



Comparative connectomics of the primate social brain

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ABSTRACT

Social interaction is thought to provide a selection pressure for human intelligence, yet little is known about its neurobiological basis and evolution throughout the primate lineage. Recent advances in neuroimaging have enabled whole brain investigation of brain structure, function, and connectivity in humans and non-human primates (NHPs), leading to a nascent field of comparative connectomics. However, linking social behavior to brain organization across the primates remains challenging. Here, we review the current understanding of the macroscale neural mechanisms of social behaviors from the viewpoint of system neuroscience. We first demonstrate an association between the number of cortical neurons and the size of social groups across primates, suggesting a link between neural information-processing capacity and social capabilities. Moreover, by capitalizing on recent advances in species-harmonized functional MRI, we demonstrate that portions of the mirror neuron system and default-mode networks, which are thought to be important for representation of the other's actions and sense of self, respectively, exhibit similarities in functional organization in macaque monkeys and humans, suggesting possible homologies. With respect to these two networks, we describe recent developments in the neurobiology of social perception, joint attention, personality and social complexity. Together, the Human Connectome Project (HCP)-style comparative neuroimaging, hyperscanning, behavioral, and other multi-modal investigations are expected to yield important insights into the evolutionary foundations of human social behavior.

1. Introduction

Behaviors related to sociality are thought to be among the key factors that drove evolution of human intelligence (Byrne and Whiten, 1988; Humphrey, 1976). A core human social cognitive ability is theory of mind (ToM), also known as mentalizing, which refers to the inference of others' mental states such as intention, belief, and emotion

(Frith and Frith, 2003). Developmental psychologists have postulated that ToM develops through eye contact and joint attention (JA) (Baron-Cohen, 1989; Mundy, 2003, 1995; Mundy and Newell, 2007; Tomasello, 1995; Tomasello et al., 2005) and linguistic abilities (Heyes and Frith, 2014). Their research investigates the ontogenic emergence of ToM, while cognitive neuroscientists are studying where and how it is implemented in brain circuits (Mahy et al., 2014). Behavioral

Abbreviations: ACC, anterior cingulate cortex; AIC, anterior insular cortex; ASD, autism spectrum disorder; DMN, default mode network; FFA, fusiform face area; YA-HCP, the young adult human connectome project; JA, joint attention; mPFC, medial prefrontal cortex; MNS, mirror neuron system; NHP, non-human primate; OFA, occipital face area; PCC, posterior cingulate cortex; STS, superior temporal sulcus; ToM, theory of mind; TPJ, temporo-parietal junction; vPM, ventral premotor cortex.

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scientists also have an important role to play, as our understanding of social behaviors will benefit from phylogenetic as well as ontogenetic approaches (Heyes, 1998; Skinner, 1966).

Social behavior is defined as any interactions between conspecifics and shaped by multiple factors ranging from inherited (e.g., genetic) to acquired (e.g., neurobehavioral adaptation to social and cultural environments). Thus, social behavior is fundamentally dynamic, flexible, and complex. The complexity of human social behaviors has led zoologists to investigate its origins in the primate lineage (Alexander, 1974; Brothers and Ring, 1992; Eisenberg, 1966; Eisenberg et al., 1972), and biologists to hypothesize mechanistic interpretations. Many candidate molecules and genes have been associated with social behaviors — serotonin and dopamine have been correlated with dominance status in monkeys (Morgan et al., 2002; Noonan et al., 2014; Raleigh et al., 1991); oxytocin and vasopressin have been linked to prosociality and social attention in monkeys and humans (Chang et al., 2012; Ebitz et al., 2013; Hovey et al., 2020; Jiang and Platt, 2018a, 2018b; Liu et al., 2015); endorphins have shown to play a role in grooming (Dunbar, 2010; Keverne et al., 1989); subtypes of vasopressin receptors are associated with individual differences of social behaviors in rodents (Phelps et al., 2017); and over 600 genetic loci are associated with autism spectrum disorder (ASD) (Waye and Cheng, 2018). However, the processes linking molecular events to phenotypes (social behavior) remain poorly understood.

The distinctiveness of primate social behavior may reflect at least two features: (i) many primates live in relatively large groups which often change in size, membership, and hierarchy (Kappeler and van Schaik, 2002); and (ii) non-kin-based relationships such as male-male and female-female bonding may be critical to the forming of coalitions (Ostner and Schülke, 2014). In support, recent behavioral studies suggest that social abilities of non-human primates (NHPs) are more sophisticated than previously thought and may represent primitive forms of human social abilities (Bourgeois-Gironde et al., 2021; de Waal and Preston, 2017; Silk and House, 2016; Suchak et al., 2016). Indeed, precursors of ToM are found in NHPs (e.g., understanding other's goals and intentions and anticipating others' false-belief) (Call and Tomasello, 2008; Hayashi et al., 2020; Heyes, 1998; Krupenye et al., 2016; Martcorena et al., 2011; Povinelli and Preuss, 1995; Premack and Woodruff, 1978). While the ability of ToM has been associated with emergence of metacognition and language in humans (Tomasello, 2003), reproductive social behaviors may largely be driven by *primitive* brain structures (e.g., the diencephalon, paleocortex, endocrine systems) in all mammals (Chen and Hong, 2018). The primate-specific social ability may be linked to increase in brain size, especially association cortex (Dunbar and Shultz, 2017, 2007; Krubitzer, 2007; Van Essen and Dierker, 2007).

Recent technical advances in neuroimaging are helping reveal macroscopic aspects of brain function and circuitry and potentially may help bridge gaps between molecules and behaviors across primate species. Here, we review our current understanding of the linkage between the underlying macroscale brain connectome and primate social behavior. We first summarize the neurobiological basis underlying primate sociality and point to a correlation between the number of neurons in the cerebral cortex and social group size in diverse primate species. Then we describe candidate brain regions and connections relevant to primate social behavior, particularly paying attention to data from resting-state networks, which recently have been correlated with individual variability in social behavior (Phelps et al., 2017). This review is focused on four categories of social behavior and their neurobiological mechanisms including perception of others, from JA to mentalization, sense of self and personality, and social complexity. Finally, we discuss future directions in comparative neuroimaging and other modalities that may yield substantial insights into evolutionary history of primate social behavior. Readers may also refer to more specific reviews on social learning (Joiner et al., 2017), aggression (Lischinsky and Lin, 2020), social stress (Sandi and Haller, 2015), empathy (Chen et al., 2018;

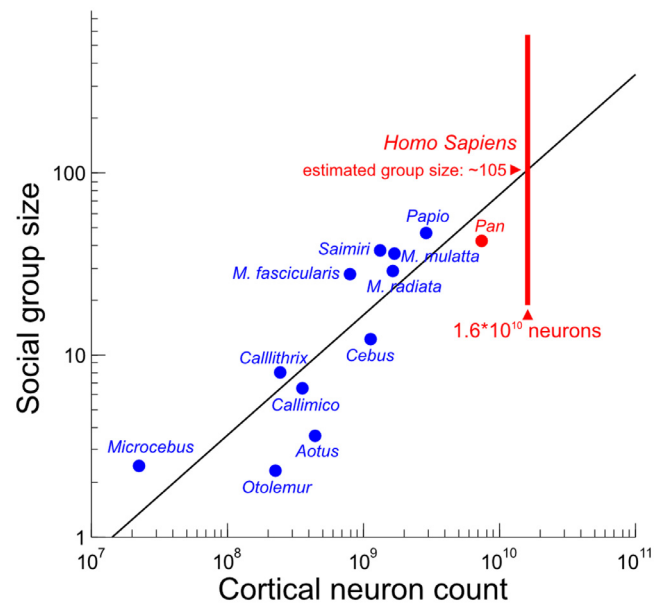


Fig. 1. Non-human primate (NHP) cortical neuron count is associated with social group size. The red vertical line indicates 95% confidence interval of human group size, predicted from the regression line of NHPs. Cortical neuron counts of monkeys (blue circle, species $N = 11$) were taken from Herculano-Houzel et al. (2015), and that of chimpanzee (red circle) from Collins et al. (2016). Social group sizes were based on DeCasien et al. (2017) except for Microcebus and Callimico (Eberle and Kappeler, 2006; Kappeler and Heymann, 1996; Nash and Harcourt, 1986). The black line indicates the regression line fitted to the logarithm of cortical neuron count and social group size. Regression slope was 0.66, which indicates that doubling social group size is associated with ~ 3 times more cortical neurons (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

de Waal and Preston, 2017), and language (Hage and Nieder, 2016; Scott, 2019).

