Common brain networks underlying human social interactions: evidence from large-scale neuroimaging meta-analysis

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Abstract:

Recent overarching frameworks propose that various human social interactions are commonly supported by a set of fundamental neuropsychological processes, including social cognition, motivation, and cognitive control. However, it remains unclear whether brain networks implicated in these functional constructs are consistently engaged in diverse social interactions. Based on ample evidence from human brain imaging studies (342 contrasts, 7,234 participants, 3,328 foci), we quantitatively synthesized brain areas involved in broad domains of social interactions, including social interactions versus non-social contexts, positive/negative aspects of social interactions, social learning, and social norms. We then conducted brain network analysis on the ensuing brain regions and characterized the psychological function profiles of identified brain networks. Our findings revealed that brain regions consistently involved in diverse social interactions mapped onto default mode network, salience network, subcortical network and central executive network, which were respectively implicated in social cognition, motivation and cognitive control. These findings implicate a heuristic integrative framework to understand human social life from the perspective of component process and network integration.

Keywords: social interaction; neuroimaging; meta-analysis; large-scale brain networks

Introduction

As social animals, human beings live in highly interactive environments, continuously engage in social interactions and have strong motivation to establish and maintain satisfying interpersonal relationships (Baumeister and Leary, 1995; Wilson et al., 2014). In accordance, our individual fitness is closely related to our capability to form strong and enduring social relationships. Initiating and maintaining felicitous social interactions require different socio-emotional and cognitive abilities, such as mentalizing, valuation, and emotion regulation. Understanding the neural signatures underlying these functions is one essential goal of social neuroscience since it could significantly advance our knowledge of neural systems that mediate everyday social life.

Social interaction refers to the process in which two or more individuals are in a meaningful contact, as a result of which their behaviors are modified (see also Merrill, 1965). This definition posits three key elements of social interaction: (i) more than one individual, (ii) reciprocal relationship among these individuals, and (iii) influence on the behavior and/or mind of the involved individuals. The past two decades have witnessed a surge of interest in determining the neural systems mediating social interactions combining research traditions rooted in psychology, neuroscience, economics, and evolutionary biology (Adolphs, 2010a; Barrett and Satpute, 2013; Cacioppo et al., 2002; Lee, 2008; Lieberman, 2007; Ochsner and Lieberman, 2001; Walter et al., 2005). Combining human brain imaging techniques with social interaction paradigms, recent studies have enriched our knowledge about the neuropsychological mechanisms underlying a wide range of social interactions (Adolphs, 2001; Fiske and Taylor, 2013; Gallese et al., 2004; Saxe, 2006), such as fairness (Feng et al., 2015; Sanfey et al., 2003),

cooperation (Rilling et al., 2008; Rilling et al., 2002), trust (King-Casas et al., 2005; Krueger et al., 2007), altruism (Feng et al., 2016; Izuma et al., 2010), social comparison (Fliessbach et al., 2007; Luo et al., 2018; Takahashi et al., 2009), competition (Beyer et al., 2015), social exclusion (Eisenberger et al., 2003), social understanding (Morelli et al., 2014), social evaluation (Cooper et al., 2014; Izuma et al., 2008), and social conformity (Izuma and Adolphs, 2013; Klucharev et al., 2009; Wu et al., 2016).

Although most brain imaging studies have endeavored to uncover neurocognitive processes underlying a specific aspect of social interactions (e.g., 'fairness'), there is a significant overlap of neural circuits engaged by a variety of social behaviors (e.g., Ruff and Fehr, 2014). Accordingly, recent overarching frameworks have delineated fundamental neuropsychological functions commonly engaged in human social behavior across varying contexts, proposing that diverse social interactions commonly recruit the engagement of brain systems important in social cognition, motivation and cognitive control (Behrens et al., 2009; Fehr and Camerer, 2007; Ruff and Fehr, 2014; Sanfey and Chang, 2008; Suzuki and O'Doherty, 2020). These frameworks have provided important insights into our understanding of human social interactions in terms of overarching processes that cut across specific tasks. Such an endeavor to uncover common or core processes engaged by different social interactive tasks dovetails with (i) long-lasting debates on the core building blocks of human social cognition (Beer and Ochsner, 2006; Happé et al., 2017; Lieberman, 2007; Schurz et al., 2020b; Seyfarth and Cheney, 2015) and (ii) more recent proposals to understand brain dysfunctions from the perspective of dimensional constructs (Cuthbert, 2014; Insel, 2014).

Together, these recent theoretical proposals highlight the importance of identifying

neurobiological systems linked to overarching dimensions of human social behaviors that cut across specific tasks. Nevertheless, these frameworks are mainly based on narrative reviews of functional activation findings, with few empirical studies quantitatively synthesizing brain regions consistently involved in various social interactions and characterizing their specific roles for social interaction in terms of network integration. Recent meta-analyses have examined neural substrates associated with specific types of social interactions including social rejection (Cacioppo et al., 2013; Rotge et al., 2015), social comparison (Luo et al., 2018), fairness (Feng et al., 2015; Gabay et al., 2014), trust (Bellucci et al., 2017), social conformity (Wu et al., 2016), social norm (Yang et al., 2019; Zinchenko and Arsalidou, 2018), deception (Lisofsky et al., 2014). These topic-specific meta-analyses provide important insights into the regions supporting specific types of social interactions, but to uncover the overarching properties of the brain systems supporting diverse social behaviors we have to go further to take into account a wider range of heterogeneous social interactions. In short, a quantitative and comprehensive synthesis of common large-scale networks involved various aspects of social interactions is greatly desired to help reveal neural organizations of multiple processes contributing to our ability to produce a wide range of social behaviors in different contexts.

A large-scale meta-analysis of brain imaging findings associated with social interactions across contexts is well-suited to address this issue by synthesizing neural substrates commonly involved in multiple forms of human social behaviors. Here, we employed a large-scale meta-analytical approach to unveil common neural circuits across varying social interactions, leveraging abundant evidence from human brain imaging studies of social interactions in the past decades. To reveal the core systems of social

interactions, this large-scale meta-analysis pools together results from studies on a wide range of heterogeneous tasks, contexts and aspects of social interactions. This approach quantitatively examines convergence across studies and provides a comprehensive overview of a research domain, while overcoming the heterogeneity and divergence of individual studies or tasks. Importantly, the current meta-analysis focus on social interactive tasks in which participants are not explicitly instructed to employ specific social cognitive strategies, but rather make their decisions in well-structured interactive games. In other words, the widely-used interactive paradigms represent experimental settings to examine how human social behaviors emerge from interactions of multiple neuropsychological processes, instead of tapping on a specific social cognitive subcomponent (e.g., mentalizing). Accordingly, pooling together previous neuroimaging studies employing various interactive tasks provide a valuable opportunity to uncover common and key neurocognitive functions inherently engaged by social interactions, without a prior assumption of specialized elements involved in social behaviors. This approach is in line with evolutionary perspective of social cognition holding that fundamental processes may have evolved to solve problems animals encounter during social interactions (Seyfarth and Cheney, 2015).

Moreover, we took a systems neuroscience perspective to characterize intrinsic functional connectivity patterns between the brain regions identified in our large-scale meta-analyses. Such a network perspective is particularly relevant to identifying neurobiological systems linked to overarching component processes commonly engaged by diverse social interactions. Indeed, it is becoming increasingly acknowledged that human social behaviors can be better understood in terms of interactions across large-

scale brain networks comprising of distributed brain locations rather than in terms of specific structures (Alcalá-López et al., 2018; Barrett and Satpute, 2013; Bassett and Sporns, 2017; Buckholtz and Meyer-Lindenberg, 2012; Bzdok et al., 2013; Kennedy and Adolphs, 2012; Wang and Olson, 2018). This novel data-driven approach can quantitatively characterize topological properties of the brain network constructed from resting-state functional connectivity (RSFC) of brain regions derived from large-scale meta-analyses. Accordingly, such a system neuroscience approach is well-suited to unravel distributed brain networks underlying fundamental psychological processes guiding various social interactions.

Specifically, we utilized large-scale coordinate-based meta-analyses to quantitatively examine whether there are common brain regions across human social interactions (342 contrasts, 7,234 participants, 3,328 foci), by identifying the convergence of brain areas involved in six commonly reported domains of social interactions: (i) social interactions compared to non-social interactions, (ii) positive social interaction compared to negative social interaction/baseline, (iii) negative social interaction compared to positive social interaction/baseline, (iv) social learning, (v) social norm alignment compared to norm violation/baseline, and (vi) social norm violation compared to norm alignment/baseline. Furthermore, the brain regions derived from a large-scale meta-analysis pooling all contrasts served as functional seeds in a subsequent modular analysis from a graph-theoretic framework to detect network connectivity patterns (i.e., modules) among the identified anatomical regions (see also Xu et al., 2016). Lastly, based on broader neuroimaging literature from the Neurosynth database (Yarkoni et al., 2011), we performed a functional decoding analysis for large-scale networks

consistently involved in social interactions in order to quantitatively infer the psychological functions of given brain networks. These complementary analytical schemes aimed to provide data-driven quantitative inference on psychophysiological functions of identified regions. Together, the current study tackles the challenge of identifying and characterizing common brain networks underlying a wide range of human social interactions by leveraging extensive neuroimaging studies on social interactions, exciting advances in human brain functional connectomic research, and increasing open access to large-scale datasets.

Methods

Literature search and selection

Following Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (http://prisma-statement.org) and best practice recommendations for neuroimaging meta-analysis (Müller et al., 2018), a systematic online database search was performed in Oct of 2018 on PubMed, ISI Web of Science and Google Scholar by entering various combinations of relevant search terms (e.g., [‘social decision making’ OR ‘social learning’ OR ‘social reward’ OR ‘social feedback’ OR ‘peer feedback’ OR ‘social norm’ OR ‘social interaction’ OR ‘social relationship’ OR ‘interpersonal interaction’ OR ‘interpersonal relationship’ OR ‘social influence’ OR ‘social observation’ OR ‘social information’ OR ‘social bonding’ OR ‘cooperation’ OR ‘competition’ OR ‘altruistic choices’ OR ‘altruistic giving’ OR ‘altruistic punishment’ OR ‘donation’ OR ‘costly punishment’ OR ‘third-party punishment’ OR ‘trust’ OR ‘reciprocity’ OR ‘reputation’ OR ‘social approval’ OR ‘social status’ OR ‘social

hierarchy' OR 'social exclusion' OR 'social acceptance' OR 'honest' OR 'social comparison' OR 'upward comparison' OR 'downward comparison' OR 'envy' OR 'gloating' OR 'Schadenfreude' OR 'equality' OR 'fair' OR 'ultimatum game' OR 'UG' OR 'inequality aversion' OR 'social preference' OR 'social conformity' OR 'confirming' OR 'herding' OR 'attitude' OR 'normative decision making'] AND ['fMRI' OR 'magnetic resonance imaging' OR 'neuroimaging' OR 'PET' OR 'positron emission tomography']).

