at lower frequencies (e.g., delta and theta). Thus, synchronization patterns both within and between the brains not only show different brain topology but also operate at different frequencies.

In an EEG hyperscanning study on spontaneous imitation of hand movements, synchronized (similar movements) compared to non-synchronized (different movements) episodes showed significant inter-brain synchronization patterns among alpha-mu, beta, and gamma frequency bands (Dumas et al., 2010). Most interestingly, model and imitator participants showed a different topology of inter-brain connectivity (with the exception of the alpha-mu band). Beta band connectivity is revealed, for example, between central sites of the model and right parieto-occipital regions of the imitator, while the connectivity within the gamma band is enhanced between right fronto-central sites of the model and right parieto-occipital regions of the imitator (Dumas et al., 2010). In an EEG hyperscanning study, where participants were interacting through speech, the inter-brain coupling in the alpha band concerned mainly frontal electrode sites for the listener and central sites for the speaker, while, in the beta band, the sites were mainly frontal for the speaker and temporal for the listener (Perez et al., 2017´). This only strengthens our assertion that inter-brain synchronous activity differs in its topology from intra-brain activity, on the one hand, and involves different regions in two (or more) interacting brains, on the other hand.

Recently, Dumas et al. (2020) revealed multiple brain networks involved in social coordination operating at different frequencies. The authors used a human dynamic clamp paradigm with a human interacting reciprocally with a virtual partner (VP), the design of which is based on an empirically grounded computational model of human coordination dynamics. Participants interacted with the VP during a session composed of 80 pseudo-randomized trials and were instructed to continue their finger movement while coordinating in-phase or anti-phase with the VP's finger. Each trial was composed of three periods: pacing (3 s), interaction (10 s), and self-report (10–20 s). During the pacing period, an auditory tone cued the required movement frequency (1.6 Hz). During the interaction period, the VP was randomly assigned a cooperative or competitive behavior for two halves of each trial. In the self-report period, the participants reported the degree to which the VP was cooperative or competitive early and later during the trial and then judged the humanness of the VP (machine vs. human). The results of this study are summarized in Fig. 5. Using power analyses on estimated cortical sources, the authors exhibited a mu-alpha suppression in the high-alpha band (10–13 Hz) over contralateral and medial rolandic regions during the execution of movement compared with rest as well as over the superior aspect of right posterior parietal areas during social coordination in comparison to a similar movement produced without a partner. In addition, they revealed an increased alpha and gamma power over the right temporo-parietal areas during emotional responses and social coordination, respectively (see Fig. 5A for details). Moreover, using cortico-motor coherence analyses with the velocity of human movement ("self") and that of VP ("other"), they revealed the significant involvement of the contralateral primary motor cortex and antero-posterior network for self- and other-related activity, respectively. This motor-related activity was found to occur in the delta/theta frequency bands corresponding to the first, second, and partly the third harmonics of the fundamental frequency of movement. The overlap of self- and other-related networks based on theta cortico-motor coherence is presented in Fig. 5B. The region specific for self-movement was located in the contralateral motor cortex (shown in red). The other's movement was associated with a large expanse of the cortex (in blue), and cortical sources related to both self- and other-related behaviors were found over right parietal areas (in bright magenta). Furthermore, the authors calculated functional connectivity between the regions in the delta-theta band (1–5 Hz) to explore how self- and other-related information may be related to humanness judgment or cooperative/competitive behaviors during social interaction. As shown in Fig. 5C, sensorimotor areas in the posterior part of the brain, predominantly in the right hemisphere, were connected to anterior areas for both humanness- and cooperation-related activities (cf. Dumas et al., 2020). The results depicted in Fig. 5 not only endorse explanations raised above that intra- and inter-brain synchronization patterns show different brain topology and operate at different frequencies, but also indicate self- and other-related networks, which could be related to different layers of the forward model.

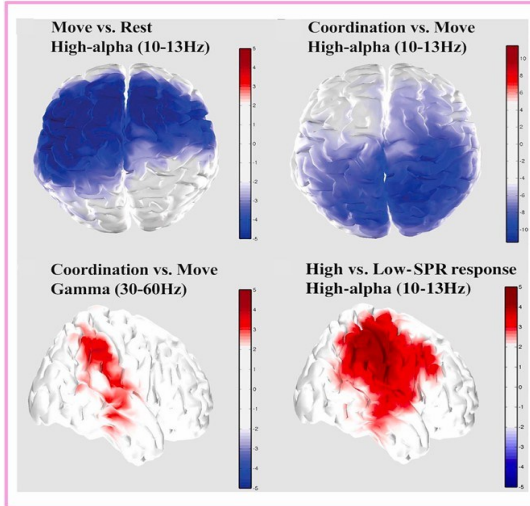### 4.3. Cross-frequency coupling for intra- and inter-brain connectivity

The next important point regarding the complex interplay of different frequencies is the use of cross-frequency coupling (CFC) for intra- and inter-brain connectivity, which together with within- frequency coupling (WFC) provides a more complete picture of hyper- brain network interaction (Acquadro et al., 2016; Müller and Lindenberger, 2014). It is well known that different frequencies are responsible for conveying different characteristics and aspects of adaptive behavior. Through CFC, these different aspects of behavior become integrated into a complex system with different behavioral facets and an operational variety of adaptive functioning on the neuronal level supporting connectivity within and between cell assemblies (Canolty and Knight, 2010; Jirsa and Müller, 2013). Using WFC and CFC in a hyperscanning study, Müller and Lindenberger (2014) investigated romantic kissing and found that the hyper-brain coupling within and between the theta and alpha frequencies are crucial for such a bonding behavior, whereby the alpha frequency was serving a cleaving or pacemaker function, binding all the frequencies in the entire hyper-frequency hyper-brain network (see more on this below). Interestingly, the brain-to-brain coupling in the alpha frequency band (8–12 Hz) was found to play a crucial role for pain alleviation in romantic partners with interpersonal touch (Goldstein et al., 2018). It has been shown that hand-holding during pain administration increases brain-to-brain coupling in a network that mainly involves the central regions of the pain receiver and the right hemisphere of the pain observer. Most importantly, brain-to-brain coupling in this network was found to correlate with analgesia magnitude and observer's empathic accuracy. Thus, inter-brain coupling in the alpha frequency band seems to play a key role during bonding and empathic behavior.