2. Primate brain and sociality

The greater social behavioral abilities of primates have long been suspected to be associated with the relatively large size of their brains among taxa (Byrne and Whiten, 1988). In particular, disproportionately enlarged neocortex relative to the rest of the brain has been shown to be predictive of social group size across primates (Dunbar, 1992; Dunbar and Shultz, 2007; Finlay and Darlington, 1995). One possibility is that primates' abilities to maintain cohesive social relations is constrained by the information capacity of the cerebral cortex and that social group sizes well outside this species-specific functional capacity are unsustainable (Dunbar and Bever, 1998).

We re-examined Dunbar's hypothesis of social group size with respect to the number of cortical neurons in the primate lineage revealed by recent quantitative analyses (Collins et al., 2016; Herculano-Houzel and Lent, 2005) (Fig. 1). Using publicly available data from 11 species of monkey and one ape species, we found a significant correlation between the number of cortical neurons and group size ($R^2 = 0.73$, $p < 0.001$) in agreement with Dunbar's hypothesis. Extrapolating the regression line from NHPs to humans with ~ 16 billion cortical neurons (Azevedo et al., 2009) predicts a human social group size of ~ 105 . This estimate falls under Dunbar's number (150) derived from a larger number of NHP species. However, a large degree of uncertainty (95% confidence interval from 19 to 585) and limited quantitative data from other ape species may require careful attention when making inferences on how apes are unique compared with monkeys (Dunbar and Bever, 1998; Lindenfors et al., 2021).

Inferences based on group size, however, remain debated (DeCasien et al., 2017; Dunbar and Shultz, 2017). For the sake of argument, this association would suggest that doubling the social group size would be associated on average with three times more cortical neurons in primates or that a single group member would be associated with an additional ~250 M neurons in humans. While such inference is certainly an oversimplification, large social group size has a foraging advantage which leads into problems dealing with complexity of social life. In contrast, a recent study argues in favor of ecological explanations that changes in diet enabled primates to grow larger brains for development of social skills (DeCasien et al., 2017). Alternatively, ecological and social factors might both contribute to the expansion of the primate neocortex but impact different circuits. For instance, the expansion of the medial orbitofrontal cortex has been associated with the ecological intelligence hypothesis (Louail et al., 2019), whereas expansion of the temporo-parietal junction (TPJ) has been associated with the social brain hypothesis (Patel et al., 2019). Regardless of the causal origins, foraging efficiency may have an advantage for a large brain. A likely consequence of an increase in cortical neuron number is an expansion of cortical neural networks (Van Essen et al., 2019) with a potential emergence of species-specific functions required for more effective problem-solving related to foraging or social interactions.

Given that several aspects of social behavior are relatively conserved across primates, their neural mechanisms may also be relatively preserved in the primate lineage. Such mechanisms may include homologous cortical areas (Brodman, 1909; Van Essen et al., 2019), structural connectivity (Markov et al., 2014; Van Essen et al., 2014), and functional networks (Buckner and DiNicola, 2019; Sallet et al., 2011) as well as conserved neurotransmitter signaling such as dopamine and serotonin (Raghanti et al., 2018, 2008; Schultz, 2007; Zilles and Palomero-Gallagher, 2017) that together drive context-dependent social functionality adaptive to social complexity.

3. Connectomics of primate social behavior

"Sociality is an integral element of mind and disappears entirely, so far at least as its symptomatic manifestations are concerned, after mutilation of the frontal lobes, and in almost all forms of mental disease in the human subject." (Bianchi and Macdonald, 1922). For over a century, neuroscientists have tried to understand the specific brain regions, particularly in the frontal lobe, and brain networks that are involved in primate sociality. Many recent neuroimaging studies have associated regions of cortex with specific social behaviors, such as medial prefrontal cortex (mPFC) and ventral premotor areas (vPM), superior temporal sulcus (STS), TPJ, which are commonly activated during different social cognitive tasks in humans (Ochsner et al., 2005; Saxe and Kanwisher, 2003; Schurz et al., 2014; Van Overwalle, 2009; Young et al., 2010) and by electrophysiological studies in NHPs (Hayashi et al., 2020; Ninomiya et al., 2020). Recent studies have correlated sets of activated regions with functional networks such as the default mode, ventral attention, and frontoparietal networks (Andrews-Hanna et al., 2014; Schurz et al., 2021). Moreover, given accumulating evidence for the ability of resting-state networks to predict other aspects of individual brain organization (Glasser et al., 2016a; Tavor et al., 2016), here we propose that individual variability in resting-state networks may correlate with individual differences in social behaviors.

We explored resting-state functional connectivity (FC) data in humans from the Young Adult Human Connectome Project (YA-HCP) (Glasser et al., 2016a) and more preliminary data in macaques (Hayashi et al., 2021), both collected and analyzed in a harmonized manner (Autio et al., 2021; Glasser et al., 2013). By seeding in corresponding areas (i.e., vPM [F5a vs 6r] and posterior cingulate/precuneus [pC/PCC]), we found two putative homologous functional network organizations that are distributed over the non-primary sensorimotor cortices and potentially associated with social behavior (Fig. 2). The FC seeded from vPM (area F5a in macaque and 6r in human)

(Belmalih et al., 2009; Gerbella et al., 2011; Neubert et al., 2014) exhibited positive correlations in the anterior inferior parietal lobules, anterior cingulate (ACC) and anterior insular (AIC) cortices. These regions overlap with a part of the 'mirror neuron system' (MNS) (Caspers et al., 2010; Iacoboni and Dapretto, 2006; Molenberghs et al., 2012; Rizzolatti and Sinigaglia, 2010). The FC seeded from pC/PCC (Vincent et al., 2007; Hayashi et al., 2021) is distributed in the posterior inferior parietal, superior temporal lobules and mPFC, which overlaps with the 'default mode network' (DMN) (Andrews-Hanna et al., 2010; Mars et al., 2012; Raichle, 2015; Spreng et al., 2020). Notably, these two neural network systems exhibit 1) spatial anticorrelation over the cortical surface, and 2) corresponding regions within the association cortex of both species: the MNS is located nearer to the primary somatomotor area, whereas the default system is situated farther from it (Margulies et al., 2016).

MNS was identified by the discovery of mirror neurons in macaque monkeys that are activated by specific actions, both when performing the action by oneself and observing the action performed by another (di Pellegrino et al., 1992; Gallese et al., 2002; Nelissen et al., 2005; Rizzolatti et al., 1996). Subsequent neuroimaging studies suggest a similar MNS network in parieto-premotor in humans (Caspers et al., 2010; Rizzolatti and Fogassi, 2014), as well as in NHPs (Nelissen et al., 2011; Rizzolatti and Craighero, 2004; Rizzolatti and Sinigaglia, 2010). The MNS is considered to unify action observation and execution, and underlie 'online' imitation of other's action when interacting with others (Caspers et al., 2010; di Pellegrino et al., 1992; Iacoboni and Dapretto, 2006; Rizzolatti and Sinigaglia, 2010). According to accumulated evidence, MNS is mainly involved in lower-level processing of observed actions rather than higher-level interpretation of observed actions (e.g., intention), as well as in domain-general visual-motor associative learning (Cook et al., 2014; Heyes and Catmur, 2021). In this review, the MNS is discussed in association with perception of others (see Section 3.1) and joint attention (Section 3.2).