In addition, we explored several other sources, including (1) direct searches on the names of frequently occurring authors, (2) the bibliography and citation indices of the included articles, and (3) the reference list of related reviews (Adolphs, 2003, 2010a; Barrett and Satpute, 2013; Bartra et al., 2013; Behrens et al., 2009; Blackhart et al., 2009; Blakemore, 2008; Cacioppo and Decety, 2011; Falk and Scholz, 2018; Fehr and Camerer, 2007; Gilam and Hendler, 2016; Hari et al., 2015; Hari and Kujala, 2009; Hari et al., 2016; Krach et al., 2010; Lee, 2008; Lieberman, 2007; Rilling and Sanfey, 2011; Ruff and Fehr, 2014; Van Overwalle, 2009; Walter et al., 2005). The search identifies 5,565 potential studies, which were further screened and assessed according to the following criteria (**Fig. 1**): (i) subjects were free from psychiatric or neurological diagnoses and pharmacological influence; (ii) subjects performed tasks in contexts having all three elements of social interaction (i.e., more than one individual, reciprocal relationship, and influence on the behavior and/or mind of the involved individuals). It should be noted that contexts concerning only vicarious valuation of options or outcomes for others were not included (e.g., empathy tasks) because of the absence of reciprocal relationship. In addition, to focus on psychological processes which are spontaneously involved in social

interactions, tasks in which participants were explicitly asked to empathize with or mentalize emotions or minds of others were also excluded (e.g., theory-of-mind tasks); (iii) fMRI or PET was used as the imaging modality; (iv) results from whole-brain general-linear-model-based analyses (rather than region of interest [ROI] analyses) were provided; (v) statistical results for appropriate contrasts of social interactions or relevant parametric analyses were reported; and (vi) activation coordinates were reported in a standardized stereotaxic space (Talairach or MNI). Note that for papers reporting Talairach coordinates, a conversion to the MNI coordinates was employed using the icbm2tal algorithm (Lancaster et al., 2007). Filtering search results according to the inclusion/exclusion criteria yielded a total of 238 published fMRI and PET study articles (247 independent samples) with 342 contrasts (3,328 foci, 7,234 participants, **Table S1**). The most common experimental tasks adopted in the meta-analyses included prisoner's dilemma game, ultimatum game, aggression tasks, trust game, cyberball game, donation tasks, social comparison tasks, dating tasks, and social conformity tasks among others (see **Fig. S1** for the distribution of different topics; see **Table S2** for a complete list of topics).

The raw contrasts identified from each included study are task-dependent, such as 'unfair vs. fair' in the ultimatum game and 'exclusion vs. inclusion' in the cyberball game. Those initial contrasts were then grouped into six high-level domains, with the following criteria: i) those high-level domains are not specific to any single paradigm in particular, and ii) there are enough studies (i.e., $n > 15$ according to a recent simulation study, Eickhoff et al., 2016) in a given domain to ensure good power for statistical analyses. Moreover, to further validate the classification of contrasts, we recruited a

sample of 40 participants to rate scenarios related to each contrast (see Table S2~S6 & Supplementary Text 1 for details), the results of which confirmed our classification. Accordingly, the neural correlates of social interactions were converged in the following meta-analyses assessing six broad domains of social interactions: (i) 64 contrasts between social interactions *vs.* nonsocial control conditions (i.e., playing a game alone or with a computer) were included to identify convergence in brain activity associated with social interactions; (ii) 85 contrasts between positive social interaction *vs.* negative social interaction/baseline were included to identify convergence in brain activity associated with positive social interactions; (iii) 100 contrasts between negative social interaction vs. positive social interaction/baseline were included to identify convergence in brain activity associated with negative social interactions; (iv) 18 parametric analyses tracking social prediction errors were included to identify convergence in brain activity related to social learning; (v) 70 contrasts between norm alignment *vs.* norm violation/baseline were included to identify convergence in brain activity associated with norm alignment; and (vi) 111 contrasts between norm violation *vs.* norm alignment/baseline were included to identify convergence in brain activity associated with norm violation.

Primary activation likelihood estimation (ALE) meta-analyses

Coordinate-based meta-analyses of reported fMRI experiments were conducted by employing the revised ALE algorithm implemented with in-house MATLAB scripts (Eickhoff et al., 2017; Eickhoff et al., 2009). Applying the ALE algorithm, the reported coordinates of brain areas associated with each meta-analysis were separately converged across different contrasts. The ALE determines the convergence of foci reported from

different neuroimaging studies with published foci in Talairach or MNI space (Laird et al., 2005; Turkeltaub et al., 2002). ALE interprets reported foci as three-dimensional Gaussian spatial probability distributions, whose widths are based on empirical estimates of the spatial uncertainty due to the between-subject and between-template variability of the neuroimaging data (Eickhoff et al., 2009). Within each included contrast, a modulated activation (MA) map is firstly created by taking the maximum probability associated with any one focus (always the closest one) for each voxel (Turkeltaub et al., 2012). An advantage of the modified ALE algorithm is that multiple foci from a single contrast will not jointly influence the individual MA value of a single voxel. Furthermore, to prevent studies with multiple contrasts based on the same subject sample influencing ALE values more than others, different contrasts from the same subject sample were combined into a single contrast rather than treated as independent contrasts for each meta-analysis (see also Turkeltaub et al., 2012). The union of these individual MA maps is then calculated to obtain an ALE map across studies. This ALE map is assessed against a null-distribution of random spatial association between studies using a non-linear histogram integration algorithm (Eickhoff et al., 2012). In addition, the average non-linear contribution of each contrast for each cluster was calculated from the fraction of the ALE values at the cluster with and without the contrast in question to control potential excessive contribution of a single contrast (Eickhoff et al., 2016) (see **Supplementary Text 2 & Table S7 - S13** for details).

It should be noted that other potential meta-analytic algorithms for brain imaging findings are available, such as Seed-based D Mapping (SDM) (Albajes-Eizagirre et al., 2019; Radua and Mataix-Cols, 2012). While both ALE and SDM share the same

fundamental idea of identifying above-chance convergence of coordinates for a particular paradigm or comparison, the two approaches are different in the implementation of this aim. While SDM integrates positive and negative effects in a same map to cancel out regions in which both are present (Radua and Mataix-Cols, 2012), the ALE detects the convergence of contrasts independent of directionality. Previous empirical and simulation studies comparing ALE with SDM have yielded similar results (Albrecht et al., 2019; Samartsidis et al., 2017). While a systematic comparison between different meta-analysis algorithms is beyond the scope of current study, we aimed to follow the best-practice recommendations commonly proposed by developers of different methods (Müller et al., 2018; Radua and Mataix-Cols, 2012).

Validation analysis

We implemented additional analyses to validate findings derived from conventional ALE meta-analyses. Specifically, we implemented a leave-one-contrast-out (LOCO) analysis for each of ALE meta-analyses to ensure that main meta-analytic results were not driven by the coordinates from a single contrast and thus validate our primary ALE meta-analysis finding (see **Supplementary Text 3** for details).

All maps were thresholded using a cluster-level family-wise error (cFWE) correction ($P < 0.05$) with a cluster-forming threshold of $P < 0.001$ (Eklund et al., 2016; Woo et al., 2014).

Modular analysis of the functional brain network

A modular analysis of the functional brain network was performed to explore the potential functionally specific relationships between regions consistently involved in various social interactions. First, nodes of the brain systems commonly involved in various social interactions were generated with the following steps. First, we conducted another meta-analysis pooling all the included studies together. Similar to the individual meta-analyses described above, all contrasts (including those contrasts inverse to each other) based on the same sample were combined into a single contrast to alleviate the issue of interdependence. This approach is suited for the purpose of the additional meta-analysis to identify brain regions consistently involved in any aspect of social interactions independent of directionality. Similar to the current study, it is a common approach for coordinate-based meta-analyses to pool together various contrasts (e.g., inverse contrasts) to determine brain regions relevant to a topic, such as to reveal aberrant activation (i.e., both hypo- and hyper-activation) among mental disorders compared to healthy controls (e.g., Li et al., 2020; McTeague et al., 2017; McTeague et al., 2020; Sha et al., 2019), to determine term- or topic-based meta-analytic maps based on Neurosynth database (Yarkoni et al., 2011), and to delineate patterns of co-activation for a pre-defined ROI using the BrainMap database (e.g., Chen et al., 2018b; Goodkind et al., 2015; Wong et al., 2019; Zhang et al., 2017b) or Neurosynth database (e.g., Chang et al., 2013; de la Vega et al., 2016; De La Vega et al., 2018).

Second, the resultant clusters were transferred into a binary mask, the parcellation of which was implemented according to the Brainnetome Atlas consisting of 210 cortical and 36 subcortical regions (Fan et al., 2016). This atlas is connectivity-based, and is therefore well-suited for regional functional connectivity and brain network analyses (Cui

and Gong, 2018; Dresler et al., 2017). iii) the parceled regions with at least 28 voxels (i.e., 0.005% of total number of voxels of the atlas) were included, resulting in 62 ROIs (see **Table S14** for details). The mean time courses of all the voxels within each ROI were extracted to calculate the Pearson correlation coefficient matrix for representing the resting brain functional network (see **Supplementary Text 4** for details), resulting in a symmetric connectivity matrix for each participant. These matrices were Fisher *z*-transformed and averaged to obtain a mean matrix used for the subsequent network analysis.

To exclude the confounding impact of spurious relationships in internal connectivity matrices, the obtained mean matrix connectivity density value was set to range from 0.19 to 0.40 with a step length of 0.01 (Xu et al., 2016). These low-value filtered matrices were performed for the modular analysis using the Graph-Theoretical Network Analysis Toolkit (Wang et al., 2015). The toolkit detects communities by maximizing the modularity Q with the spectral optimization algorithm, which has been introduced as a measure to assess the goodness of a partition (Newman, 2006; Newman and Girvan, 2004). Finally, the number of modules and the membership of each ROI belonging to which module were obtained.

To validate the resultant subnetworks (i.e., modules) derived from our modular analyses, the ensuing modules were overlaid onto seven canonical functional cortical networks and a collection of subcortical areas (Choi et al., 2012; Liu et al., 2018; Yeo et al., 2011). Canonical networks include the fronto-parietal network, dorsal attention network, ventral attention network (i.e., salience network), somatomotor network, visual network, cortical affective network, and default mode network, in addition to a

subcortical network (Yeo et al., 2011). The relative distribution was computed by the proportion of activated voxels of a given network versus all activated voxels; while the absolute distribution was calculated by the proportion of activated voxels of a given network versus voxels of a given canonical network (see also Chen et al., 2018a; Zhang et al., 2017a). Lastly, the relationship between the resultant subnetworks and each domain of social interactions we identified—i.e., social interactions vs. nonsocial control conditions, positive social interaction vs. negative social interaction/baseline, negative social interaction vs. positive social interaction/baseline, social prediction errors, norm alignment vs. norm violation/baseline , and norm violation vs. norm alignment/baseline —was established by computing the relative and absolute distributions, in a similar manner described above except that clusters derived from the six domains of social interactions were used as templates.

Functional decoding for ensuing modules

To better understand the functional correlates of behavioral phenotypes across identified modules (i.e., networks), a functional decoding analysis based on Neurosynth was performed to map the semantic topics representing psychological states to the topography of identified modules. Neurosynth, a framework for large-scale fMRI meta-analysis composed of nearly 11,500 studies, uses a machine learning approach to estimate the likelihood that defined modules are associated with specific psychological terms (Yarkoni et al., 2011). To investigate plausible psychological topics most relevant to each module, we performed decoding analysis based on the version 0.6 of the Neurosynth database (Yarkoni et al., 2011) consisting of 11,406 fMRI studies and over 410,000

activation peaks covering all published neuroimaging literature in the database. Each observation contains the peak activations reported in a study's table and the frequency of all words in the article abstract. Notably, a set of 60 topics selected by De La Vega et al. (2018) were used here, which was derived by the latent Dirichlet allocation topic modeling to remedy the redundancy and potential ambiguity in word terms (Blei et al., 2003).

Next, we performed functional decoding by training a naïve Bayes classifier using all fMRI studies. Following the pipeline of De La Vega et al. (2018), two sets of studies which activated at least 5% of voxels and which did not activate any voxel of the given module were selected respectively as the positive and negative samples for training the model. The area under the receiver operating characteristic curve was used to measure the performance of the model with a 4-fold cross-validation. After training the model by each psychological topic and the presence of activation in the corresponding area, each topic got a conditional probability coefficient for activating the module. Log odds ratio (LOR) represents the log of the ratio between the probability of a given topic activating the module and the probability of that topic not activating the same module. Here, the LOR of each topic was extracted from the trained naïve Bayes classifier and used to generate functional decoding profiles. Values greater than zero indicate that the presence of a given topic in a study positively predicts activity in a module. Only the topics surviving multiple comparisons thresholding using FDR with $P < 0.01$ by a permutation test were reported.