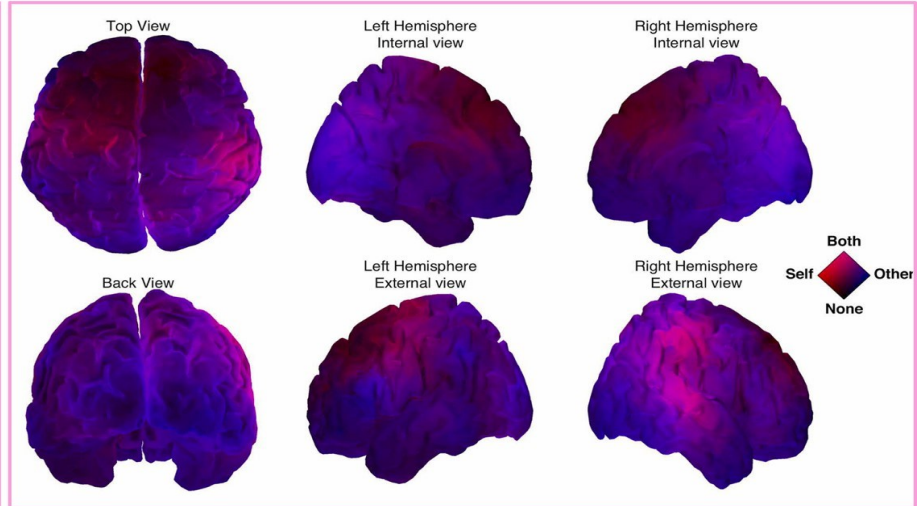### 5. Hyper-brain network topology dynamics

Given hyper-brain synchronization patterns comprising intra- and inter-brain synchronous activity, network analyses can be carried out by means of the graph-theoretical approach (GTA). Although GTA is intensively used in modern neuroscience (see Avena-Koenigsberger et al., 2018; Bassett and Sporns, 2017; Bullmore and Sporns, 2009; Fornito et al., 2015; Lynn and Bassett, 2019; Sporns, 2011; Stam, 2014, for reviews), its application in hyperscanning studies remains rare. Nevertheless, it has been shown that hyper-brain network analyses provide important information about network structure and network topology dynamics with regard to intra- and inter-brain connectivity (Astolfi et al., 2020; De Vico Fallani et al., 2010; Müller et al., 2013, 2018b; Müller and Lindenberger, 2014, 2019; Sänger et al., 2012). De Vico Fallani et al. (2010) showed that hyper-brain networks of two-defector couples in an Iterated Prisoner's Dilemma game had significantly lower hyper-brain connectivity (determined by in- and out-strengths) than those of pure cooperation and tit-for-tat couples. Moreover, it has been shown that hyper-brain networks of two-defector couples were characterized by lower network efficiency, but higher modularity and divisibility (both indicating higher separability of the common network into two individual brains). Thus, defection strategies were above all characterized by reduced inter-brain connectivity affecting the entire hyper-brain network structure and its functionality (De Vico Fallani et al., 2010).

As shown in hyperscanning studies with musicians, hyper-brain networks emerging when playing the guitar in duet (Müller et al., 2013; Sänger et al., 2012) or quartet (Müller et al., 2018b) exhibit small-world network properties with a high clustering coefficient (CC) and a short characteristic path length (CPL), indicating the high segregation and high integration of neuronal processes within the hyper-brain
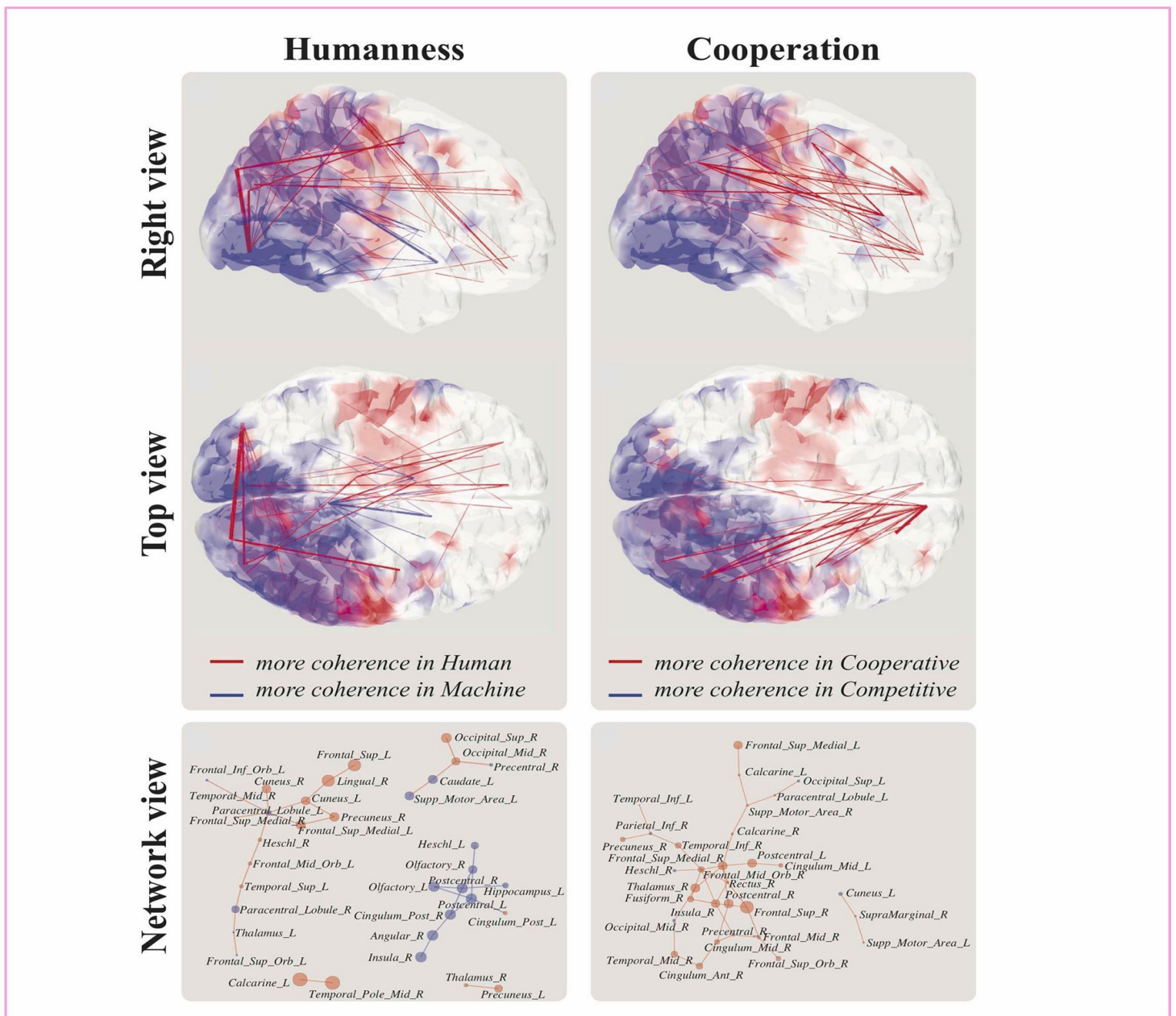
A Power spectral activity