Conversely, the DMN has been associated with higher-level social behavior. It is mainly active during 'offline' or default state (Raichle et al., 2001), and is often de-activated during tasks that require mental (sensory) orientation to external information (Andrews-Hanna et al., 2010; Mars et al., 2012; Raichle, 2015; Spreng et al., 2020). The DMN is associated with a sense of self and personality (see Section 3.3) and social group size (Section 3.4). Both MNS and DMN have been associated with mentalizing (Mars et al., 2012; Schurz et al., 2021) (see also Section 3.2). The spatiotemporal organization of the networks (Fig. 2) is in line with the putative contrasting functions: the MNS is more engaged in 'online' unifying perception and action at lower-level, whereas the DMN is more associated with an 'offline' state of higher-level social cognition including a sense of self and personality and social complexity.

3.1. Perception of others

Social behavior requires extracting socially relevant information from the external world, especially from other individuals in the social group. In primates, the face is a particularly important source of social information. Ever since face responsive neurons were first reported in the inferotemporal cortex of macaque monkeys (Gross et al., 1972), the neural basis of face perception has been extensively studied in diverse primate species. Neurophysiological studies found that macaque monkeys have several areas specifically processing face visual information, often referred as "face patches", along STS (Hesse and Tsao, 2020; Tsao et al., 2006). These face selective responses along STS were confirmed using neuroimaging in marmosets (Fig. 3a) (Hung et al., 2015; Schaeffer et al., 2020) and macaques (Fig. 3b) (Bell et al., 2011; Fisher and Freiwald, 2015; Russ and Leopold, 2015). A similar arrangement has been reported in humans (Fig. 3c) (Allison et al., 2000), suggesting that the temporal face processing network is a common feature in primates (Tsao et al., 2008). However, the precise homologies among these face patches remain unclear. Human face-selective areas

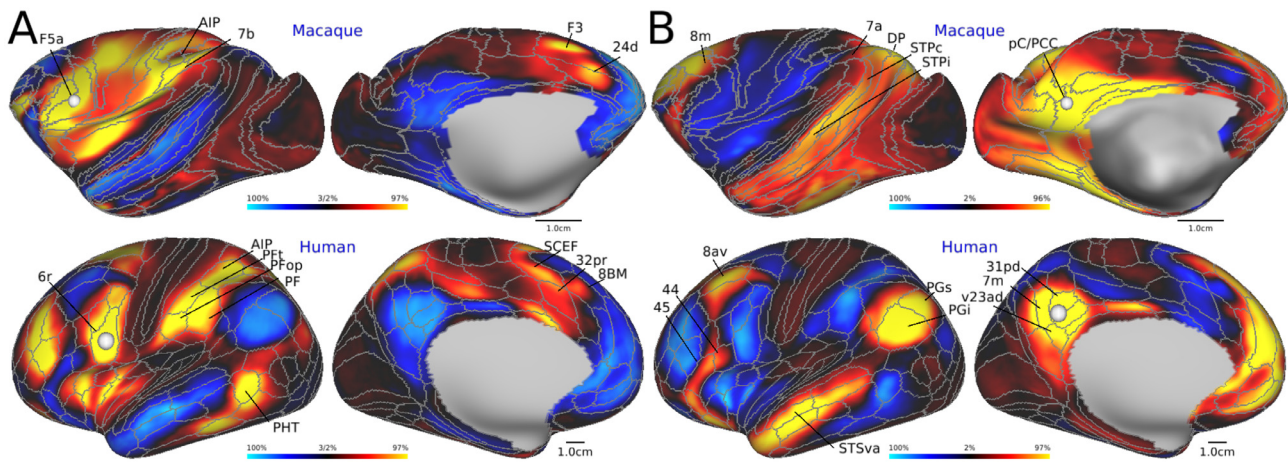


Fig. 2. Two contrasting brain network homologs in the primate cortex.

Putative homologs of functional networks in the left hemispheres of macaque (top) and human (bottom) cerebral cortices. (A) Dense functional connectivity (FC) seeded from the left ventral premotor (vPM) cortex (areas F5a and 6r in macaque and human, respectively) reveals a fronto-parietal network mostly localized near to the primary sensory cortex. Note that positive FC extends over premotor, inferior parietal and insular cortices whereas anticorrelation extends over temporal and prefrontal cortices. (B) FC seeded from the left posterior cingulate cortex/precuneus (pC/PCC) reveals another fronto-parieto-temporal association network that exhibits positive FC in the angular gyrus (parietal area G inferior, PGI), parietal area G superior (PGs) and medial prefrontal cortices. Interestingly, the vPM and pC/PCC FC are spatially anticorrelated in both species. Annotations of cortical areas and boundaries (gray color) are according to M132 (Markov et al., 2014) and the Young Adult Human Connectome Project (YA-HCP) (Glasser et al., 2016b) parcellations in macaque and human, respectively. Human data is from the YA-HCP S1200 Release whereas the macaque data ($N = 30$) was obtained using standardized HCP-style data acquisition and preprocessing (Autio et al., 2020; Glasser et al., 2013; Hayashi et al., 2021,) and standardized in a CIFTI greyordinate space in each species (see Section 4.3). Fig. 2b was reproduced from Hayashi et al. (2021). Note that while the human HCP_MMP cortical parcellation was created based on multimodal MRI data including functional connectome, the macaque parcellation is created based on neuroanatomy but often disagrees with functional maps in some of the areas, e.g., posterior cingulate cortex (Vogt et al., 1987, 2006). Data at <https://balsa.wustl.edu/MxZ8N> (A, Macaque), <https://balsa.wustl.edu/qNG6m> (A, Human), <https://balsa.wustl.edu/B45Zp> (B, Macaque), <https://balsa.wustl.edu/ILV2K> (B, Human).

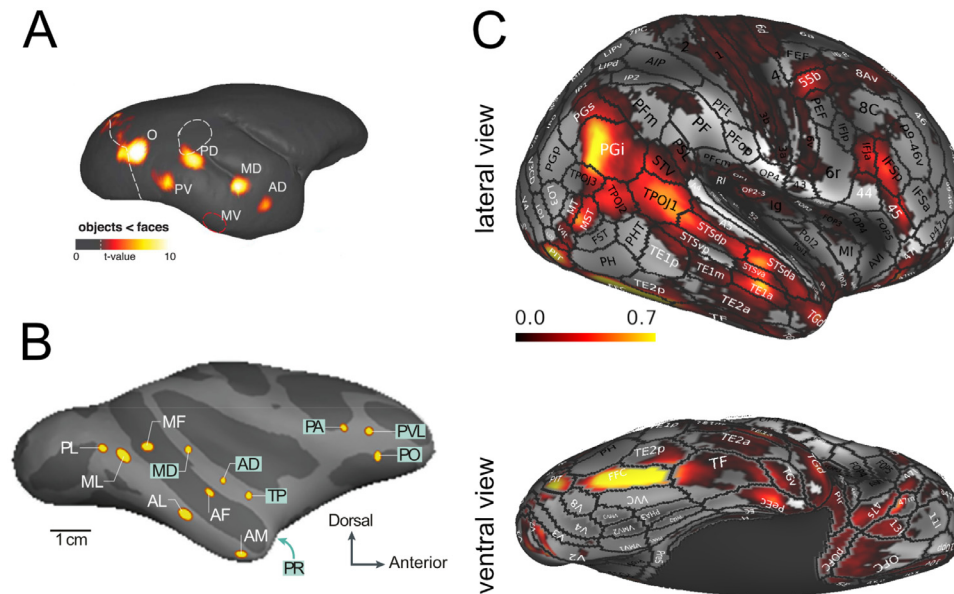


Fig. 3. Face-selective patches in marmosets, macaques, and humans.