Results

Primary ALE meta-analysis results

The brain regions consistently involved in each domain were identified by the corresponding individual meta-analyses. To indicate the distribution of the ensuring regions in canonical brain networks, the brain regions identified for each domain were overlaid onto seven canonical functional cortical networks and a collection of subcortical areas (Choi et al., 2012; Liu et al., 2018; Yeo et al., 2011). Below we report the identified regions for each domain and their distributions in the canonical networks.

Social interaction vs. non-social interaction. Consistent maxima for social interactions were found in dorsomedial prefrontal cortex (dmPFC)/anterior cingulate cortex (ACC), right temporoparietal junction (TPJ)/posterior superior temporal sulcus (pSTS), left inferior frontal gyrus (IFG), bilateral anterior insula (AI), ventral striatum (VS), left inferior parietal lobule (IPL), posterior cingulate cortex, precuneus, and lingual gyrus (**Table 1 & Fig. 2**). These regions were primarily distributed in the default mode network (relative: 43.85%; absolute: 3.73%), fronto-parietal network (relative: 23.52%; absolute: 3.09%) and ventral attention network (relative: 14.40%; absolute: 2.70%) (see **Fig. S2a** for canonical network distribution of the identified clusters).

Positive social interaction vs. negative social interaction/baseline. For positive social interactions, consistent maxima were found in VS and ventromedial prefrontal cortex (vmPFC) (**Table 2 & Fig. 3**). These regions were primarily distributed in the subcortical network (relative: 70.43%; absolute: 8.57%) and default mode network (relative: 22.75%; absolute: 0.83%) (**Fig. S2b**).

Negative social interaction vs. positive social interaction/baseline. For negative social interactions, consistent maxima were found in bilateral AI, dorsal anterior cingulate cortex (dACC), left middle temporal gyrus, and vmPFC (**Table 3 & Fig. 4**). These regions were primarily distributed in the ventral attention network (relative: 43.34%; absolute: 9.15%), fronto-parietal network (relative: 27.46%; absolute: 4.05%) and default mode network (relative: 25.35%; absolute: 2.42%) (**Fig. S2c**).

Social prediction errors. Consistent maxima were found in VS and right AI (**Table 4 & Fig. 5**). These regions were primarily distributed in the subcortical network (relative: 59.80%; absolute: 3.38%) and ventral attention network (relative: 22.16%; absolute: 0.83%) (**Fig. S2d**).

Norm alignment vs. norm violation/baseline. For norm alignment, consistent maxima were found in VS and right vmPFC (**Table 5 & Fig. 6**). These regions were primarily distributed in the default mode network (relative: 55.76%; absolute: 0.40%) and subcortical network (relative: 42.86%; absolute: 1.03%) (**Fig. S2e**).

Norm violation vs. norm alignment/baseline. For norm violation, consistent maxima were found in bilateral AI, dACC, dmPFC, left IPL, and vACC (**Table 6 & Fig. 7**). These regions were primarily distributed in the ventral attention network (relative: 35.65%; absolute: 7.74%), fronto-parietal network (relative: 30.01%; absolute: 4.56%) and default mode network (relative: 28.26%; absolute: 2.78%) (**Fig. S2f**).

Validation results

The results of the LOCO approach corroborated the main findings of our primary ALE meta-analysis (see **Fig. S3-S9** & **Supplementary Text 3** for details).

Network analysis for identified regions

An additional meta-analysis was conducted by pooling all included studies together, which identified brain regions constantly involved across various human social interactions, independent of directionality (**Fig. 8 & Fig. S10**). Afterwards, we performed a modular analysis (i.e., a community detection algorithm) to detect the connectivity patterns between the identified regions. Four stable network modules were detected, for which the modules' partitioning maintained good consistency across different connectivity strengths. These four modules, based on the location and functions of the involved regions, are labeled as i) salience network module, ii) subcortical network module, iii) default mode network module, and iv) central executive network module. It is noteworthy that these modules were derived from the network analysis, and similarity in the names between these modules and canonical networks reflect the overlap between corresponding modules and canonical networks (see below).

Specifically, the salience network (SN, red) module mainly comprised bilateral AI, and dACC. The subcortical network (SCN, green) module contained bilateral striatum. The default mode network (DMN, yellow) module mainly consisted of vmPFC, dmPFC, and TPJ. The central executive network (CEN, blue) module included left dorsolateral PFC (dlPFC) and IPL (**Fig. 9A, B & Table S14**). For the connectivity density of 0.40, a spring embedder layout model for straight-line representations was applied — grouping together or pulling apart nodes according to their connectivity patterns (Brandes and Wagner, 1997). The spring-like layout of the four network modules was characterized by the Euclidean distance between each pair of nodes (reflecting the graph-theoretic distance)

and the thickness of lines (representing the connection strength of the edges) (**Fig. 9D**). The RSFC for which ROIs were sorted by modules demonstrated that the modules were more strongly connected internally than externally (**Fig. 9C**).

Notably, the subnetworks derived from our modular analyses fit well with the canonical brain networks (**Fig. 10A & Fig. 10B**). Specifically, the SN module was primarily distributed in the canonical ventral attention network (relative: 55.58%; absolute: 12.28%). The SCN module was primarily distributed in the canonical subcortical network (relative: 100.00%; absolute: 10.84%). The DMN module was primarily distributed in the canonical default mode network (relative: 68.40%; absolute: 8.14%). The CEN module was primarily distributed in the canonical dorsal attention network (relative: 51.33%; absolute: 3.15%) and canonical fronto-parietal network (relative: 48.03%; absolute: 2.30%).

Finally, these subnetwork modules were differentially engaged by the six broad domains of social interactions we identified (see **Table S14** for the involvement of each module in each domain). In particular, the SN module was mainly engaged by negative social interaction vs. positive social interaction/baseline, norm violation vs. norm alignment/baseline, and social vs. non-social domains. The SCN module was mainly involved in positive social interaction vs. negative social interaction/baseline, prediction error, and norm alignment vs. norm violation/baseline. The DMN module was mainly recruited by social vs. non-social, norm violation vs. norm alignment/baseline, positive social interaction vs. negative social interaction/baseline, negative social interaction vs. positive social interaction/baseline, and norm alignment vs. norm violation/baseline. The

CEN module was mainly engaged by social vs. nonsocial and norm violation vs. norm alignment/baseline.

Quantitative functional profiling of identified networks

The functional decoding analysis revealed that the SN module was mainly linked to the psychological topics of reward, decision-making, errors, pain, conflict, and inhibition. The SCN module was predominantly associated with the psychological functions of reward, decision-making and pain. The DMN module was predominantly associated with the psychological topics of mentalizing, communication, decision-making, emotion, reward, and memory. The CEN module was involved in topics of arithmetic, conflict, attention, switching, language, and working memory. The LOR between the probability of a given topic activating the network and the probability of the topic not activating each network was displayed in a functional decoding profile for each network ($P < 0.01$, FDR corrected) (**Fig. 10C**).

Discussion

The past two decades have witnessed a surge of interest in uncovering brain mechanisms underlying human social interactions by employing diverse tasks from various disciplines. Although different types of social interactions are usually examined separately from each other, there is a growing consensus that social behaviors as a whole are supported by a set of common neurocognitive processes engaging large-scale distributed brain networks. In light of this hypothesis, the current study aimed to reveal the neural organization associated with a wide range of social interactions combining a large-scale meta-analysis

with brain network analysis. Based on 342 contrasts (3,328 foci, 7,234 participants) from 238 published fMRI and PET articles, the current meta-analysis quantitatively synthesized previous neuroimaging findings to identify key and common brain regions consistently involved in various social interactions. Our findings revealed that brain regions consistently involved in broad domains of social interactions — social interactions vs. non-social contexts, positive social interaction vs. negative social interaction/baseline, negative social interaction vs. positive social interaction/baseline, social learning, social norm alignment vs. norm violation/baseline, social norm violation vs. norm alignment/baseline — were organized into four stable modules corresponding to the DMN, SN, SCN and CEN modules. Our functional decoding findings further indicated that these large-scale brain networks were respectively implicated in social cognition, motivation, and cognitive control.

The current study provides meta-analytic evidence of common brain networks supporting a wide range of social interactions, as well as unravels the functional structure of brain systems implicated in social interactions in terms of network integration rather than regional specialization. The current findings suggest that heterogeneous social interactions share common neural circuits for social, cognitive, and affective processes, thus highlighting an overarching framework for neuropsychological functions mediating human social life. In line with the current study, there is a long-lasting debate on the structure of social cognition, that is, what processes constitute the building blocks of social processing (Beer and Ochsner, 2006; Happé et al., 2017; Schurz et al., 2020b; Seyfarth and Cheney, 2015). Indeed, a growing body of evidence has indicated that social processes might be better understood in terms of high-level dimensional processes (i.e.,

component processes) that are co-recruited across diverse tasks (e.g., Schurz et al., 2020a; Schurz et al., 2020b). In this regard, brain regions and networks revealed in the current study might correspond to the dimensional functional constructs that are commonly and spontaneously engaged by a broad range of social interactions. Accordingly, the current findings shed light on the building blocks of human social interactions by employing a novel data-driven approach. Notably, it is likely that those higher-order functional constructs are embedded in large-scale networks, rather than localized brain regions (Alcalá-López et al., 2018; Barrett and Satpute, 2013; Bassett and Sporns, 2017; Buckholtz and Meyer-Lindenberg, 2012; Bzdok et al., 2013; Kennedy and Adolphs, 2012; Wang and Olson, 2018). As discussed below, brain regions and networks revealed in the current study contribute to widespread functional constructs that are related to different dimensions of human social behaviors.

First, the DMN module we identified mainly consisted of vmPFC, dmPFC, and TPJ, which overlapped with canonical default mode network and was associated with social cognition, such as mentalizing, attribution, and emotion communications as revealed by functional decoding analyses. In accordance, the relationship between DMN and social cognitive processes has been well documented in a large body of literature (Amft et al., 2015; Buckner and DiNicola, 2019; Raichle, 2015; Schilbach et al., 2012; Spreng et al., 2009). For instance, resting-state activity and functional connectivity of DMN predict individual differences in learning new social (but not nonsocial) information (Meyer et al., 2019) and self-reported social skills (Spunt et al., 2015). Likewise, altered functional organization of the DMN represents prominent neurobiological features of mental disorders (e.g., autism) characterized by social cognitive deficits (Padmanabhan et al.,

2017). Moreover, spontaneous fluctuations in DMN activity scales with the speed of mental state (but not physical) attribution on a trial-by-trial basis (Spunt et al., 2015), and functional connectivity profiles of the DMN are modulated according to the socio-affective tasks (Göttlich et al., 2017). Notably, the DMN is comprised of at least two subsystems, such that the vmPFC and PCC contribute mostly to affectively-focused social processes (i.e., empathy), while the dmPFC and TPJ are primarily related to cognitively-focused social processes (i.e., mentalizing) (Bzdok et al., 2013; Li et al., 2014; Lieberman et al., 2019). It is convincible that these social cognitive and affective processes mediated by the DMN play a critical role in various social interactions, in with the involvement of the DMN module in almost every aspect of social interactions (except for encoding social prediction errors) identified in the current study. Accordingly, functional connectivity patterns of the DMN contribute to guiding human social interactions (Fareri et al., 2020), and a growing body of studies has indicated that intrinsic DMN properties predict individual variations in social behaviors, such as trust, reciprocity, deception, and costly punishment (Bellucci et al., 2019; Feng et al., 2018; Hahn et al., 2015; Lu et al., 2019; Tang et al., 2018). Together, our findings indicate that DMN is commonly involved in a wide range of social interactions, which implies that social cognitive processes are a fundamental component of human social interactions.