Move vs. Rest
High-alpha (10-13Hz)

Coordination vs. Move
High-alpha (10-13Hz)

Coordination vs. Move
Gamma (30-60Hz)

High vs. Low-SPR response
High-alpha (10-13Hz)

B Overlap of self- and other-related networks

Top View

Left Hemisphere
Internal view

Right Hemisphere
Internal view

Back View

Left Hemisphere
External view

Right Hemisphere
External view

Both

Self — Other

None

C Right parietal cortex as a hub between self- and other-sensorimotor brain networks

Humanness

Cooperation

Right view

Top view

— more coherence in Human
— more coherence in Machine

— more coherence in Cooperative
— more coherence in Competitive

Network view

Occipital_Sup_R
Frontal_Sup_L
Occipital_Mid_R
Frontal_Inf_Orb_L
Precentral_R
Cuneus_R
Lingual_R
Temporal_Mid_R
Cuneus_L
Caudate_L
Paracentral_Lobule_L
Precuneus_R
Supp_Motor_Area_L
Frontal_Sup_Medial_R
Frontal_Sup_Medial_L
Heschl_R
Heschl_L
Frontal_Mid_Orb_L
Olfactory_R
Temporal_Sup_L
Olfactory_L
Postcentral_R
Hippocampus_L
Paracentral_Lobule_R
Cingulum_Post_R
Postcentral_L
Thalamus_L
Cingulum_Post_L
Angular_R
Frontal_Sup_Orb_L
Insula_R
Calcarine_L
Thalamus_R
Temporal_Pole_Mid_R
Precuneus_L

Frontal_Sup_Medial_L
Calcarine_L
Occipital_Sup_L
Temporal_Inf_L
Paracentral_Lobule_L
Parietal_Inf_R
Supp_Motor_Area_R
Precuneus_R
Temporal_Inf_R
Calcarine_R
Frontal_Sup_Medial_R
Postcentral_L
Heschl_R
Frontal_Mid_Orb_R
Cingulum_Mid_L
Thalamus_R
Rectus_R
Fusiform_R
Insula_R
Postcentral_R
Cuneus_L
Occipital_Mid_R
Frontal_Sup_R
SupraMarginal_R
Precentral_R
Frontal_Mid_R
Temporal_Mid_R
Cingulum_Mid_R
Supp_Motor_Area_L
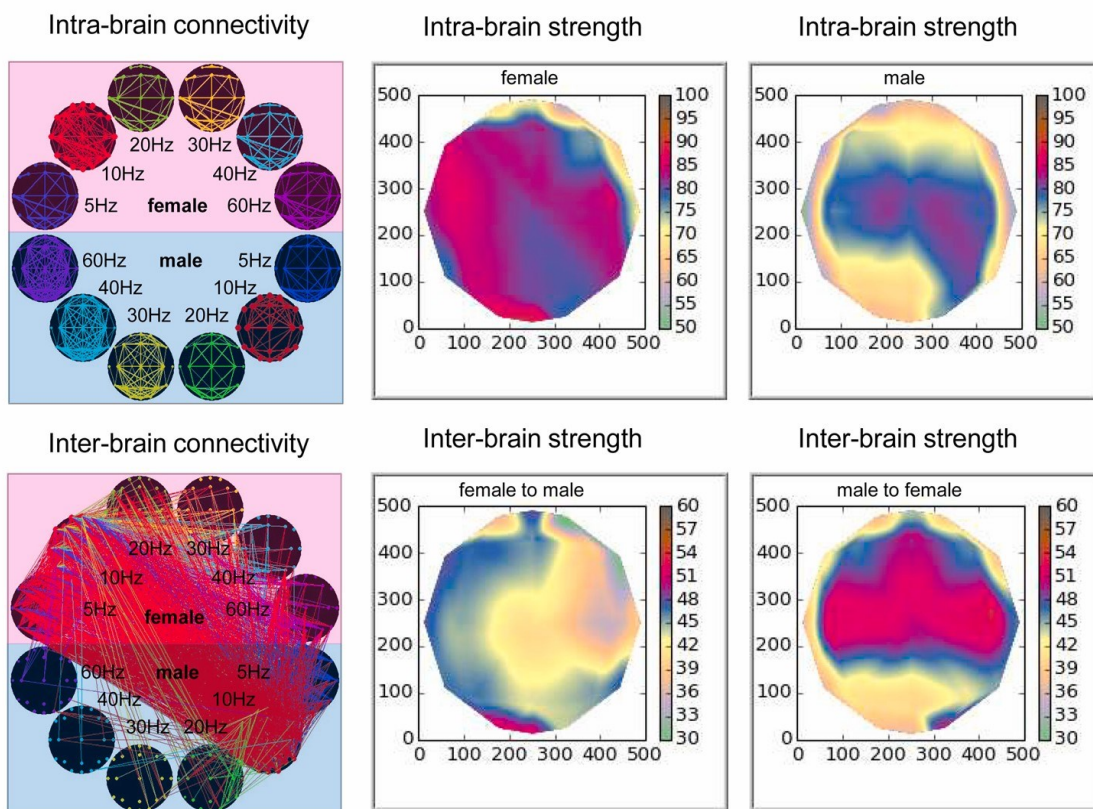*Cingulum_Ant_R*
Frontal_Sup_Orb_R

(caption on next page)