(A) Face-selective areas overlaid on the marmoset cortical surface (reproduced from Hung et al., 2015) and (B) the macaque inflated cortical surface (reproduced from Hesse and Tsao, 2020). (C) The contrast of face stimuli minus average of all stimulus classes in the working memory task in the Young-Adult Human Connectome Project S1200 (Glasser et al., 2016a). Upper: lateral view; lower: ventral view of right hemisphere. Abbreviations: AD, anterior dorsal; AF, anterior fundus; AL, anterior lateral; MF, middle fundus; ML, middle lateral; PL, posterior lateral are the six canonical face patches in the inferotemporal cortex of macaque monkey. AD, anterior dorsal; MD, middle dorsal; MV, middle ventral; O, occipital; PA, prefrontal pre-arcuate; PD, posterior dorsal; PO, prefrontal orbital; PR, perirhinal; PV, posterior ventral; PVL, prefrontal ventrolateral; TP, temporal pole are additional face related regions. Data of panel C available at <https://balsa.wustl.edu/Vj9mN>.

are found in the ventral to lateral cortical surface including the occipital face area (OFA), fusiform face area (FFA), and STS (Deen et al., 2015; Kanwisher et al., 1997; Puce et al., 1996), whereas monkey face-selective patches are mainly located in the lateral cortical surface along the inferior temporal gyrus and within the STS (Fisher and Freiwald, 2015; Taubert et al., 2020) (Fig. 3). Interestingly, the human STS respond to facial and body movements (Pinsk et al., 2009), human voice (Aglieri et al., 2018; Kriegstein and Giraud, 2004; Pernet et al., 2015), and language (Hickok and Poeppel, 2007), which is regarded as “the third visual pathway” specialized for social perception (Pitcher and

Ungerleider, 2021). Responsiveness to conspecific vocal cues in STS is also found in NHPs, including macaques (Petkov et al., 2008) and marmosets (Sadagopan et al., 2015). Preferential encoding for body parts, or gaze have also been identified in distinct subdivisions of the macaque STS (Bell et al., 2011; Marciniak et al., 2014; Popivanov et al., 2014). A recent macaque fMRI study revealed a distinct response to moving and static faces along a dorsal-ventral gradient in the face patches, which may correspond with the lateral (STS) - ventral (OFA and FFA) distinction of human face-processing pathways (Fisher and Freiwald, 2015). There are also areas associated with emotional face perception, such as

the amygdala and the ACC, insular, and orbitofrontal cortices, which are reported in both humans (Krolak-Salmon et al., 2004; Morris et al., 1996; O'Doherty et al., 2003) and NHPs (Taubert et al., 2020).

3.2. From joint attention to mentalization

3.2.1. Gaze as social signal

Other's gaze towards the self provides salient information for vertebrates, and is particularly prominent in primates (Emery, 2000). The human eye gaze can elicit gaze aversion as an arousal-reducing cut-off action in human children (Coss, 1979) and induces defensive behaviors in infant rhesus monkeys (Kalin and Shelton, 1989). On the other hand, a preference for a conspecific's gaze in early development can occur in humans (Farroni et al., 2002), chimpanzees (Bard et al., 2005), and macaques (Ferrari et al., 2009; Simpson et al., 2019). Chimpanzees (Myowa-Yamakoshi et al., 2003) and macaques (Simpson et al., 2016) also show cross-species preferences of human eye gaze. Moreover, mutual gaze in mother-infant interactions often signal intention in communication in humans (Cary, 1978; Csibra, 2010), apes (Goodall, 1986; Idani, 1995; Tomasello and Call, 1997; Yamagiwa, 1992), and macaques (Ehardt and Blount, 1984).

3.2.2. Eye contact, joint attention, and theory of mind as milestones of development of social cognition

Eye contact is one of the most salient and most straightforward types of mimicry, unconscious or automatic imitation of movement. Two individuals must coordinate their eye movements to make eye contact (Prochazkova and Kret, 2017). Eye contact is a communicative signal that mediates information transfer regarding emotional and mental states (Emery, 2000). Joint attention (JA) is the ability to coordinate attention between interactive social partners on a third significant object (Mundy et al., 1986), which emerges in human infants around ten months of age (Corkum and Moore, 1998). There are two aspects of JA: responding to JA refers to an individual's ability to follow another individual's direction of gaze; initiating JA refers to an individual's ability to spontaneously create a shared point of reference by the use of alternating gaze between objects and another individual with eye contact (Mundy et al., 2009). It is a critical behavioral milestone in development of human social cognition because it may be a prerequisite for language acquisition (Tomasello, 2003) and a precursor of the theory of mind (Tomasello, 1999). A lack of JA, particularly initiating JA, may be an early predictor of ASD (Mundy et al., 2009). ToM explicitly emerges at around the age of 4 years when children pass the false-belief task, while it operates to implicitly attribute intention and other mental states at around 18 months of age (Frith and Frith, 2003). In sum, eye contact is the basis of JA, which is the precursor of ToM. Considering JA is one of the biomarker candidates of ASD (Mundy and Crowson, 1997), elucidation of network-level representation of these psychological constructs is of clinical importance.

3.2.3. Neural substrates- single brain approach

Studies based on analyzing the brain of one individual at a time have reported candidate neural substrates of eye contact, JA, and ToM. Eye contact activates many regions of the social brain, including the fusiform gyrus, anterior and posterior superior temporal gyri, mPFC, orbitofrontal cortex, and amygdala in humans (Calder et al., 2002; Conty et al., 2007; Kawashima et al., 1999; Pelphrey et al., 2004; Sato et al., 2004; Schilbach et al., 2006; Senju and Johnson, 2009; Wicker et al., 2003) and NHPs (Hoffman et al., 2007; Mosher et al., 2014; Perrett et al., 1982; Schaeffer et al., 2020; Shepherd and Freiwald, 2018). The neural substrates of JA are the mPFC, middle temporal gyrus, and the posterior portion of STS, TPJ, and subcortical areas including cerebellum (Caruana et al., 2015; McKenzie et al., 2006; Oberwilling et al., 2016; Pfeiffer et al., 2014; Redcay et al., 2012, 2010; Schilbach et al., 2013, 2010; Tanabe et al., 2012; Williams et al., 2006).

A meta-analysis of ToM studies (Van Overwalle, 2009) showed that "inferring temporary states such as goals, intentions, and desires of other people engages the TPJ. Inferring more enduring dispositions of others and the self, or interpersonal norms and scripts engages the mPFC". Thus, human ToM is associated with regions that code gaze-mediated social interaction. A cross-species comparative study using MRI revealed that human TPJ has a functional connectivity profile with cortical areas similar to that of the macaque's middle STS which is known to code social information mediated by eye movements (Mars et al., 2013). In addition, the human TPJ and the middle STS in macaques share computational properties. Modulation of activity in both regions reflects social prediction error (Behrens et al., 2008; Koster-Hale and Saxe, 2013; Roumazeilles et al., 2020). Similarly comparative functional connectivity analysis has revealed similar connectivity patterns in the mPFC in humans and macaques (Neubert et al., 2015; Sallet et al., 2013). Electrophysiological recordings and fMRI studies in macaques have revealed distinct contributions of the different subdivisions of the mPFC region to social cognition, from social valuation, to processing social interactions, to social communication and learning from others (Chang et al., 2013; Haroush and Williams, 2015; Seo et al., 2014; Shepherd and Freiwald, 2018; Sliwa and Freiwald, 2017; Yoshida et al., 2016, 2012). These data suggest that similar circuits mediate social information processing in human and non-human primates.