Second, the SN and SCN modules we identified mainly comprised of AI, dACC and VS in the canonical ventral attention and subcortical networks, which were associated with salience detection and motivation. Social interactions can be a great source of pleasure and distress, representing one of fundamental motivations of human behaviors. We often experience pleasant feelings when encountering positive social interactions,

such as when we are treated fairly, helped, accepted, trusted, or endorsed by others, or when we help, cooperate with, or bond with others. Conversely, negative feelings are often evoked by negative social interactions, such as unfair treatment, rejection, disapproval, or betrayal from others. The SN and SCN respectively encode these rewarding or punishing aspects of social life as control signals to regulate behavioral adjustment in complex social world (i.e., social learning) (Behrens et al., 2008; Klucharev et al., 2009). Notably, the SN and SCN register social reward/punishment independent of financial payouts, such that mutual cooperation, altruistic giving, and costly punishment consistently involve the engagement of VS node in the SCN, even though those normative behaviors often result in a financial loss for oneself (De Quervain et al., 2004; Spitzer et al., 2007). In contrast, norm violation induces negative feelings and triggers error-like signals in the dACC and AI nodes of SN, which drive people to change their behaviors or internal states in line with social norms (Luo et al., 2018; Montague and Lohrenz, 2007; Wu et al., 2016). That is, human social behaviors are not only driven by self-interest but also social norms that are often at odds with maximizing personal payoff.

Accordingly, the SN and SCN are thought to constitute a common neural motivation system regulating human decision-making across various individual and social contexts (Grabenhorst and Rolls, 2011; Gu et al., 2019; Izuma et al., 2008; Levy and Glimcher, 2012; Lin et al., 2012; Rangel et al., 2008; Saxe and Haushofer, 2008). However, it should be noted that our findings indicate that the SN module was mainly engaged by negative social interaction and norm violation while the SCN module was mainly engaged by positive social interaction and norm alignment. These findings are generally

in line with the critical role of SN and SCN in encoding negative experience and rewarding events, respectively (Feng et al., 2015; Gabay et al., 2014; Luo et al., 2018).

Lastly, the CEN module we identified included dlPFC and IPL, corresponding to the fronto-parietal and dorsal attention networks that were related to a variety of high-level cognitive control processes ranging from control of attention and memory to response and emotion. Specifically, the CEN is thought to contribute to task-set maintenance, long-term planning, and response suppression/selection, and information integration (Cole et al., 2014; Cole et al., 2013; Menon, 2011). These cognitive control processes are frequently required to achieve a harmonious social interaction, since people often have to suppress self-interest or immediate pleasure in order to reap long-term or common benefits for both the self and other(s). This conflict engages CEN mediated cognitive control processes that integrate different sources of information and maintain goal-directed behavior (Fehr and Camerer, 2007; Feng et al., 2015). Accordingly, the CEN is involved in various regulatory functions in social contexts, including emotion regulation (Goldin et al., 2008), and inhibiting one's own experience and making strategic choices when taking into account the mental states of other individuals (Bhatt et al., 2010; Samson et al., 2005; Vogeley et al., 2001). Moreover, neurostimulation evidence has indicated that transient regulation of activity in CEN nodes (e.g., dlPFC) causes changes in human social behaviors, such as norm enforcement, trust, and deception (Baumgartner et al., 2011; Knoch et al., 2006; Knoch et al., 2009; Mameli et al., 2010; Maréchal et al., 2017; Ruff et al., 2013; Tang et al., 2017). These findings have led to the hypothesis asserting that the CEN might be associated with integration and selection of various sources of information for optimal decisions during social interactions (see also

Buckholtz and Meyer-Lindenberg, 2012; Miller and Cohen, 2001). In line with this conjecture, the CEN is mostly involved in social (vs. nonsocial) interactions and norm violation, highlighting its roles in incorporating information in the social contexts and mediating conflicts in norm violation situations.

In summary, our findings implicated four common brain networks across human social interactions — including the DMN, SN, SCN and CEN modules— which mediate social cognition, motivation, and cognitive control during various interactive contexts. In light of recent studies (Alcalá-López et al., 2018; Schurz et al., 2020b), these large-scale brain networks might be involved in hierarchical processing associated with social interactions. In particular, the DMN might be implicated in modeling feelings, intentions, and traits of others to simulate, explain, and predict others' behaviors (Frith and Frith, 1999; Krueger et al., 2009). The SN and SCN probably act as a generic motivational system to encode rewarding/punishing properties of social options and outcomes, with reference not only to self-interest but also normative social principles (Luo et al., 2018; Montague and Lohrenz, 2007; Xiang et al., 2013). Finally, the CEN might be involved in integrating information encoded in DMN (mental states) and SN (motivational relevance) to optimize one's social behaviors (Buckholtz and Marois, 2012; Krueger and Hoffman, 2016). This conjecture is consistent with the functional profiles of these brain networks, which indicate that they are respectively involved in social cognitive processes, motivation, and cognitive control. However, it should be noted that the above descriptions of interactions among brain networks are tentative and provide only one possible way of how these networks might interact to support social behaviors, with the aim to offer an intuitive framework to understand human social interactions from the

perspective of network integration. Indeed, it is likely that these large-scale brain networks interact with each other in a flexible way according to different social contexts. Future studies on this topic could assess the correspondence of functional connectivity across social interactions to uncover whether there are common patterns of functional couplings among brain networks across various social interactive tasks.

In addition to the brain networks identified in the current study, other brain regions and/or systems have also been implicated in human social behavior and cognition, such as the amygdala (e.g., Adolphs, 2010b), the cortical affective network (e.g., the orbital frontal cortex, Ruff and Fehr, 2014), the cerebellar regions (Hoche et al., 2016; Van Overwalle et al., 2014), the somatomotor network (Molenberghs et al., 2012; Van Overwalle et al., 2015) and the occipito-temporal regions (Lieberman, 2007; Yang et al., 2015). It remains unclear why the current study did not identify the consistent involvement of these brain systems in human social interactions, which could be attributed to multiple factors including the experimental settings and contrasts used in the social interactive tasks. Indeed, even for the DMN, SN, SCN and CEN modules revealed in the current study, their involvement in different aspects of human social interactions is asymmetric (see also **Table S14**), suggesting that the nature of the contrast reported in a study would impact the networks identified. To achieve a better understanding of these unidentified networks in human social interactions, it might be important to consider evidence from studies employing other paradigms as well as evidence form lesion, brain stimulation and neuropharmacological studies.

Several limitations related to the current study should be noted. First, the current approach did not allow for addressing the issue of social specificity. The functional

profiles indicate that the identified large-scale networks implement domain-general functions, but it should be noted that social specificity could manifest at different levels, such that the same brain network might be engaged by both social and non-social domains but implement different algorithms for these domains (Lockwood et al., 2020). In this regard, the current findings should be considered as the evidence indicating where in the brain social-related processes are implemented, while the specific algorithms implemented by these brain networks require further investigation with the model-based approaches to neuroimaging (Konovalov et al., 2018; Suzuki and O'Doherty, 2020). Second, the common brain networks identified in our study do not imply that differences in neurocognitive processes between tasks are negligible. In fact, both common and distinct functional profiles across social behaviors could be discovered within the hierarchical framework of social processing (Alcalá-López et al., 2018; Schurz et al., 2020b). Both common and specific neural underpinnings are important for a more comprehensive understanding of hierarchical structure of social processing, which could help to explain both correlation and heterogeneity across human social behaviors. Third, there are important aspects of social interactions not included in the current meta-analyses due to the limited number of studies, such as social learning that does not depend on prediction errors but engages other (e.g., Bayesian) learning algorithms. The absence of these domains by no means suggests that they are trivial, and a better understanding of social interactions await further studies from diverse perspectives and techniques. Lastly, to uncover task-overarching brain networks mediating diverse social behaviors, the current meta-analyses were conducted to synthesize heterogeneous findings, such that (i) heterogeneous contrasts were grouped into broad domains to

increase the power of analyses and that (ii) some broad domains address very general aspects of social interactions (e.g., social vs. non-social), whereas others address more specific aspects of social interactions (e.g., prediction errors). The consistent involvement of brain networks identified despite of the heterogeneity between studies and domains implicates the robustness of current findings, although it should be noted that some important brain systems might be missed due to the heterogeneity.

Despite of these limitations, our study identified common brain networks engaged in a broad range of social interactions, which are implicated in fundamental neuropsychological processes underlying human social behaviors, i.e., initial social stimuli processing, social cognition, motivational processes and cognitive control. These findings implicate a heuristic integrative framework to understand human social life from the perspective of component process and network integration and shed lights on the building blocks of social processing.

Figures and Tables

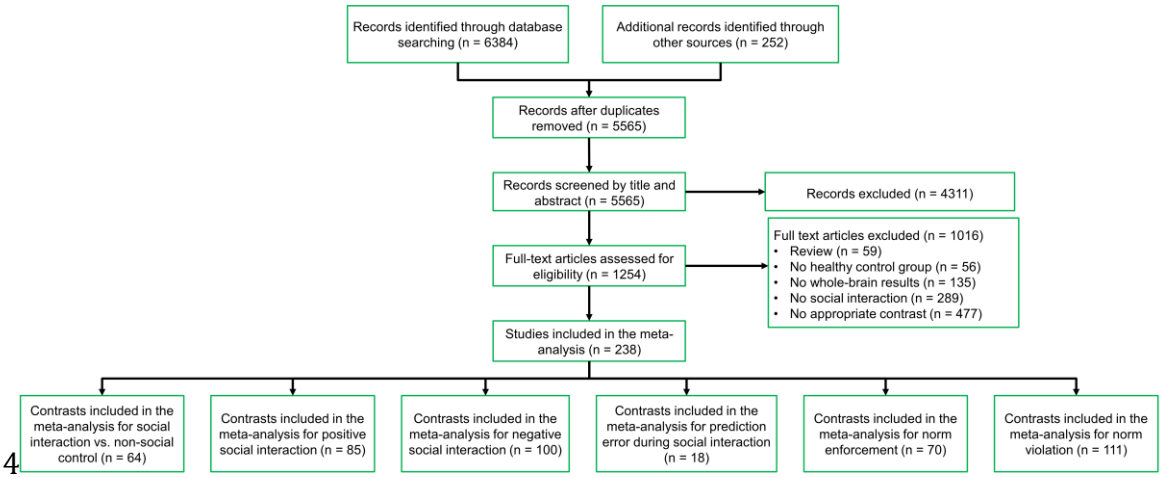

Figure 1. Flowchart of literature search and selection process.