Fig. 5. Self- and other-related brain activity during coordinated finger movement in a human dynamic clamp paradigm. (A). The modulation of the spectral activity of cortical sources. High-alpha suppression over fronto-central regions during the execution of movement without a virtual partner (VP) (Move vs. Rest), decrease of high-alpha activity over parieto-occipital cortex (predominantly right), and increase of gamma activity over right parietal cortex during interaction with VP (Coordination vs. Move), and modulation of high-alpha activity by the emotional responses of the participants as measured by Skin Potential Response (High vs. Low SPR) are presented. Color indicates clusters of cortical sources that were significantly modulated in each contrast. (B) Overlap of self- and other-related brain networks. Red and blue code for the "Self versus Scrambled" and "Other versus Scrambled" contrasts, respectively. Bright magenta codes the brain areas that correspond to cortical sources related to both self- and other-related behaviors. (C) Right parietal cortex as a hub between self- and other-related sensorimotor brain networks. Humanness attribution and cooperation are related to changes in large-scale brain dynamics. Coherence between posterior and anterior brain structures in the delta/theta band (1–5 Hz) increased when participants judged the VP as being human rather than a machine (Humanness) and when VP was cooperative rather than competitive (Cooperation). Panels on the bottom show the networks of brain structures implicated during Humanness and Coordination, respectively. Line width and circle size indicate the modulation strength of coherence and power in the theta band (adapted with permission from Dumas et al., 2020).
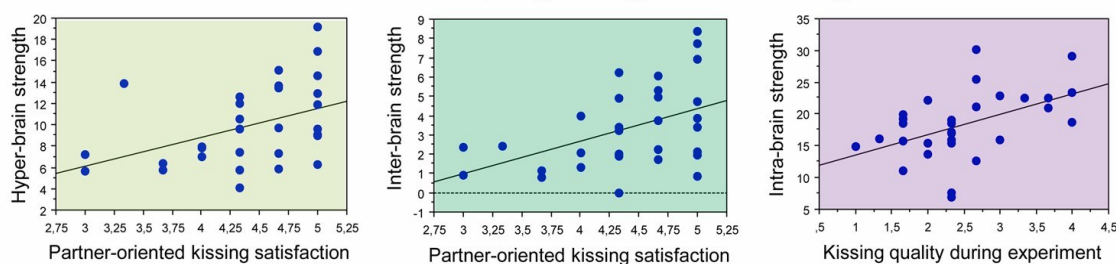

A Hyper-brain modules emerging during playing guitar in duet and quartet
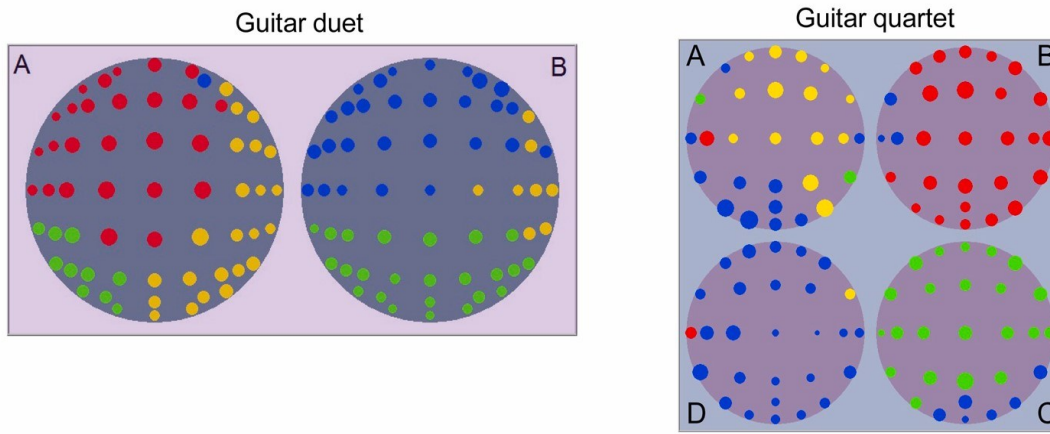
Guitar duet

Guitar quartet

B Theta-alpha subnetworks and coupling strengths emerging during kissing

Intra-brain connectivity

Intra-brain strength
female

Intra-brain strength
male

Inter-brain connectivity

Inter-brain strength
female to male

Inter-brain strength
male to female

C Correlations between coupling strengths and kissing satisfaction

Fig. 6. Hyper-brain modules and theta-alpha subnetworks representation. (A) Representation of hyper-brain modules emerging during guitar playing in duet and quartet. The different modules in two (guitar duet) and four brains (guitar quartet) are coded by color. In a guitar duet, there are three hyper-brain modules (blue green, and yellow) with electrodes distributed across two brains, while one module (red) is restricted to the brain of guitarist A. In a guitar quartet, there are four hyper-brain modules, and one of them (blue) is distributed across all four brains. (B) Representation of theta-alpha subnetworks and coupling strengths emerging during kissing. A hyper-frequency hyper-brain network based on within- and cross-frequency coupling is represented here. The brain maps at the top represent connectivity at six different frequencies within the female and male brains, respectively. The brain maps at the bottom represent the between-brain connectivity within and between the six frequencies. It can be seen that the strongest connections are found in the theta (blue) and alpha (red) frequency bands, and between them. These connections build the so-called theta-alpha subnetwork binding the two brains together. The topological distribution of coupling strength represents the overall within- and cross-frequency connectivity strengths within and between the brains. (C) Correlations between coupling strengths and kissing satisfaction and kissing quality. Partner-oriented kissing satisfaction correlated significant positively with hyper- and especially inter-brain strength determined for 5-Hz oscillation nodes. Kissing quality during the experiment correlated significantly positively with intra-brain strength determined for 10-Hz oscillation nodes. Note that (A) is adapted from Müller et al. (2013, 2018), and (B) and (C) are adapted from Müller and Lindenberger (2014).

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network binding the guitarists' brains together. These processes were also frequency-dependent with high integration but lower segregation hyper-brain network properties at lower frequencies (e.g., delta and theta) as compared to the high frequencies (e.g., beta and gamma). Similar results (at least with respect to the integration processes) were also found in the study by Astolfi et al. (2020) comparing joint action with the two individual control conditions. A further interesting result reported in the studies mentioned above (Müller et al., 2013, 2018b; Sänger et al., 2012) was the occurrence of so-called *hyper-brain modules* or communities sharing nodes or electrode sites from different brains (see Fig. 6A). By definition, the connections between the nodes within the modules are the strongest, so the hyper-brain modules comprising nodes located in different brains must have an important functional meaning. Mainly, those hyper-brain modules support the information flow within the hyper-brain network, comprising the within- and between-brains connectivity.