3.2.4. Neural substrates – two-brain approach with hyperscanning fMRI

For behaviors that involve interactions between individuals, network-level analysis should ideally not be restricted to just one individual, but should instead include the brains of others involved in the interaction (Redcay and Schilbach, 2019). For example, hyperscanning fMRI (scanning more than one individual performing an interacting multi-subject task at the same time) enables analyses of inter-brain synchronization within a multi-subject task. Inter-brain synchronization may be explained by predictive coding theory in terms of sharing the internal model or prediction (Friston and Frith, 2015). This approach proposes that neuronal representations in higher cortical hierarchies predict the representations in lower levels (Friston, 2008; Mumford, 1992; Rao and Ballard, 1999). The comparison of top-down predictions (forward model) with representations at the lower level forms a prediction error fed back up the hierarchy to update higher representations. This recursive exchange of signals suppresses prediction error at every level to provide a hierarchical explanation for sensory inputs. According to the predictive coding account, iterative updating processes result in the inter-brain neuronal synchronization during reciprocal interaction of the agents (Friston and Frith, 2015). This schema also predicts that the location of inter-individual neuronal synchronization differs according to the different levels of the internal model sharing.

The hyperscanning approach has been used to evaluate a proposed modular model of ToM (Baron-Cohen, 1994; Perrett and Emery, 1994). The four modules included a direction of attention detector (DAD), intentionality detector (ID), mutual attention mechanism (MAM) for detecting mutual gazes, and ToM mechanism. In this model, the eye contact, as MAM, links JA with the ToM to infer the volitional states.

The hyperscanning evaluation of this model includes three approaches. First, a study during eye contact found that the limbic MNS (the ACC and AIC) (Cattaneo and Rizzolatti, 2009) and cerebellum mediate mutual interaction (Koike et al., 2019a), which constitutes MAM.

Second, in a study during the JA task, Koike and colleagues found inter-brain synchronization of the task-specific activity in the right AIC (Koike et al., 2019b). Recent theoretical and experimental approaches suggest that inter-individual synchronization represents a forward model (Friston and Frith, 2015; Miyata et al., 2021). Koike et al. (2019b) concluded that the right AIC represented sharing "intention in attention" as a pair-specific forward internal model through JA activity.

Third, a study was conducted during a verbally-mediated JA task (Yoshioka et al., 2021). As the triadic representation relationship involves shared attitude (attend, goals, desire, etc.),

Baron-Cohen (1995) hypothesized that ToM is triggered in development by taking triadic representations from JA and converting them into meta-representations through linguistic interaction. A longitudinal study showed that gaze following, a critical component of JA, at 10.5 months of age, predicted the use of mental-state terms at 2.5 years; the latter predicted ToM at 4.5 years (Brooks and Meltzoff, 2015). The authors hypothesized that gaze following fueled children's linguistic coding of psychological concepts, which in turn supported the ontogenesis of an explicit "ToM". Based on this hypothesis, Yoshioka et al. (2021) conducted verbally mediated JA without exchanging eye-gaze. They found that the right AIC showed pair-specific inter-individual neural synchronization of task-specific activities, replicating the gaze mediated JA finding of Koike et al. (2019a). Furthermore, the right AIC also showed inter-individual synchronization of the residual time-series data, along with the right TPJ and dorso-medial prefrontal cortex—the core components for mentalization and the DMN (Fig. 2). They interpreted this background synchronization as representing a higher-level forward model, sharing the belief of sharing the situation. They concluded that shared visual experiences are represented by coherent and hierarchical coordination between the DMN and salience network linked through the right AIC.

Thus, the combination of hyperscanning fMRI with predictive coding may account for hierarchical aspects of the social brain network. This experimental approach was recently extended to nonhuman primates (Cléry et al., 2021; Gilbert et al., 2021), allowing for neurobiological understanding of interactive theory for social cognition and behavior (see Section 4.1).

3.3. Sense of self and personality

3.3.1. Sense of self

The sense of self (e.g., self-awareness) is a stable sense of self-identity that is required for adapting one's own behavior to the dynamic social environment (Bahrami et al., 2010). Self-awareness therefore may be critical for advanced social cognition that is specific to humans (Fabbro et al., 2015; Gallup, 1982). Despite controversy on self-awareness in NHPs, self-recognition has been investigated using a range of behavioral paradigms. In particular, a widely-used mirror self-recognition test has revealed that human children and apes can inherently exhibit self-exploratory behaviors that relate to self-awareness (Gallup, 1970; Papoušek and Papoušek, 1974; Swartz et al., 1999; Ujhelyi et al., 2000) whereas monkeys cannot (Anderson, 1994; Boccia, 1994; Gallup, 1977; Hauser et al., 2001; Heschl and Burkart, 2006). However, monkeys can react differently to mirrors and strangers (de Waal et al., 2005; Itakura, 2001; Platt and Thompson, 1985), and also exhibit self-awareness-related behaviors when they are extensively trained on self-recognition tests (Chang et al., 2015; Heschl and Burkart, 2006; Jorgensen et al., 1995) or when a highly salient mark is present on their body (Rajala et al., 2010). Therefore, monkeys may have primitive abilities of self-awareness (also known as *pre-conceptual* self) (Jorgensen et al., 1995) and thus NHPs are useful models to understand neural mechanisms of self-awareness.

The sense of self has been linked to the DMN (Fig. 3b) (Buckner et al., 2008; Buckner and DiNicola, 2019; Fox et al., 2005; Gusnard and Raichle, 2001). Perceived social isolation is associated with variation in structural and connectivity profiles of the DMN (Spreng et al., 2020). The internal representation of the self is associated with the dorsal part of the mPFC, a part of the DMN (Gusnard et al., 2001; Lou et al., 2017; Ochsner et al., 2005). The ventral part of the mPFC is thought to integrate the internal self (visceromotor responding and self-conscious emotion) and apply it to the decision-making process, given its anatomical connections with the subcortical limbic systems and the brainstem (Bechara et al., 1997; Mitchell et al., 2005; Ongür and Price, 2000). The posterior medial cortex is active during autobiographical memory (Kim, 2012), mind-wandering, and future-oriented thinking (Andrews-Hanna et al., 2010; Brewer et al., 2013; Mason et al., 2007). More-

over, the posterior lateral cortex around the posterior end of the lateral and superior temporal sulci is thought to be associated with unaware self-processing (Tadikowski et al., 2017). The DMN-like resting-state network is found in several species of NHPs (Hayden et al., 2009; Kojima et al., 2009; Liu et al., 2019; Mantini et al., 2011; Mars et al., 2012; Sallet et al., 2011) and distributed in a manner comparable to humans (Hayashi et al., 2021; Vincent et al., 2007). It may therefore represent the ability of self recognition shared across primate species (Itakura, 2001; Jorgensen et al., 1995), although detailed knowledge of homology and divergence remains unknown until cross-species brain registration is established (see Section 4.3).

3.3.2. Personality

Social behavior trait (or personality) is a characteristic pattern of individual behaviors for interacting with others, which is relatively stable throughout the lifespan but variable across individuals, groups, and species. Personality in NHPs has been described as several trait dimensions extracted from multiple behavioral phenotypes, which are considered continuous behavioral styles across time and contexts (Uher, 2011). NHPs may be a powerful model for understanding personality and related brain networks.