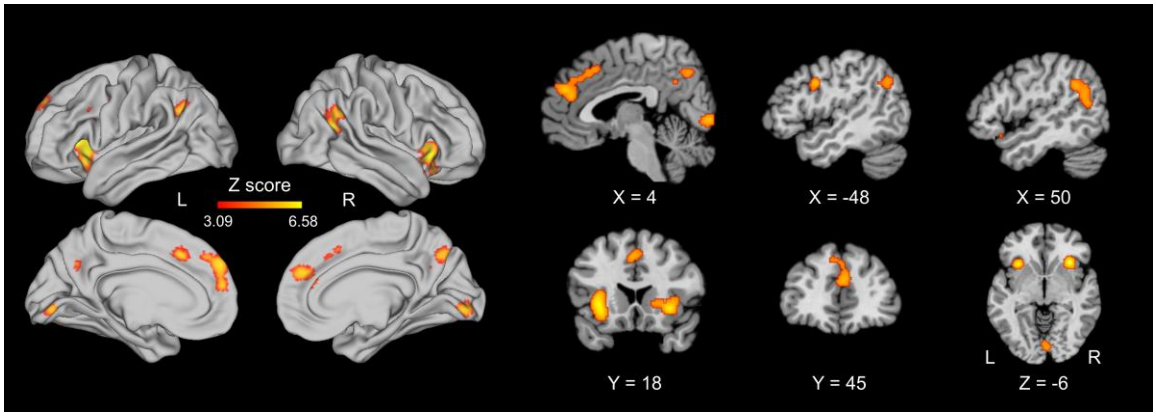

Figure 2. Significant clusters from the primary coordinate-based ALE (activation likelihood estimation) meta-analysis (cluster-level family-wise error correction ($P < 0.05$) with a cluster-forming threshold of $P < 0.001$ using 10,000 permutations) for social interactions vs. nonsocial control conditions. Consistent maxima were found in dorsomedial prefrontal cortex/anterior cingulate cortex, right temporoparietal junction/posterior superior temporal sulcus, left inferior frontal gyrus, left inferior parietal lobule, anterior insula, ventral striatum, posterior cingulate cortex, precuneus, and lingual gyrus. L, left; R, right.

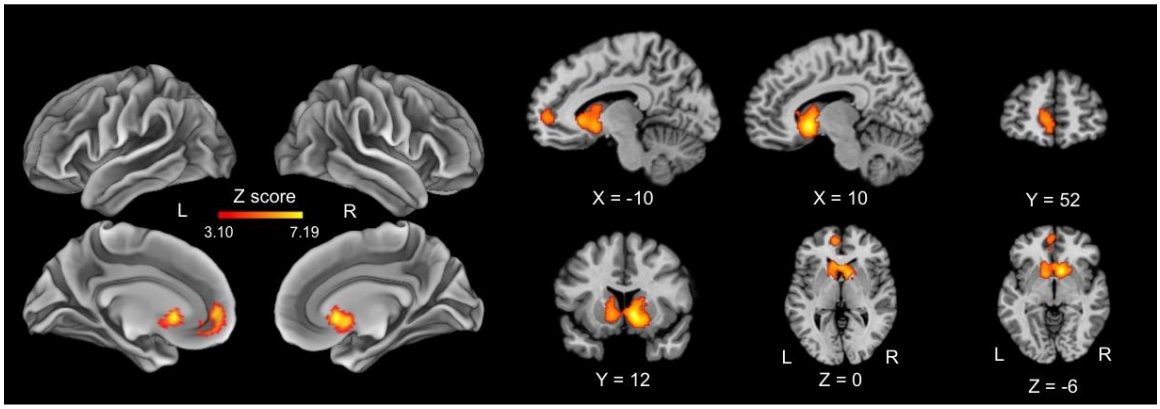

Figure 3. Significant clusters from the primary coordinate-based ALE (activation likelihood estimation) meta-analysis (cluster-level family-wise error correction ($P < 0.05$) with a cluster-forming threshold of $P < 0.001$ using 10,000 permutations) for positive social interaction vs. negative social interaction/baseline. Consistent maxima were found in ventral striatum and ventromedial prefrontal cortex. L, left; R, right.

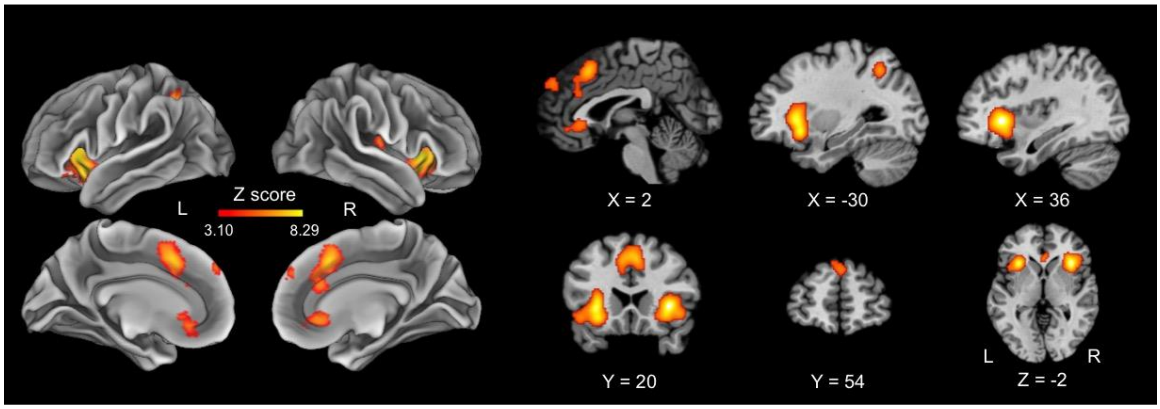

Figure 4. Significant clusters from the primary coordinate-based ALE (activation likelihood estimation) meta-analysis (cluster-level family-wise error correction ($P < 0.05$) with a cluster-forming threshold of $P < 0.001$ using 10,000 permutations) for negative social interaction vs. positive social interaction/baseline. Consistent maxima were found in bilateral anterior insula, dorsal anterior cingulate cortex, left middle temporal gyrus, and dorsomedial prefrontal cortex. L, left; R, right.

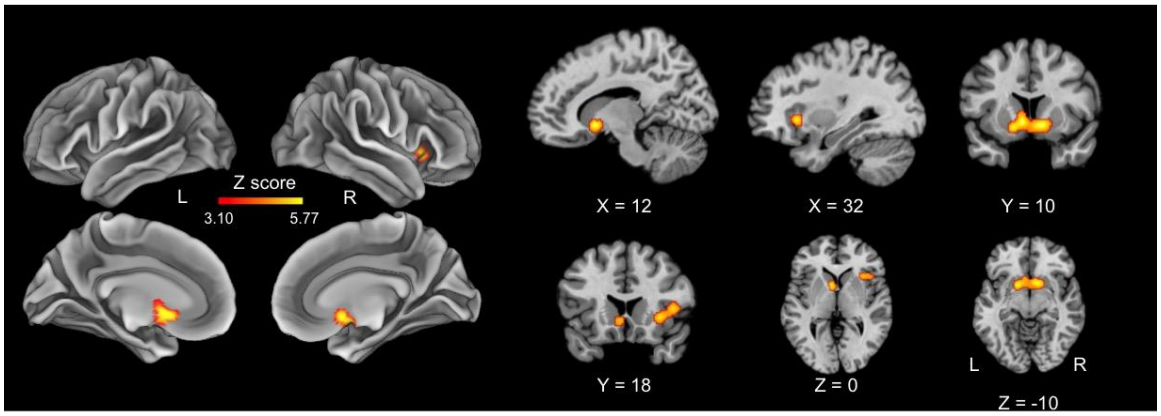

Figure 5. Significant clusters from the primary coordinate-based ALE (activation likelihood estimation) meta-analysis (cluster-level family-wise error correction ($P < 0.05$) with a cluster-forming threshold of $P < 0.001$ using 10,000 permutations) for prediction error during social interactions. Consistent maxima were found in ventral striatum and right anterior insula. L, left; R, right.

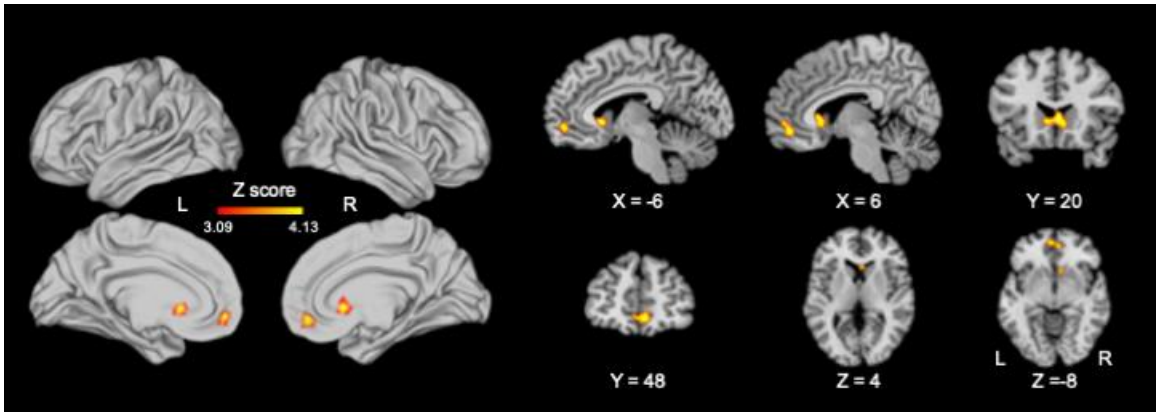

Figure 6. Significant clusters from the primary coordinate-based ALE (activation likelihood estimation) meta-analysis (cluster-level family-wise error correction ($P < 0.05$) with a cluster-forming threshold of $P < 0.001$ using 10,000 permutations) for norm alignment vs. norm violation/baseline during social interactions. Consistent maxima were found in ventral striatum and ventromedial prefrontal cortex. L, left; R, right.

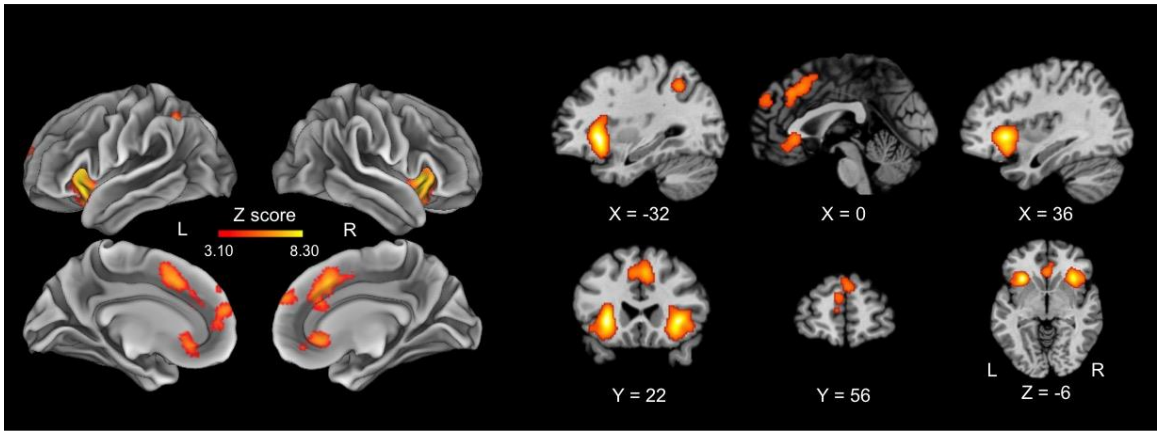

Figure 7. Significant clusters from the primary coordinate-based ALE (activation likelihood estimation) meta-analysis (cluster-level family-wise error correction ($P < 0.05$) with a cluster-forming threshold of $P < 0.001$ using 10,000 permutations) for norm violation vs. norm alignment/baseline during social interactions. Consistent maxima were found in bilateral anterior insula, ventral anterior cingulate cortex, dorsal anterior cingulate cortex, dorsomedial prefrontal cortex, and left L inferior parietal lobule. L, left; R, right.