Hyper-brain modules were also found in hyper-frequency hyper- brain networks during kissing (Müller and Lindenberger, 2014). In this study, within- and cross-frequency couplings were used for hyper-brain network construction. The hyper-brain modules mainly encompassed the coupling within and between the theta and alpha frequencies and were called theta-alpha subnetworks (Fig. 6B). Importantly, hyper-brain and especially inter-brain strengths of 5-Hz oscillation nodes correlated positively with partner-oriented kissing satisfaction and intra-brain strengths of 10-Hz oscillation nodes correlated with kissing quality during the experiment (see Fig. 6C). It has been suggested that 5-Hz oscillation nodes represent the social (partner-oriented) aspect of interaction during kissing whereas the 10-Hz oscillation nodes represent much more the individual or satisfying aspect of kissing, whereby both these oscillation nodes are integrated in a common subnetwork playing a crucial role during kissing (Müller and Lindenberger, 2014). Interestingly, in this study, the authors used oscillatory activity of lip muscles, which synchronized between man and woman as well as with their cortical EEG activity. But the nodes, reflecting muscle-muscle and muscle-brain synchrony in the common hyper-brain network, did not correlate with partner-oriented kissing satisfaction or kissing quality during the experiment. This indicates that inter-brain synchrony is the main player in this joint game of emotions and satisfaction. Against backdrop of our theoretical considerations (i.e., forward model and functional system theory), kissing is a human action based on a very close physical, emotional, physiological, etc. interaction (with multiple feedback loops in the autonomic nervous system and the brain). All three levels of the forward model have to be engaged in order to achieve the common goal, i.e., to satisfy and to bring each other closer emotionally and physically. This is also the result that the functional systems in both interaction partners strive for. When all the information flows of the afferent synthesis are analyzed and integrated, the acceptor of the results takes control of the action, and the actions are continuously corrected and advanced by this block. Kissing satisfaction, which is strongly correlated with inter-brain strengths, is both the goal and the result of the action or interaction – it is predicted and also fed back as an action result. Whether the inter-brain coupling is a driving force of kissing or only a result of this action is an open research question that remains to be resolved.

Recently, Müller and Lindenberger (2019) investigated the coupling between brains and instruments. Based on the coupling within and between the musicians' brains and guitars, they constructed an *extended* hyper-brain network including all these interactions (i.e., guitar-guitar, guitar-brain, and brain-brain interactions). Modularity analyses of the extended hyper-brain networks revealed hyper-brain modules or extended hyper-brain modules sharing not only nodes from the two guitarists' brains, but also nodes from their guitars. The authors suggested that this complex interplay between brains and instruments combine the musicians' actions to produce sounds with their instruments and the influences of these sounds on the musicians themselves through sensory and sensorimotor pathways. It has been shown that such interaction loops and corresponding extended hyper-brain networks change their structure dynamically depending on the musical situation and music rhythm (Müller and Lindenberger, 2019). In line with the forward model and the functional system approach discussed above, hyper-brain networks reflect different interaction steps and information flows underlying intentions, predictions, motor actions, and results of actions. These are represented in sensory and motor systems and corresponding sensorimotor pathways, which are temporally adjusted and integrated in a common neurocognitive space.

6. Group interaction as a superorganism or superordinate system

As highlighted by Hasson and Frith (2016), "interactions with other members of a group can fundamentally shape the way we behave in the world, and alignment is a ubiquitous feature of such interactions" (Hasson and Frith, 2016, p. 2). In biological studies of insects regarding collective behavior and swarm cognition, interactions among the individual insects as well as between the insects and their environment result in seemingly cognitive behavior of an insect swarm that is often considered as a "superorganism" (Trianni et al., 2011). The concept of a superorganism was proposed by the entomologist William M. Wheeler (1911) who argued that an ant colony behaves like an organism or superorganism (cf. Hoffecker, 2013). As stressed by Detrain and Deneubourg (2006), one of the biological features of an ant superorganism is the ability to function as a whole and to take collective decisions. The ability to function as a whole is also a representative feature of human group behavior. In a study investigating choral singing, it has been suggested that "the choir functions as a superordinate system, or superorganism, that imposes boundary conditions on the dynamic features of the individual singers" (Müller et al., 2018a, p. 85). Noble (2012) argued that superordinate systems enclosing all other systems in a given time and space are characterized through multilevel dynamics as well as upward and downward causation (cf. Müller et al., 2019). Activity synchronization and oscillatory processes represent a further important property of superorganism. For example, such processes appear in ant societies in widely varying contexts and can have periods from a few seconds to hours and even days and weeks. This synchronized activity can emerge simply from mutual activation through direct physical contacts (Detrain and Deneubourg, 2006).

6.1. Group brain dynamics

Studies on human group brain dynamics are very rare and still in their infancy. There are some hyperscanning studies investigating four people playing a "Bridge-like" card game, wherein an EEG was obtained simultaneously from four participants' brains (Astolfi et al., 2010; Babiloni et al., 2007a, 2007b). Unfortunately, the EEG analyses in these studies were restricted to single- or dual-brain analyses but excluded group dynamics. Astolfi et al. (2010) showed, for example, that the signals estimated from the prefrontal areas (BA8) of the first players were connected to several regions of the brain of their companions in a Granger-causality sense, while the anterior cingulate cortex (ACC) of the second players of the team was strongly connected to the signals estimated in different cortical areas of the first players of the same team. Using functional near-infrared spectroscopy (fNIRS) hyperscanning, Duan et al. (2015) investigated collective drumming in a group of nine people, where the participants were instructed to try their best to make their beats consistent with each others'. The authors used multi-brain network analyses on ROI-averaged data (ROI, regions of interest) that were correlated among the nine nodes indicating the drumming participants. This hyper-brain network was described in terms of graph-theoretical measures, such as network degree, local and global efficiency, and nodal betweenness. In an EEG hyperscanning study, Dikker et al. (2017) investigated classroom social dynamics and found that the brain-to-brain synchrony across students predicts both student

class engagement and social dynamics. The authors suggested that brain-to-brain synchrony is a possible neural marker for dynamic social interactions, likely driven by shared attention mechanisms (Dikker et al., 2017). Another classroom study by Bevilacqua et al. (2018) found that students' brain-to-brain synchrony and their content retention were higher for videos than for lectures, while the brain-to-brain synchrony between the teacher and students varied as a function of student engagement as well as teacher likeability. The authors suggested that social factors such as perceived closeness are reflected in, or appear to drive, brain-to-brain synchrony in real-world group settings and can predict cognitive outcomes such as students' academic performance (Bevilacqua et al., 2019). This evidence was also confirmed in a conceptual learning study using fNIRS measured in instructor–learner dyads (Pan et al., 2020). They observed that brain-to-brain coupling was correlated with learning outcomes, and appeared to be driven by specific scaffolding behaviors on the part of the instructors (e.g., asking guiding questions or providing hints).

The study about hyper-brain synchrony in the guitarist quartet mentioned above revealed strong intra- and inter-brain connectivity, which differed in each of the four guitarists' brains (Müller et al., 2018b). Changes in connectivity patterns were accompanied by corresponding changes in the modular organization of the quartet's hyper-brain network, indicating that the hyper-brain network consisting of four different brains is a dynamic structure with nonstationary coupling dynamics and network architecture that is highly adaptive to external, and probably also internal, situations requiring different network or brain states (Müller et al., 2018b). Another hyperscanning study examined saxophone quartets, but did not investigate group dynamics or inter-brain synchronization (Babiloni et al., 2012). The authors only reported on EEG spectral power density changes during playing and observation of playing compared with the resting state and their relations to the musicians' empathy.