In common marmosets, Yokoyama et al. (2013) quantified social behavioral traits using multiple tests of encountering unfamiliar conspecifics and analyzed the relationship of the traits to regional serotonergic function. Three factors of social behavior were identified by factor analysis: aggressiveness, friendliness, and anxiousness. An association with serotonin neurotransmission was found for aggressiveness and friendliness in the PCC and for anxiousness in the ACC, as revealed by positron emission tomography (PET) using a specific radioligand for the serotonin transporter, ¹¹C-DASB. Neural activity was assessed in the same subjects using PET with a metabolic ligand ¹⁸F-fluorodeoxyglucose (¹⁸F-FDG), while animals were in freely moving conditions and adapting to different social contexts (familiar vs unfamiliar conspecifics are encaged next to the test subjects). Interestingly, neural activity and connectivity of ACC and PCC were altered depending on these social contexts, respectively. These results suggest a close link between the serotonergic system, midline cortical functional connectivity, and social behavior. The marmoset PCC was identified as a core region of the DMN by resting-state fMRI (Liu et al., 2019) and the ACC as a critical region for emotion and motivation regulation (Alexander et al., 2019; Wallis et al., 2017), resembling its human homolog (Schaeffer et al., 2019).

As for the neurobiology of human personality, scientists have been attempting to use population datasets such as the YA-HCP to relate scores based on the five-factor model of human personality (Costa Jr. and McCrae, 2008) to cortical structures (Lewis et al., 2018; Privado et al., 2017; Riccelli et al., 2017; Toschi and Passamonti, 2019) and the functional connectome (Cai et al., 2020; Dubois et al., 2018; Nostro et al., 2018; Passamonti et al., 2019; Toschi et al., 2018). One dimension of personality, "openness to the experience" is positively associated with gyrification in the PCC, but negatively associated with cortical thickness and myelination in the ACC (Riccelli et al., 2017; Toschi and Passamonti, 2019). Another dimension, "conscientiousness," is positively associated with cortical thickness in the precuneus. Therefore, variability of personality may be correlated with structural changes in cortical areas including the DMN, which suggests a possible link to inherent and developmental variations in these areas. Personality was also associated with functional networks including the DMN (Cai et al., 2020; Nostro et al., 2018; Passamonti et al., 2019); however, results are often inconsistent across studies, and there is a debate over the reliability of the predictive value of functional MRI (Dubois et al., 2018).

Comparative neuroimaging combined with personality traits may provide a tool for the field of personality neuroscience if the personality measures are fully objective and validated (see Section 4.2). Nevertheless, a questionnaire-based approach like the five-factor model used in human has been applied to NHPs (Inoue-Murayama et al., 2018; King and Figueredo, 1997; Koski et al., 2017; Weiss et al., 2011, 2021),

in which animals' social behaviors are rated by caregivers or researchers who are familiar with the subjects. This evaluation is likely reliable and supported by objective (task-based) personality evaluation in many species of NHPs (Freeman et al., 2013; Garai et al., 2016; Šlipogor et al., 2021, 2020, 2016; Úbeda and Llorente, 2015; Verspeek et al., 2019). Combining subjective (questionnaire) and objective (task or observation) approaches may improve the robustness of behavioral measurements of personality both in humans and NHPs.

3.4. Social complexity

The primate social environment is characterized by the large size of social groups and high complexity of social hierarchy, which requires navigating through a multi-agent environment. Social group size is thought to be a key evolutionary drive (Section 2) and also may be related to inter-individual differences in brain structure and function. The higher the number of friends, the larger gray matter volume in a set of brain areas located principally within the DMN (Bickart et al., 2014; Noonan et al., 2018; Sallet et al., 2011; Von Der Heide et al., 2014). Furthermore, gray matter in the ventral part of the mPFC varied with both social network size and ToM competence, demonstrating a correlation between these two facets of primate social life (Lewis et al., 2011). While the direction of cause and effect was not tested in human studies, a manipulation of the social network size in macaques showed that changes in the social environment caused alteration of gray matter volumes in the prefrontal and temporal cortex (Sallet et al., 2011). This neuroimaging finding of structural plasticity might reflect several mechanisms (Zatorre et al., 2012). The social environment not only impacts distinct brain areas but also influences the interaction between brain areas. For instance, the larger the social network, the stronger the coupling between the STS and the perigenual ACC (Sallet et al., 2011).

Social groups are hierarchically organized where individuals vary in their level of power, influence, skill, or dominance (Koski et al., 2015). Social dominance is a major feature of primate societies (Chiao, 2010; Sapolsky, 2005). Individuals with higher status in a social group receive more resources and benefits than others (e.g., mates, foods, social learning). The social hierarchy is also clearly present in human culture (Sidanius and Pratto, 1999). In humans, the amygdala has been shown to be important for learning and representing hierarchies between social agents (Kumaran et al., 2012; Zink et al., 2008). In macaques, its neural correlates partially overlap in the temporal cortex regions sensitive to social network size, including the amygdala and the cortex of the mid-STS (Noonan et al., 2014; Sallet et al., 2011). Subcortical structures have also been identified using deformation-based morphometry analysis, including in the lateral hypothalamus and the raphe nuclei (Noonan et al., 2014). While they play a key role in social cognition (Noritake et al., 2021), addressing questions about their roles in brain networks may benefit from combined studies with functional neuroimaging.

Mathematical approaches have been used to understand the complexity of primate social networks. For example, concepts derived from graph theory developed in sociology and anthropology, such as centrality and betweenness parameters, are now being used in studies of primate sociality (Brent, 2015). This detailed level of analysis could be combined with multi-voxel pattern analysis (MVPA). MVPA is a method that has attracted interest in neuroimaging because it analyzes distributed patterns of activity and allows detecting differences between conditions with higher sensitivity than conventional univariate analysis. Applied to social network analysis, it revealed that several defining parameters associated with social agents within their social network are extracted spontaneously and represented in different brain regions principally located within the DMN (Parkinson et al., 2017). Social distance is represented in the posterior STS, centrality in the mPFC and PCC/precuneus, and constraint (i.e., a measure of how influential a social agent is) in the STS. Embeddedness is more related to the saliency and limbic network (Schurz et al., 2021).

4. Future directions and challenges in linking behavior to the brain connectome

4.1. Shifting the point-of-view from observer to interactor

The behavioral approach of social neuroscience originated from conceptual theories, but experimental validation of theoretical framework is constrained by methodological limitations due to challenges in making ecologically valid investigations on real-time interaction between individuals (Keysers and Gazzola, 2007; Pfeiffer et al., 2013; Schilbach et al., 2010; Sperduti et al., 2014). Inference of others' mental states has been explained by simulation-theory and theory-of-theory (Caspers et al., 2010; Rizzolatti and Sinigaglia, 2010). Both rely on spectator theories of social cognition, which assume that knowing others is gained specifically through perceiving them. Accordingly, experimental paradigms require participants to observe others and think about others' mental states rather than engage directly. A first-person or simulationist account of social cognition has been linked to the involvement of the MNS (Davies and Stone, 1995; Doherty, 2009), whereas a third-person or theorist account of social cognition to the ToM network (Frith and Frith, 2010). Importantly, both accounts are essentially related to perception, without direct engagement, and their neural activation patterns are depicted by the single brain approach. In contrast, interactive theory (Fuchs and De Jaegher, 2009; Gallagher, 2008; Tanaka, 2017) is based on a phenomenological approach based on the idea that humans perceive others directly through interaction before making inferences or simulations (Gallagher, 2012). Considering the importance of social interaction over observations during development, (Schilbach, 2014) argued the need to identify the neurobiological basis of social interactions, and its relation to those of social observation. As discussed in Section 3.3, the social brain connectome analysis with hyperscanning of the interacting participants is expected to provide a methodological basis for probing the nature of interactive theory across humans (Koike et al., 2016, 2019a,b) and NHPs (Gilbert et al., 2021).