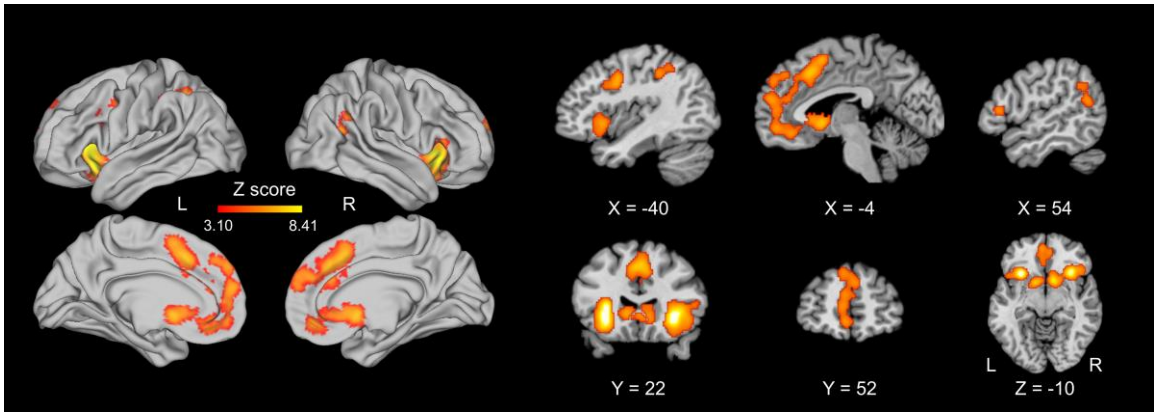

Figure 8. Significant clusters from the primary coordinate-based ALE (activation likelihood estimation) meta-analysis (cluster-level family-wise error correction ($P < 0.05$) with a cluster-forming threshold of $P < 0.001$ using 10,000 permutations) pooling all included studies. Consistent maxima were found in bilateral anterior insula, ventral striatum, dorsal anterior cingulate cortex, left inferior frontal gyrus and left inferior parietal lobule, and right temporoparietal junction/posterior superior temporal sulcus. L, left; R, right.

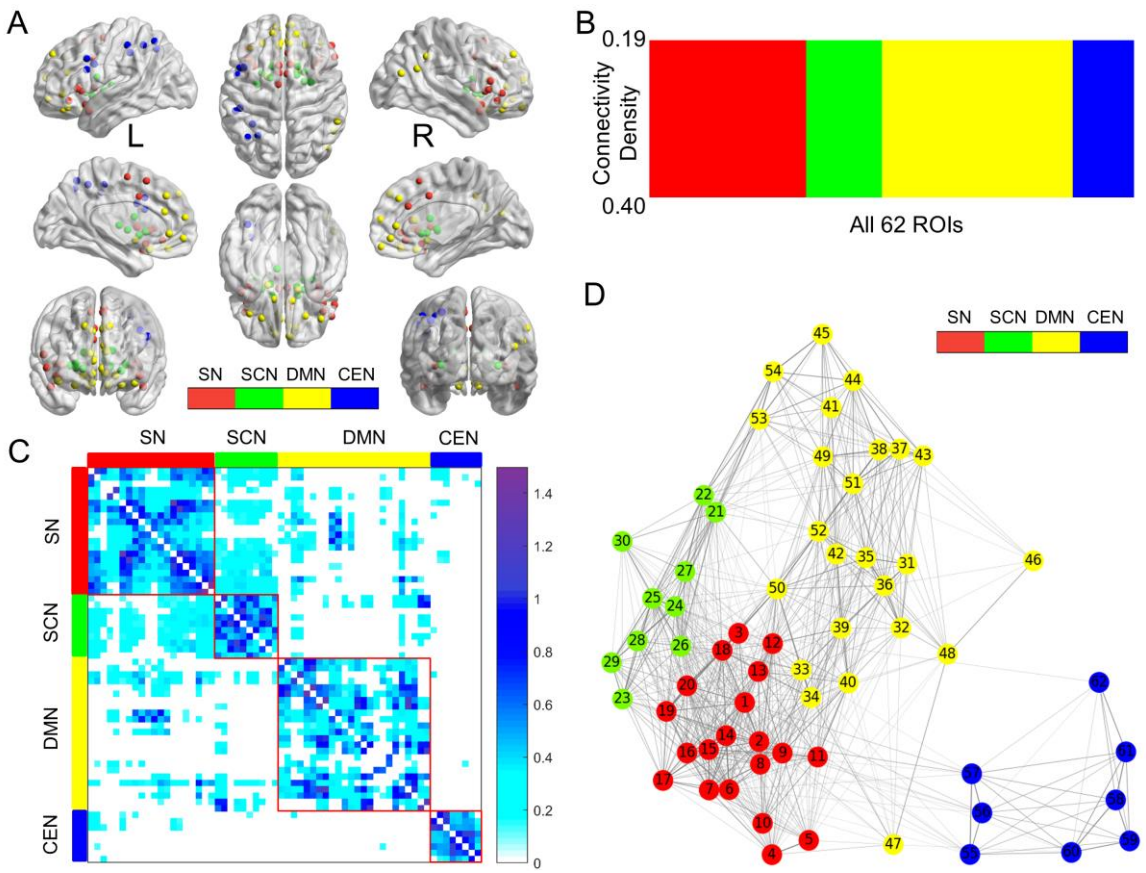

Figure 9. Four network modules detected for social interactions. A) Brain regions in the salience network (SN, red), subcortical network (SCN, green), default mode network (DMN, yellow), and central executive network (CEN, blue). B) The modular analysis determined three stable modules from ROIs shown in the same color under connectivity density levels ranging from 0.19 to 0.40 by increments of 0.01. C) Functional connectivity matrix for a connectivity density of 0.40 (ROIs are sorted by modules) showing a stronger strength of edges within than those between modules. D) Layout of the four network modules. The correspondence between the number (ROI label) and brain location can be found in Table S14.

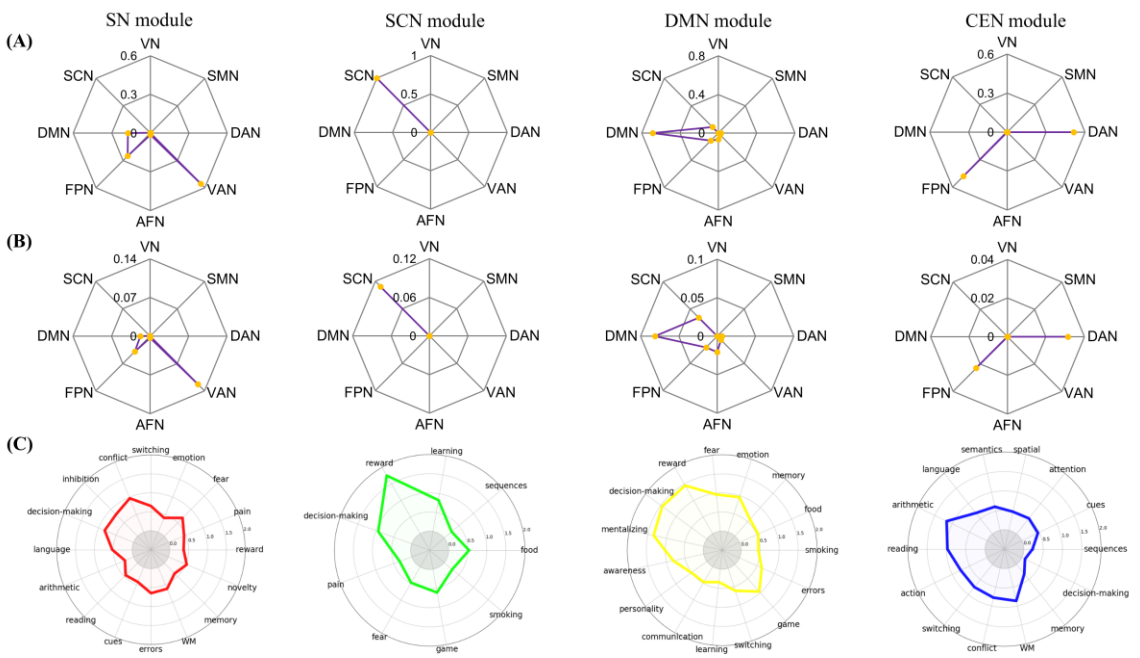

Figure 10. Network distributions and quantitative functional profiling of identified modules. A) Relative distribution of salience network (SN) module, subcortical network (SCN) module, default mode network (DMN) module, and executive-control network (CEN) module in canonical brain networks including visual network (VN), SCN, DMN, fronto-parietal network (FPN), cortical affective network (AFN), VAN, dorsal attention network (DAN), and somatomotor network (SMN). B) Absolute distribution of SN, SCN, DMN, and CEN modules in canonical brain networks. C) Functional profiling of SN, SCN, DMN, and CEN modules. WM, working memory.

Table 1. ALE meta-analysis results for social interaction vs. nonsocial control conditions

Brain Regions	BA	MNI Coordinates (mm)			peak Z score	Cluster Size (voxels)
		x	y	z		
R AI/VS	47	32	22	-6	6.59	500
L AI	13; 47	-34	18	-2	6.29	453
L Inferior Frontal Gyrus	9	-44	4	32	6.19	187
R TPJ/pSTS	39	54	-60	14	5.39	334
dmPFC/ACC	9; 32	-2	22	42	5.22	768
Lingual Gyrus	18	2	-86	-2	4.93	163
PCC	7; 31	0	-54	34	4.57	99
L Inferior Parietal Lobule	40	-52	-62	34	4.29	156
R Precuneus	7	8	-66	40	4.41	108

BA, Brodmann area; L, left; R, right; AI, anterior insula; TPJ, temporoparietal junction; pSTS, posterior superior temporal sulcus; dmPFC, dorsomedial prefrontal cortex; ACC, anterior cingulate cortex; PCC, posterior cingulate cortex. Cluster-level family-wise error correction ($P < 0.05$) with a cluster-forming threshold of $P < 0.001$ using 10,000 permutations.

Table 2. ALE meta-analysis results for positive social interaction vs. negative social interaction/baseline

Brain Regions	BA	MNI Coordinates (mm)			peak Z score	Cluster Size (voxels)
		x	y	z		
VS	-	10	12	-8	6.88	1204
vmPFC	10	-8	52	0	4.87	279

BA, Brodmann area; L, left; R, right; VS, ventral striatum; vmPFC, ventromedial prefrontal cortex. Cluster-level family-wise error correction ($P < 0.05$) with a cluster-forming threshold of $P < 0.001$ using 10,000 permutations.

Table 3. ALE meta-analysis results for negative social interaction vs. positive social interaction/baseline

Brain Regions	BA	MNI Coordinates (mm)			peak Z score	Cluster Size (voxels)
		x	y	z		
L AI	47; 13	-30	18	-12	7.87	967
R AI	47; 13	36	22	-2	7.34	1087
dACC	32	6	22	42	6.48	938
L Middle Temporal Gyrus	21	-56	-30	-8	4.83	97
vmPFC	32; 24	2	28	-4	4.62	216

BA, Brodmann area; L, left; R, right; VS, AI, anterior insula; dACC, dorsal anterior cingulate cortex. Cluster-level family-wise error correction ($P < 0.05$) with a cluster-forming threshold of $P < 0.001$ using 10,000 permutations.

Table 4. ALE meta-analysis results for prediction error during social interactions

Brain Regions	BA	MNI Coordinates (mm)			peak Z score	Cluster Size (voxels)
		x	y	z		
VS	-	-6	8	-4	5.66	518
R AI	47; 13	32	20	-4	5.27	205

BA, Brodmann area; R, right; VS, ventral striatum; AI, anterior insula.
Cluster-level family-wise error correction ($P < 0.05$) with a cluster-forming threshold of $P < 0.001$ using 10,000 permutations.

Table 5. ALE meta-analysis results for norm alignment vs. norm violation/baseline

Brain Regions	BA	MNI Coordinates (mm)			peak Z score	Cluster Size (voxels)
		x	y	z		
VS		-6	18	-2	4.1261	163
vmPFC	10; 11	6	48	-10	3.9886	128

BA, Brodmann area; L, left; R, right; VS, ventral striatum; vmPFC, ventromedial prefrontal cortex. Cluster-level family-wise error correction ($P < 0.05$) with a cluster-forming threshold of $P < 0.001$ using 10,000 permutations.