In summary, the study of group brain dynamics has been shown to provide further information on human interaction and improve our understanding of complex social networks that are highly adaptive and likely driven by shared attention mechanisms. These networks are likely to be related to people's engagement and likeability.

6.2. Group physiological system dynamics

As noted by Bashan et al. (2012), "The human organism is an integrated network where complex physiological systems, each with its own regulatory mechanisms, continuously interact, and where failure of one system can trigger a breakdown of the entire network" (p. 1). The authors also showed that different physiological states are characterized by specific network structures and coupling strengths between systems, demonstrating a robust interplay between network topology and function (Bashan et al., 2012). Müller and Lindenberger (2011) investigated interpersonal oscillatory couplings among 11 singers and 1 conductor engaged in choir singing and found that phase synchronization both in respiration and heart rate variability increase significantly during singing relative to a rest condition. Phase synchronization was also higher when singing in unison than when singing pieces of music in parts. Müller et al. (2018a) refined the analyses on choir singing and used WFCs and CFCs, respectively, of respiratory, cardiac, vocalizing, and motor subsystems. Interestingly, they found that coupling strengths in the choir were higher when singing a canon in unison than when singing it in parts, but only for WFC. In contrast, the choir's cross-frequency connections were particularly strong when singing a canon in parts, apparently supporting the interaction and coordination of the different canon entries. Moreover, the authors constructed a hyper-frequency network (HFN) by using WFC and CFC between all choir members and all four subsystems investigated in the study, which were all synchronized within and between the choir members. As suggested by Bashan et al. (2012), the choir HFNs demonstrated a robust interplay between network topology and function. Specifically, when analyzing the modularity structure of the choir HFN, it has been found that the number of hub nodes (characterized by strong connectivity within the modules) and connector nodes (responsible for strong connectivity between different modules) in the network increased when the canon was sung in parts compared to singing in unison, while the singing conditions did not differ in the number of modules in the network. It has been suggested that singing a canon in parts represents a more complex coordination action and, therefore, requires more hub and/or connector nodes. A follow-up analysis (Müller et al., 2019) revealed further differences in the HFN topology between different singing conditions: The clustering coefficient as well as the local and global efficiency were highest and characteristic path length, correspondingly, was shortest when the choir sang a canon in parts compared to singing it in unison. The authors argued that the choir network is more segregated and, at the same time, more integrated when singing the canon in parts as compared with singing in unison. "High segregation indicates that choir members build smaller clusters in the choir (e.g., canon groups singing different parts), while high integration can indicate that notwithstanding the high segregation of the choir, its members remain strongly connected to each other (e.g., attending to the singers in the other groups)" (Müller et al., 2019, p. 10). Furthermore, coupling strengths and HFN topology metrics revealed a significant relationship to the individual heart rate, as an indicator of arousal, and to an index of heart rate variability indicated by the LF/HF ratio (power spectral density at low and high frequencies, respectively), reflecting the balance between sympathetic and parasympathetic activity.

Codrons et al. (2014) investigated arm movements, respiration, and cardiac responses at rest and during spontaneous, music-, and metronome-associated arm-swinging. They found that group synchronization occurs without explicit instructions, at least for arm movements in the metronome-associated condition and for breathing, particularly at rest and in the music-associated condition. Group synchronization of autonomic (cardiovascular and respiratory) rhythms while listening to music in a live concert was reported by Bernardi et al. (2017). The authors concluded that "simple rhythms and melodies largely dominate the choice of music during rituals and mass events, situations in which the value of group cohesion is highlighted" and that "this choice may be based on the fact that it is precisely this kind of music that has the maximum potential to synchronize bodily rhythms across individuals, hence creating the biological soil for an elevated sense of togetherness" (Bernardi et al., 2017, p. 9). Konvalinka et al. (2011) previously reported that collective rituals may enhance social cohesion and that their effects are not limited to those actively performing, but affect the audience as well. In their study regarding a Spanish fire-walking ritual, synchronized arousal assessed by heart rate dynamics was found between active participants and related spectators, but not between the participants and other members of the audience. The authors suggested that the synchronized arousal of the two groups of peoples cannot be explained by a "direct exchange of matter or energy, leaving only the information available to spectators and participants as the basis of the coupling". They concluded that "the shared heart rate dynamics are thus the consequence of socially modulated information-mediated coupling" (Konvalinka et al., 2011, p. 8518). A fNIRS hyperscanning study by Hou et al. (2020) observed that the popularity of a violin performance was strongly associated with averaged left-temporal inter-brain synchrony between the violinist and the audience. Thus, music appreciation is related to a temporally aligned network in the brains of music producers and perceivers. This relation may serve as an underlying mechanism for the positive reception of musical performance (cf. Hou et al., 2020).

Taking the reported results in this paragraph together, coupling strengths and network topology dynamics of autonomic nervous system have proved to be a crucial determinant of group behavior and may represent a potent biomarker for group physiological system dynamics (Müller et al., 2018a).