4.2. Experimental design for social brain connectomics

4.2.1. An evolving role for task fMRI

Task fMRI has been a major tool to map whole-brain patterns of brain activation and deactivation in both humans and NHPs. It has often been combined with additional scans for localizing functional areas, for example, visual presentation of images of face/body and places/scenes was used to map discrete patches in the occipito-temporal cortex which respond categorically and selectively (Grill-Spector and Weiner, 2014). Localized areas are often used as functional landmarks in volume space or on the cortical surface, but the functional landmark location is variable across subjects, raising the question of whether the variability in functional localization is due to limitation of the registrations or to true biological variation across individuals. In macaques, 3D volumetric alignment of cortical folding patterns has limitations, although NHPs have less variation in folding patterns than humans (Hayashi et al., 2021). A more recent and more sophisticated approach is to apply cortical surface reconstruction using structural images, combined with cortical surface registration using folding or functional features in human brains (Coalson et al., 2018; Glasser et al., 2016a, 2013). Cortical surface reconstruction and folding-based surface registration have recently extended to NHPs (Autio et al., 2020; Donahue et al., 2016), and the usefulness of the surface registration based on functional features in macaques remains to be investigated. Thus, future studies ideally should include additional resting-state fMRI scanning to obtain intrinsic and spontaneous functional connectivity organization over the entire cortex to use as a functional localizer as well as registration modality. To increase the reproducibility of resting-state fMRI, a potential approach may be to use visual presentation with minimal stimuli (e.g., natural or artificial images/movies) during movie fMRI scan without a specific task, which has proven useful in children (Vanderwal et al., 2015) and

NHPs (Russ and Leopold, 2015; Sliwa and Freiwald, 2017), as well as comparative analysis between humans and NHPs (Hori et al., 2021; Mantini et al., 2012).

4.2.2. Common fMRI tasks across species

Designing structured task experiments for cross-species comparison has its own challenges in terms of what features should be matched across species. As Tinbergen pointed out, “to put different species in exactly the same experimental arrangement is an anthropomorphic kind of standardization” (Tinbergen, 1951). Many cognitive tasks may be difficult and require intensive training for monkeys but are easily executed by humans. Matching the task difficulty by modifying task parameters (stimulus features, temporal sequence, number of possible choices, etc.) would be helpful. However, that is not enough insofar as behavior and neural responses also depend on the context of the task. For example, the same face image elicits different neural responses depending whether the subject is focusing on the identity, emotion, or social status (Aglinskas and Fairhall, 2020). The challenge is that it is much more difficult to control task context in NHPs. Since it is not possible to explicitly instruct NHPs, they learn tasks through training and incentives (often food or liquid reward), which can affect task context. To minimize such discrepancies, it is important to match experimental designs across species (Boesch, 2007).

Quantifying NHP behavior is another challenge because NHPs cannot be asked questions verbally and therefore objective assessment of behavior is essential. Task responses, reaction times, gaze locations are all valuable measures for behavior that enable quantitative analysis. Social interactions often provoke autonomic responses such as heart rate, skin conductance, pupil dilation, which would help objective evaluations (Bradley et al., 2008; Critchley, 2005; Kreibitz, 2010; Mauss and Robinson, 2009; Wallis et al., 2017). Measuring the same behavioral parameters also in humans would be valuable for cross-species comparisons. Personality assessment based on questionnaires is used for not only humans but also NHPs, which should be validated by objective assessments in both cases (Freeman et al., 2013; Garai et al., 2016; Šlipogor et al., 2021, 2020, 2016).

4.2.3. Causality of the social brain and connectivity

Assessments of causality associated with task-related fMRI activations and functional connectivity is a prominent approach in NHP studies, which can rarely be addressed in the human brain. Besides classical surgical or chemical (neurotoxic) lesions or reversible pharmacological manipulations (Basile et al., 2020; Roy et al., 2014; Rudebeck et al., 2006; Wallis et al., 2017), other methods that address causal roles of brain connections or areas include a double viral method (Kinoshita et al., 2012), and Designer Receptor Exclusively Activated by Designer Drug (DREADD) (Roth, 2016). Eldridge et al. (2016) revealed that the connection between orbitofrontal and rhinal cortices in primates is engaged in the retrieval of relative stimulus values from memory by reversibly disconnecting two regions of the brain using hM4Di-DREADD. A similar approach was used to clarify the causal role of prefrontal connections in social behaviors in primates. Hayashi et al. (2020) trained macaques for a task testing the ability to attribute false belief to others, which is considered as a milestone of ToM. They combined an anticipatory-looking false belief paradigm with DREADDs and demonstrated that the medial prefrontal cortex may have a causal role of the false belief attribution-like behaviors, suggesting the importance of this region underlying ToM. Ninomiya et al. (2020) demonstrated that the vPM to mPFC connection, supposed to be within the mirror neuron system, is involved in monitoring another's actions. Delta-band coherence was found between these two areas during action execution and action observation, and information flow, analyzed by Granger causality, increased from vPM to mPFC. Selective blockade of the vPM-to-mPFC pathway using a double viral vector infection technique impaired the processing of observed, but not executed, actions.

Recent technical developments in transcranial focused ultrasound can offer a novel approach to non-invasively modulating neural processing in not only superficial but also deep structures of the brain (Klink et al., 2021; Rabut et al., 2020). In particular, low-intensity and low-frequency focused ultrasound was reported to impact brain activity via its mechanical action on neurons and glial cells (Kubaneck et al., 2018; Oh et al., 2019). This technique has been used in monkeys to investigate causal role of deep brain structures such as the anterior cingulate gyrus (Folloni et al., 2019; Fouragnan et al., 2019), amygdala (Folloni et al., 2019), basal forebrain (Khalighinejad et al., 2020) and medial frontal cortex (Verhagen et al., 2019). Since these areas are all implicated in a part of the social brain, future studies are needed to reveal direct association with social behaviors. Since this technique was also shown to safely modulate activity in localized regions in humans (Legon et al., 2020, 2014), it may also be valuable for comparative social neuroscience and therapeutic use in future.

4.2.4. Population neuroscience in NHPs

Addressing individual variability of social behaviors and brain connectomics requires collection of data from a relatively large population. Recent large-scale imaging initiatives have collected data from ~1 k up to ~100 k human subjects (Casey et al., 2018; Miller et al., 2016; Van Essen et al., 2013). Comparable large-scale data collections are not feasible in NHPs due to economical, technical and ethical reasons, although the NHP neuroimaging and neuroanatomy project (NHP_NNP) is underway to collect a more modest number of non-invasive high-quality imaging, social behaviors, and genetics in macaques and marmosets ($N \approx 100$) (Hayashi et al., 2021). However, it remains unclear how many subjects are required to link variations in social behavior and genetics to variations in connectomes in NHPs. A second approach is to identify an animal model demonstrating an outlier of social behavior (e.g., an autistic trait) and to investigate related features of brain connectivity. This approach was indeed taken by combining a single neuron analysis, whole brain genomics, and behavioral assessments in an autistic macaque monkey (Yoshida et al., 2016). A third approach is to establish harmonized scanning protocols across different scanners and imaging centers, and apply high-quality preprocessing and harmonization statistics, adapted by recent clinical studies (Casey et al., 2018; Koike et al., 2021). Similar efforts are underway in the international collaborative primate neuroimaging project, PRIME-DRE (Milham et al., 2018; PRIMatE Data Exchange Global Collaboration Workshop and Consortium, 2020). Since the quality of the data acquisition and preprocessing in NHPs has lagged behind that in humans, establishing high-quality data collection across imaging centers remains a crucial issue (Autio et al., 2021). Fourth is to estimate longitudinal changes of the brain connectome during developmental phases of NHPs, potentially providing important insights for developments of social behaviors. Indeed, a longitudinal study of structural MRI data in postnatal macaques demonstrated developmental changes associated with sociality (Becker et al., 2021; Young et al., 2017).