Table 6. ALE meta-analysis results for norm violation vs. norm alignment/baseline

Brain Regions	BA	MNI Coordinates (mm)			peak Z score	Cluster Size (voxels)
		x	y	z		
L AI	47; 13	-32	20	-8	8.28	926
R AI	47; 13	34	22	-4	7.63	1031
dACC	32	6	24	40	6.08	975
L Inferior Parietal Lobule	7	-30	-54	44	5.10	106
vACC	32	0	28	-6	5.04	219
dmPFC	10	-6	58	20	4.64	147

BA, Brodmann area; L, left; R, right; AI, anterior insula; dACC, dorsal anterior cingulate cortex; vACC, ventral anterior cingulate cortex; dmPFC, dorsomedial prefrontal cortex. Cluster-level family-wise error correction ($P < 0.05$) with a cluster-forming threshold of $P < 0.001$ using 10,000 permutations.

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fig1

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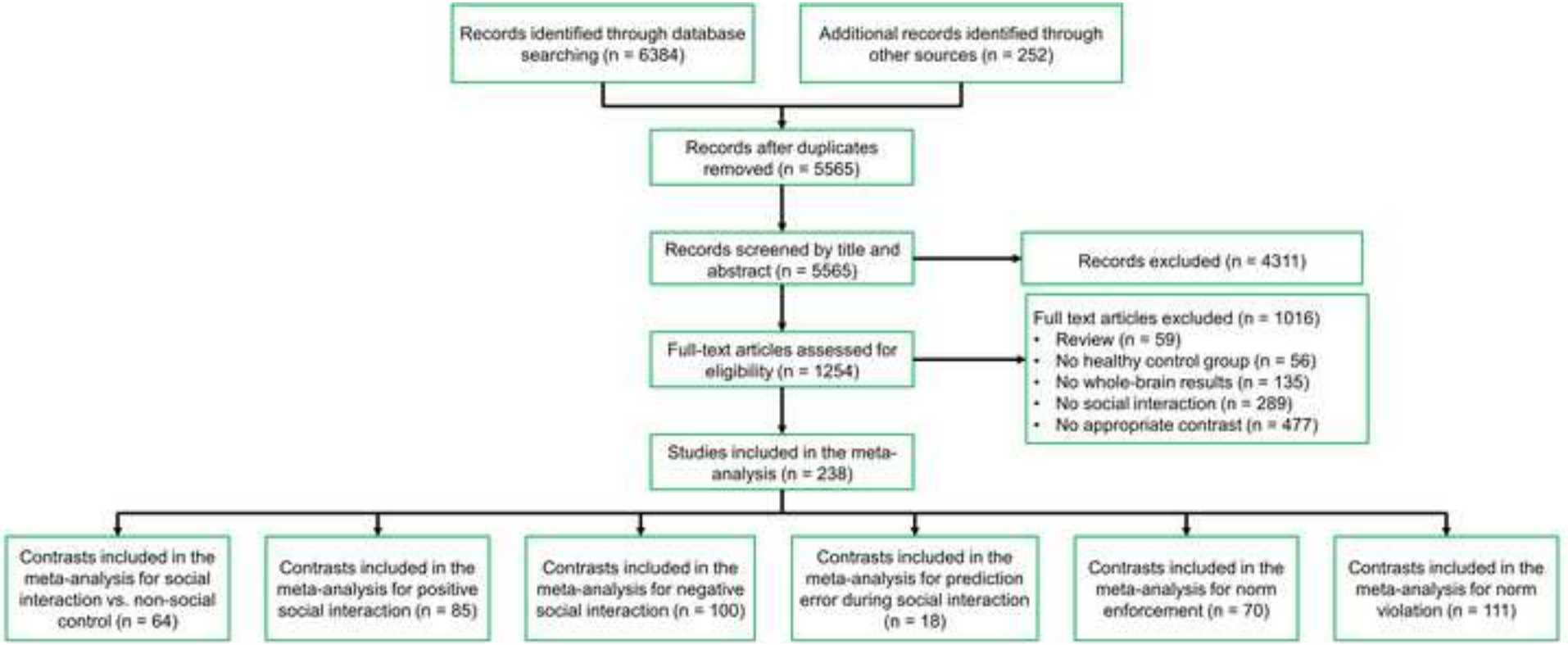

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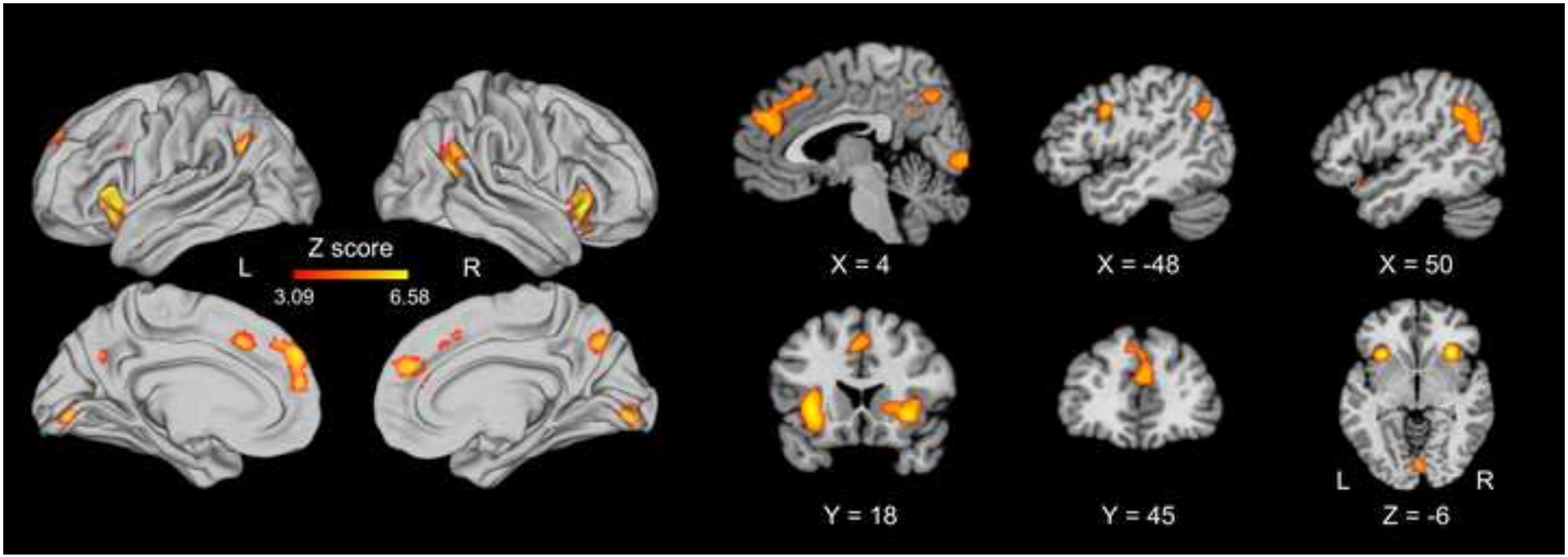

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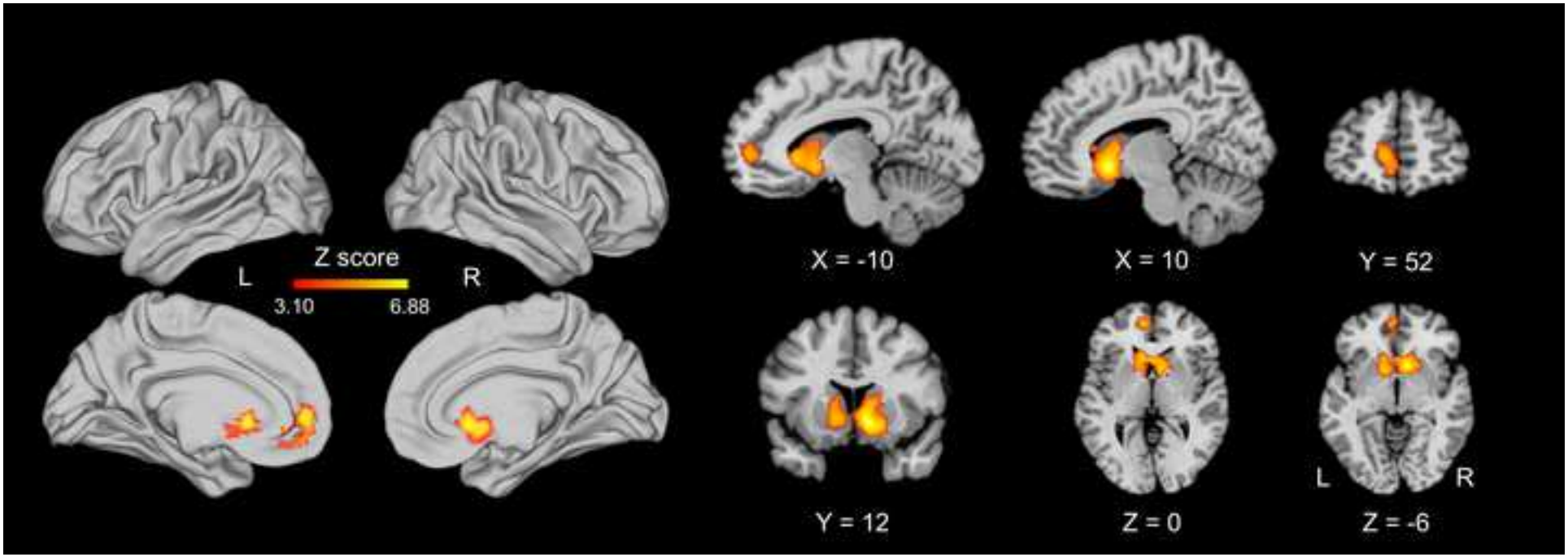

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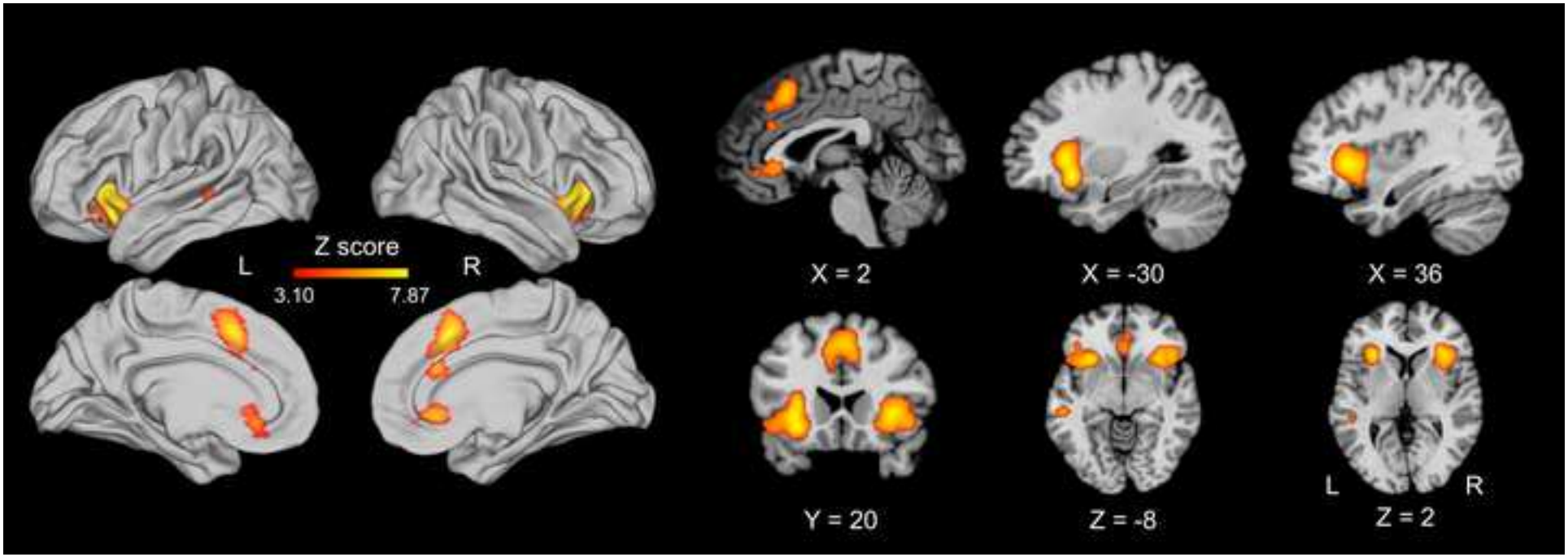