6.3. Group body movement dynamics

"A social group is not only a set of people, the relations between them, and the social structure, but also the continuous process of synchronization of gestures, looks, acts, and communication" (Nowak et al., 2017, p. 8). Badino et al. (2014) investigated music coordination in quartets using Granger-causality analysis to examine the musicians' head movements and found strong relations between musical complexity and the amount of communication among musicians. The authors suggested that musicians coordinate behavior by maximizing their coordinative efforts in specific and critical moments in time. The fact that high demands on musical coordination increase within- and between-brain synchronous activity in guitarist duets (Lindenberger et al., 2009; Müller et al., 2013; Sänger et al., 2012) and also guitarist quartets (Müller et al., 2018b) only strengthens this observation. In line with these observations, a study on string quartets using motion capture showed that the performers' rating of the "goodness" of performance was positively correlated with the overall degree of body sway coupling between the string quartet members, indicating that communication through body sway reflects perceived performance success (Chang et al., 2017). Moreover, the authors found that assigned leaders exerted significantly greater influence on others and were less influenced by others compared with followers. This effect was present regardless of whether or not the quartet members could see each other, but was nevertheless enhanced by visual information, indicating systemic influences of the musical role (leader vs. follower) on quartet performance and its organization (Chang et al., 2017). In another study on string quartets, Wing et al. (2014) used a time series analysis of successive tone onset asynchronies to estimate correction gains for all pairs of players in two different string quartets. Although both quartets exhibited on average near-optimal gain, the first violinist in one quartet exhibited less adjustment to the others compared with their adjustment to him/her and, in the second quartet, the levels of correction by the first violinist matched those exhibited by the others. The authors suggested that these correction patterns may reflect contrasting strategies of a first-violin-led autocracy versus democracy (Wing et al., 2014). D'Ausilio et al. (2012) investigated movement synchronization (in the Granger causality sense) of eight violinists and two orchestra conductors when playing five different Mozart pieces. The musicians' and conductors' kinematics were assessed using an infrared optical system with passive markers placed on the upper end of the violinists' bows and the end tip of the conductors' baton. The authors showed that the increase of conductor-to-musicians influence in parallel with the reduction of musician-to-musician coordination were associated with the quality of musical execution, as assessed by the judgments of musical experts. They discussed the results in terms of the aesthetic quality of music and visual communication efficacy (D'Ausilio et al., 2012). In a study of the movements of six-member groups who rocked their chairs while seated in a circle facing the center, the cluster-phase method (introduced by Frank and Richardson, 2010) was used to analyze movement data in trials where group members either had no information about each others' movements (their eyes were closed) or they had their eyes open and gazed at a marker in the center of the group. The group level synchrony measure proved able to distinguish between these two situations (eyes closed vs. eyes open). Moreover, the authors were able to determine whether and how strong the movements of any one group member were synchronized to the movements of a group as a whole (Richardson et al., 2012). Recently, Chauvign´e et al. (2019) investigated group synchronization of 13 expert folk dancers while the availability of either auditory (the beat of music), visual (seeing their fellow dancers), or haptic (holding hands in a circle) coupling was manipulated. Using 3D motion capture recordings and following cluster phase analysis for group synchrony, the authors demonstrated that selective inhibition of any one of the three types of sensory coupling significantly reduced group synchrony, whereby haptic coupling had the strongest effect on movements and group synchrony, at least in the medio-lateral and antero-posterior axes. Thus, this study endorses the significance of sensory couplings and underlying sensory input and motor output in group synchrony and joint action performance.

In summary, this subsection showed that in addition to brain and physiological group dynamics, body movements (e.g., body sway, hand and head movements, etc.) become synchronized if the participants are involved in joint action. Furthermore, sensory couplings play a crucial role in group synchrony and joint action performance.

6.4. Group dynamics of rhythmic applause

As mentioned above, a performance, especially a good performance, affects the audience. An audience expresses appreciation for a good performance through the strength of its applause or by thunderous synchronized clapping (N´eda et al., 2000b). This synchronization process provides a wonderful and interesting example of social self-organization that is also observed in numerous systems in nature (Neda et al., 2000a´) and collective behavior, e.g., synchronous flashing in fireflies, fish schooling, honey bee swarm gathering, etc. (cf. Detrain and Deneubourg, 2006; Sumpter, 2006). N´eda et al. (2000a) describe the applause dynamics as follows: "Our measurements offer an insight into the mechanism of synchronized clapping: during fast clapping, synchronization is not possible owing to the large dispersion in the clapping frequencies. After period doubling, as mode II clapping with small dispersion appears, synchronization can be and is achieved. However, as the audience gradually decreases the period to enhance the average noise intensity, it slips back to the fast clapping mode with larger dispersion, destroying synchronization" (N´eda et al., 2000a, p. 849). This is the reason why the two main desires of the spectators (optimal synchronization and maximal applause intensity) cannot both be fulfilled at the same time (N´eda et al., 2000b). Thus, there is a controversy or incompatibility between the optimal synchronization and the intensity of the applause. This leads us to assume that such controversy or exclusionary regularity exists in other physiological or social systems as well. As Buzsaki pointed out in his well-known book "Rhythms of the brain": "The waxing and waning nature of rhythmic hand clapping is reminiscent of numerous transient oscillatory events in the brain, especially in the thalamocortical system" (Buzsaki, 2006´, pp. 168–169). There is also a trade-off between neural computation and oscillatory coordination. It has been suggested that independent neural firing can drastically reduce oscillatory coordination, whereas complete synchronization practically eliminates the possible computational contribution of individual neurons (Peterson and Voytek, 2018).

In an experimental study, Thomson et al. (2018) recorded applause in different groups (from a few individuals to over 200) who were instructed to clap in unison. The authors reported that every single group that was analyzed (over 30 in total) tended to increase the frequency of the collective rhythm after synchrony was achieved and that this increase in frequency occurred more rapidly in larger groups. The authors also found that the tendency of humans to clap in unison or in sync by speeding up is an epiphenomenon of inter-individual behavior and not a consequence of some collective desire to increase noise intensity, for example (Thomson et al., 2018). Ott and Antonsen (2017) present a simple model for synchronization via a combination of frequency and phase synchronization dynamics that can be reduced to a low dimensional dynamical system as observed in synchronized clapping, but also firefly flashing, and cricket chirping. They proposed this model for a frequency adaptation of populations of coupled oscillatory units and conclude that "evolution might, in some cases, favor the development of frequency adaptation in organisms for which synchronization has a functional benefit" (Ott and Antonsen, 2017, p. 4).

In summary, we show that synchronized clapping as an audience expression of appreciation for a good performance functions as a social self-organizing system that mostly exhibits specific dynamics with different phases (e.g., fast clapping, synchronization, and slipping back to the fast clapping) and corresponds to the trade-off between optimal

synchronization and maximal applause intensity, which can be expressed in the African proverb: "To go fast, go alone. To go far, go together." Overall, the findings reviewed in this section that social behavior emerges through the interaction of the subsystems at different levels organized in accordance with the principles of self-organization and self-regulation, multilevel dynamics as well as upward and downward causation, and functioning as a superorganism or superordinate system.

7. Theoretical concepts and their possible relations to neurophysiological data
7.1. Forward model, functional system theory, and superorganism concept

In this subsection, we would like to explain the three concepts presented above in terms of their similarities and discrepancies. First of all, it should be emphasized that the forward model and functional system theory have many similarities that we have not yet mentioned before and would like to present here. Common goal and action intentions at all three layers of the forward model belong to the afferent synthesis of the functional system and are mainly related to motivation as the leading internal need of the system. The role of motivation is to form a goal and support goal-directed behavior. The goal, or the common goal, is also strongly associated with the valuable result of the system serving as the system-building factor. The external effects in the forward model can be related to contextual and starting afferentation in the afferent synthesis. Action prediction (also at the three layers) can be realized at the three stages of the functional system: afferent synthesis, decision making, and acceptor of action results. The acceptor of action results also includes an efference copy and other's and joint actions as well as corresponding expectation effects from these actions, while the motor command rather belongs to the action program with a set of efferences. Sensory feedback in the forward model could then be equivalent to the backward afferentation or reafference in the functional system. This brief comparison of these two approaches shows their advantages and disadvantages. If the three layers of representation (individual, other's and joint forward model) in the forward model can be considered individually, they are not separated and represented in their unity in the functional system approach. The functional system approach, however, has a more detailed representation of the processes taking place during an action or interaction. Moreover, the hierarchical and holographic principles of organization are another advantage of functional system theory, which allows one to evaluate systems and subsystems in their entirety.