4.3. Brain registration across individuals and species

Addressing intersubject variability in social ability and brain structure, function, and connectivity requires an improved standardized brain coordinate system. Indeed ToM-associated activations in TPJ revealed high variability in 3D coordinates across studies (Geng and Vessel, 2013; Schurz et al., 2014) and species (Noonan et al., 2017). Human TPJ is located close to the inferior border of the inferior parietal lobe where cytoarchitectonic parcellations aligned across subjects in the volume also have substantial uncertainty in 3D coordinates (Caspers et al., 2008) and historical heterogeneity in its definition (Niu et al., 2021). Indeed, it is not at all clear what cortical areas are activated in many human functional neuroimaging studies that use volume-based smoothing and cross-subject cortical alignment, including the vast majority of the functional neuroimaging studies cited above

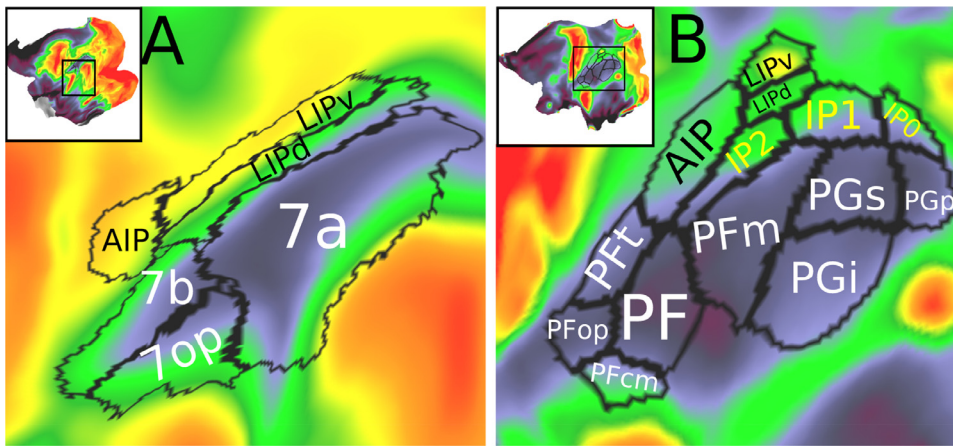


Fig. 4. Cortical myelin flat-maps and inferior lateral parietal areal boundaries for (A) macaque and (B) human. Black labels: same areas in both species. White labels: Proposed modular differentiation, more in human than macaque. Yellow labels: Areas emergent in human but not macaque via hypothesized areal duplication or de novo areal evolution. Data available at <https://balsa.wustl.edu/Z4LMz> (panel A) and <https://balsa.wustl.edu/VjXD9> (panel B) (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.).

(Coalson et al., 2018; Glasser et al., 2016b). Major parts of the social brain networks in humans are distributed across association areas of the neocortex where the folding patterns and locations of areas relative to folds are highly variable across subjects (Coalson et al., 2018; Hayashi et al., 2021). Inter-subject variability should be systematically addressed using an improved brain coordinate system, CIFTI *greyordinates*, in which 2D coordinates are used to capture the geometry of the cortical ribbon and 3D coordinates are used for globular subcortical structures (Coalson et al., 2018; Glasser et al., 2013; Robinson et al., 2018). The CIFTI greyordinate system in combination with multi-modal MRI enables improved cortical surface alignment across subjects using cortical features (e.g., myelination and functional connectivity) thereby providing compelling improvement in the accuracy of inter-subject alignment (Coalson et al., 2018; Robinson et al., 2018). Recent studies in NHPs have also adapted the CIFTI *greyordinate* system (Autio et al., 2021; Donahue et al., 2016; Hayashi et al., 2021), although the inter-subject variability in NHPs appears smaller in comparison to humans.

Addressing interspecies difference in the social brain areas is very important, but our evolutionary understanding may also benefit from improved cross-species comparisons. Social brain areas are mainly located in the association cortex, which has enormously expanded in humans relative to NHPs. This expansion may reflect a larger number of human cortical areas, a larger average size of individual areas, or a combination of both. For example, Fig. 4 shows macaque and human lateral parietal myelin maps with boundaries and labels for 3 types of area: (i) Presumed homologues LIPd, LIPv, and AIP are located in moderately myelinated (green, yellow) intraparietal cortex and reflect species differences in areal size, but not identity. (ii) Three macaque areas and 8 human areas are located in lightly myelinated (blue, indigo) lateral parietal cortex that exemplify the “modular differentiation” hypothesis in which an area of lightly myelinated cortex in a common ancestor became heterogeneous, with internal sub-areas expanding quasi-isotropically in both lineages, diversifying in architecture, function, connectivity, and/or topography into several distinct areas in the macaque (7a, 7b, and 7op) and expanding even further and diversifying more extensively into 8 distinct areas in the human ‘PG and PF complex’. (iii) For the 3 intervening human areas IP0 - IP2 (yellow labels), we hypothesize they emerged as new areas, either ‘de novo’ or by ‘areal duplication’ (akin to gene duplication). For example, area AIP in the common ancestor remained AIP in the macaque, but may have split in the human lineage into a medial area that remained AIP whereas the more lateral one differentiated into IP2, and similarly for LIPd and IP1, and IP0 and its dorsal stream visual neighbors. Finding correspondence could be made even more difficult in case of a cortical reorganization. For instance, the emergence of linguistic abilities during primate evolution may have contributed to migration of the MT Complex that lies within the STS in macaque (Mars et al., 2018a, 2018b), to its more lateral and posterior part of the temporal cortex in humans.

A complementary approach involves interspecies surface-based registration between macaque and human cerebral cortices. Early application of this approach suggested that specific functional domains (e.g., cognitive cortical areas) have disproportionately expanded in the human lineage (Van Essen and Dierker, 2007). This work inspired several novel cross-species registration methodologies including sulcal mapping (Amiez et al., 2019), cortical myelin (Eichert et al., 2020), diffusion tractography (Mars et al., 2018), and functional connectivity (Xu et al., 2020). Multimodal integration would be beneficial to interspecies registration and consistent parcellation across species (Van Essen et al., 2019). These studies suggest that there are important interspecies differences in some regions that are related to social cognitive function in the human brain, including areas for language (Eichert et al., 2019; Mars et al., 2018) and the default mode network (Xu et al., 2020). Thus, future studies achieving registrations using finer and richer information may provide us a clue to understand the correspondence of the social brain areas across species.

5. Conclusions

Recent advances in MR neuroimaging provide valuable tools to an emerging field of comparative connectomics. However, much remains to be done to bridge the gap between primate social behavior, a sound theoretical framework, brain function and structure, and genetic factors. Due to evolutionary proximity, NHP models may provide important means to improve upon our current understanding of neurobiology and causality of social interaction and help address the evolutionary origins of our social behavior.

Credit authorship contribution statement

Chihiro Yokoyama: Formal analysis, Investigation, Writing – original draft, Writing – review & editing. **Joonas A. Autio:** Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. **Takuro Ikeda:** Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **David C. Van Essen:** Methodology, Formal analysis, Writing – original draft, Writing – review & editing, Funding acquisition. **Matthew F. Glasser:** Methodology, Formal analysis, Writing – review & editing, Visualization. **Norihiro Sadato:** Conceptualization, Writing – original draft, Funding acquisition. **Takuya Hayashi:** Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization, Resources, Supervision, Project administration, Funding acquisition.

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Data code availability

Data is partly available at BALSa <https://balsa.wustl.edu/>. Analysis pipeline is available at <https://github.com/Washington-University/NHPPipelines>. Protocols are available at <https://brainminds-beyond.riken.jp>.

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