The superorganism approach, or concept, is an interesting and important complement to the two previous approaches. The superorganism approach refers to a complex interaction involving several organisms (although a two-person interaction can also be considered as a kind of superorganism). Important properties of this concept are self- organization, synchronization, multilevel dynamics, and upward and downward causation (Detrain and Deneubourg, 2006; Hoffecker, 2013; Noble, 2012; Trianni et al., 2011; Wheeler, 1911). The two principles of functional system theory that we have explained before (i.e., hierarchical and holographic principles) have certain parallels with multilevel dynamics and upward and downward causation mentioned above. Moreover, functional systems are, like superorganisms, self-organizing and auto-regulating systems. Self-organization outlines a spatiotemporal pattern that is not explicitly fixed in the individual components of the system, but results from the numerous interactions between them (Trianni et al., 2011). Interaction between individual components and their synchronization is a key feature that is common for all approaches that we discuss here. In the superorganism approach, such terms as "Swarm Cognition" (Trianni et al., 2011) or "super-brain" (Hoffecker, 2013) emerge that assume the function of making collective decisions. But the main question remains: How is this self-organization achieved and how is information about goals, plans, actions, and results represented and processed in such systems (Kazansky, 2015)? The valuable result as a system-building factor may be one possible solution, showing how the components can be organized to form a system.

7.2. Possible relationships between theoretical concepts and experimental data

The three concepts or approaches described above represent important theoretical tools to explain or understand experimental data. However, there is a large gap between neural and behavioral data, and we do not know exactly by which perceptual and/or action moments individuals are linked. For example, consider the situation of playing the guitar in quartet shown in Fig. 4. The within- and between-brain connectivity and strength distribution maps are different in the four guitarists' brains (see Fig. 4 for details). Besides the auditory, visual, and sensorimotor brain regions, representing corresponding sensory and motor information channels, fronto-parietal brain regions, representing the mirror neuron system and other (cognitive) brain functions, are also involved in the four guitarists to differing extents. Given the relatively low spatial resolution of EEG, we can only speculate that enhanced intra- brain connectivity at left central sites in guitarists B, C, and D is related to the right-hand activity, as to be expected in guitar playing (note that guitarist A is drumming on the deck of the guitar with both hands). But even if this is the case, we cannot say exactly what fraction of a person's neural connections is devoted to representing the forward model of his/ her action over that of the other person, or even the joint action. Similarly, using the functional system approach, we cannot state precisely which stage of the system (afferent synthesis, decision making, or acceptor of action results with program of action) is related to the right- hand synchronization pattern. Further, there is also a certain uncertainty whether this synchronization pattern represents the action itself with a corresponding efference copy or is a representation of action results with a corresponding reafference. In addition, if we now look at the between-brain connectivity map, it becomes evident that the connections do not communicate among the same brain regions in the four different brains but there are mostly different brain regions in contact with each other. This means that an auditory channel in one brain is in contact with a visual or another channel in another brain, and so on. Moreover, it can contact a visual channel in one brain and a sensorimotor or another information channel in a further brain. Thus, the overall hyper-brain network consisting of different intra- and inter-brain connectivity or synchronization patterns can have different configurations dependent on internal and external conditions. How these synchrony patterns are related to different layers of the proposed forward model or different processing stages of the functional system is an open research question requiring more insights into the cognitive and neural mechanisms underlying such processes.

In accordance with the superorganism concept and also the theory of functional systems, the guitarist quartet is a self-organizing system with upward and downward causation. This means that (1) only those neuronal connections that are adaptive for the system or lead to the certain result become active and (2) each action of each guitarist influences the whole quartet and vice versa, all changes that occur in the quartet itself have a certain effect on the quartet members. It stands to reason that the synchronization patterns shown in Fig. 4 have specific adaptive meaning and represent the adaptively best action for the four guitarists and the quartet as a whole. We only need to properly understand and represent the associations between these actions and neural processes. For this understanding, further research is needed to close the gap between behavioral and neural and also other (physiological and physical) representations or features.

8. Concluding remarks

Coordinated social interaction is an essential and ubiquitous part of human everyday life (Keller et al., 2014; Sänger et al., 2011). Neural

mechanisms of this interaction are far from being understood. In this review, we presented common roles for how coordinated behavior can be comprehended in terms of the extended forward model, functional system theory, and the superorganism approach. We find it important to consider the three representation levels of social behavior simulating own, others', and joint actions as presented in the extended forward model. Functional system theory approach indicates different operation blocks representing the system architectonics that is driven by a valuable result strived for by the system and functioning as a system-building factor (Anokhin, 1974). We also showed that systems function in accordance with isomorphic, hierarchical, and holographic principles of organization. In line with other research, we emphasized the important role of inter-brain synchronization as a crucial neural mechanism of social interaction. We also showed that the interplay of the two types of couplings (intra- and inter-brain), resulting in hyper-brain activity, offers a better way to understand the neural processes activated during interpersonal interaction. This integrated synchronous activity of interacting brains, or hyper-brain activity, in connection with the graph-theoretical approach and network analyses, provides further crucial information about hyper-brain neural actions and underlying mechanisms of dynamic cortical representations. Finally, we described potential basic underlying processes of group brain and group physiological system interactions that show that groups of individuals function as superordinate systems, or superorganisms, that impose boundary conditions on the dynamic features of the groups' agents based on multilevel dynamics as well as upward and downward causation (Noble, 2012). This view has also been validated on group body movements and rhythmic applause or synchronized clapping that have possible implications for other complex social systems and self-organization mechanisms. We recognize that this review is not able to cover the entire hyperscanning literature; on the other hand, we also note that this growing field of research has certain knowledge gaps, making it difficult to provide an all-encompassing exhaustive view on social interaction behavior and its neural mechanisms.

Clearly, further sophisticated research is needed to deepen our understanding of these highly interesting and complex phenomena. Most importantly, different brains are coupled to one another through perception and action. Thus, hyperscanning techniques need to be combined with dense recordings of behavioral and perceptual cues to better understand the mechanisms that give rise to intra- and inter-brain synchrony, and physiological systems' and subsystems' synchronous activity.

Declaration of Competing Interest

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

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