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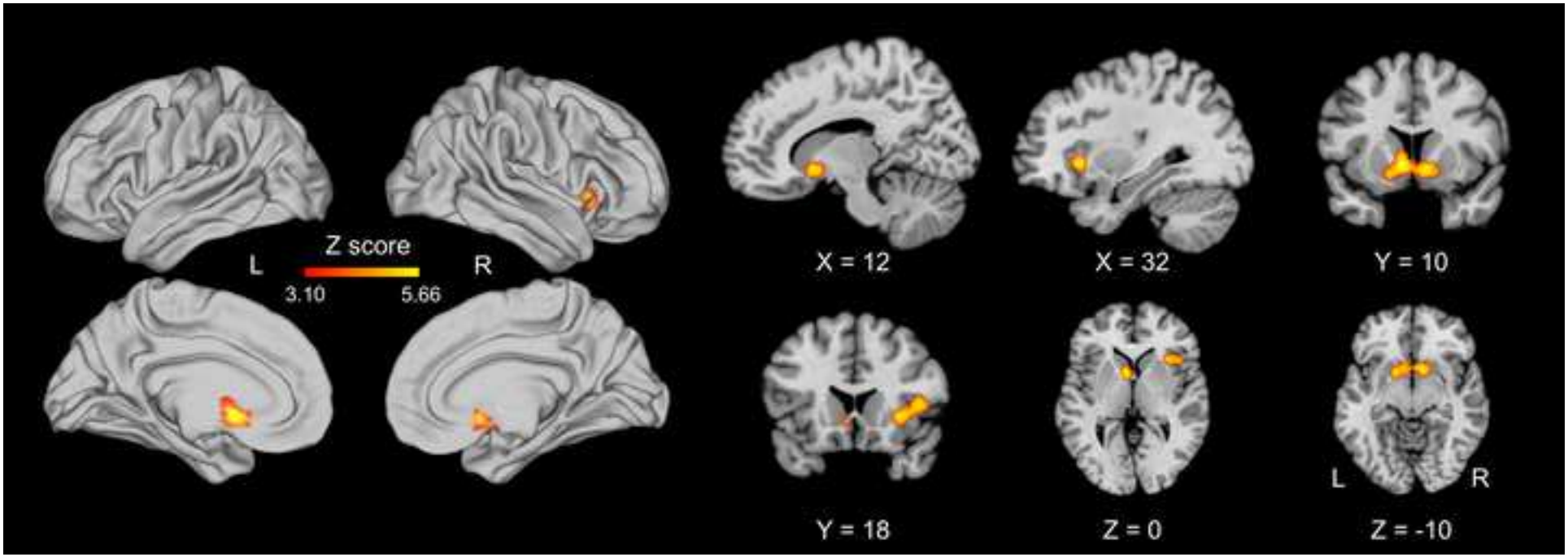

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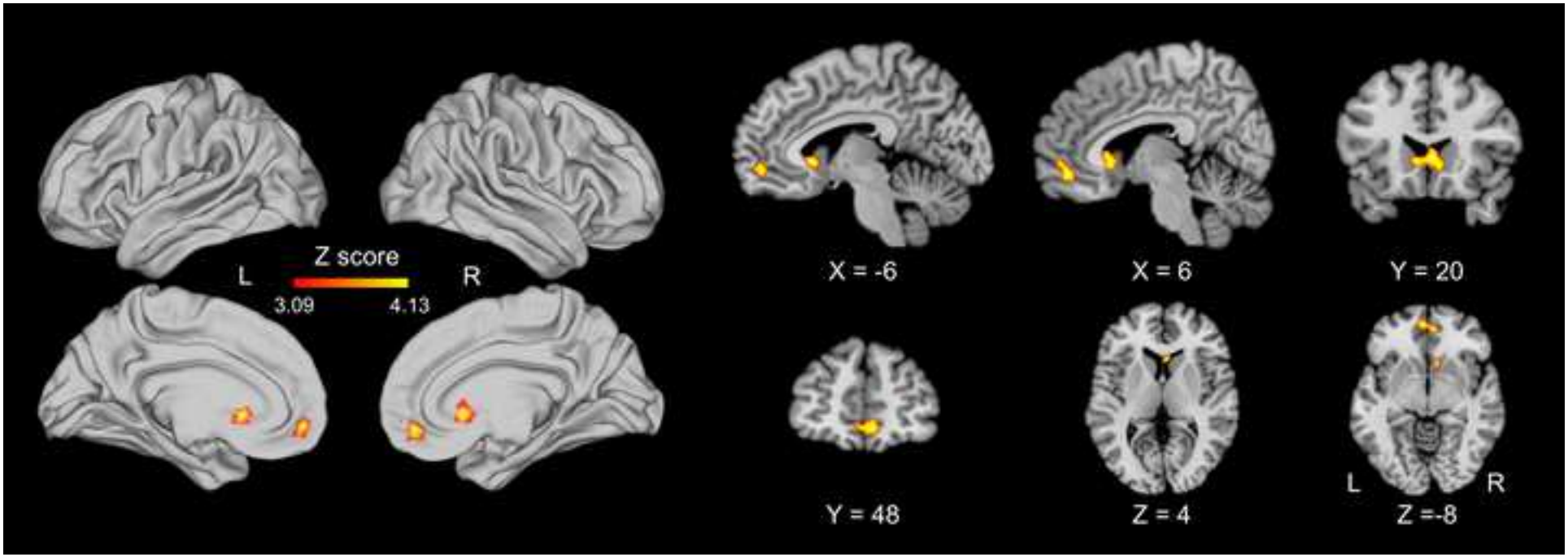

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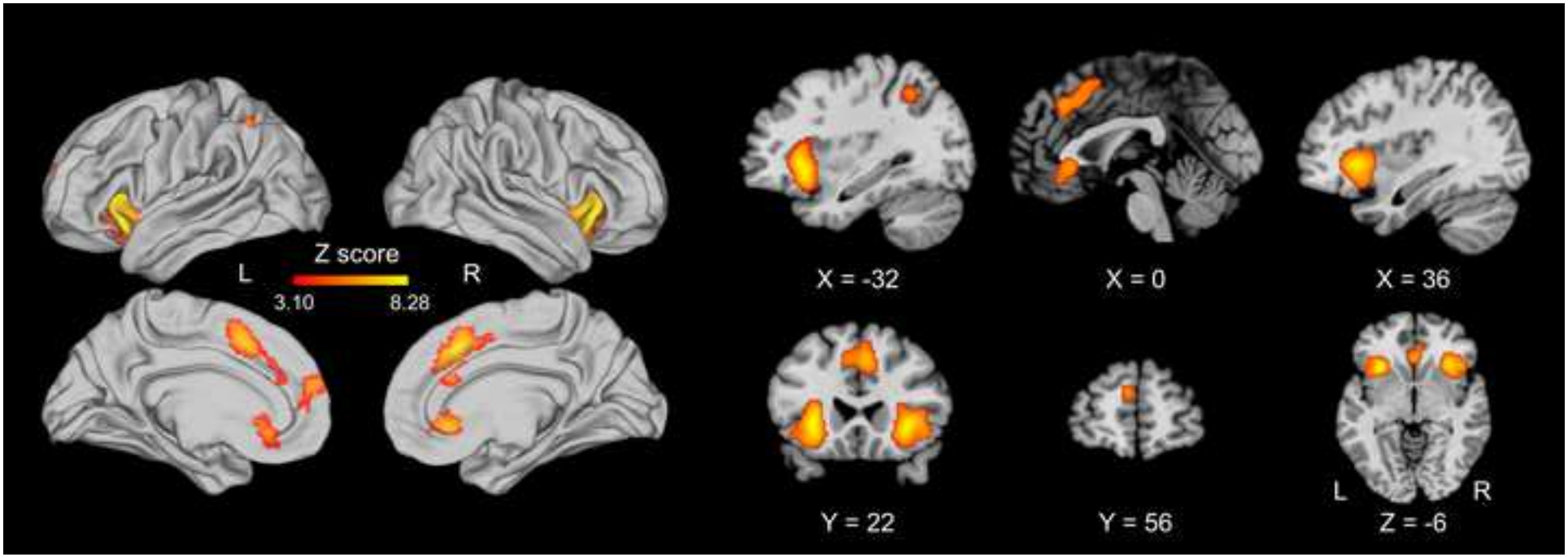

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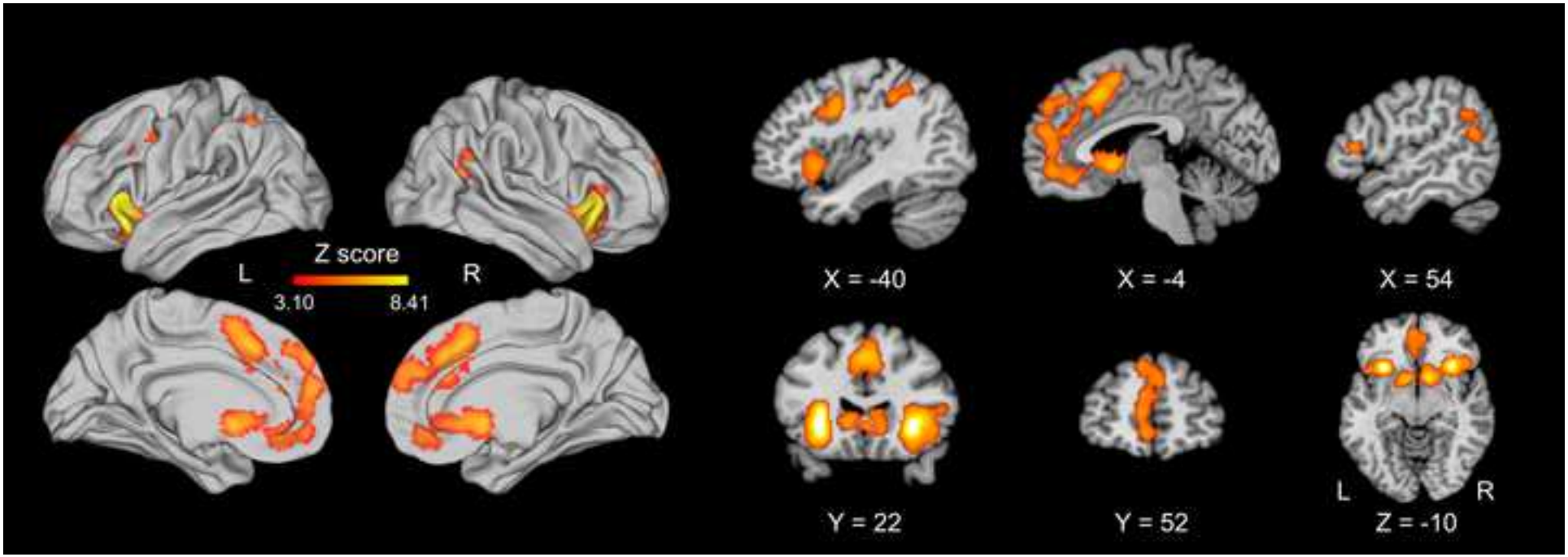

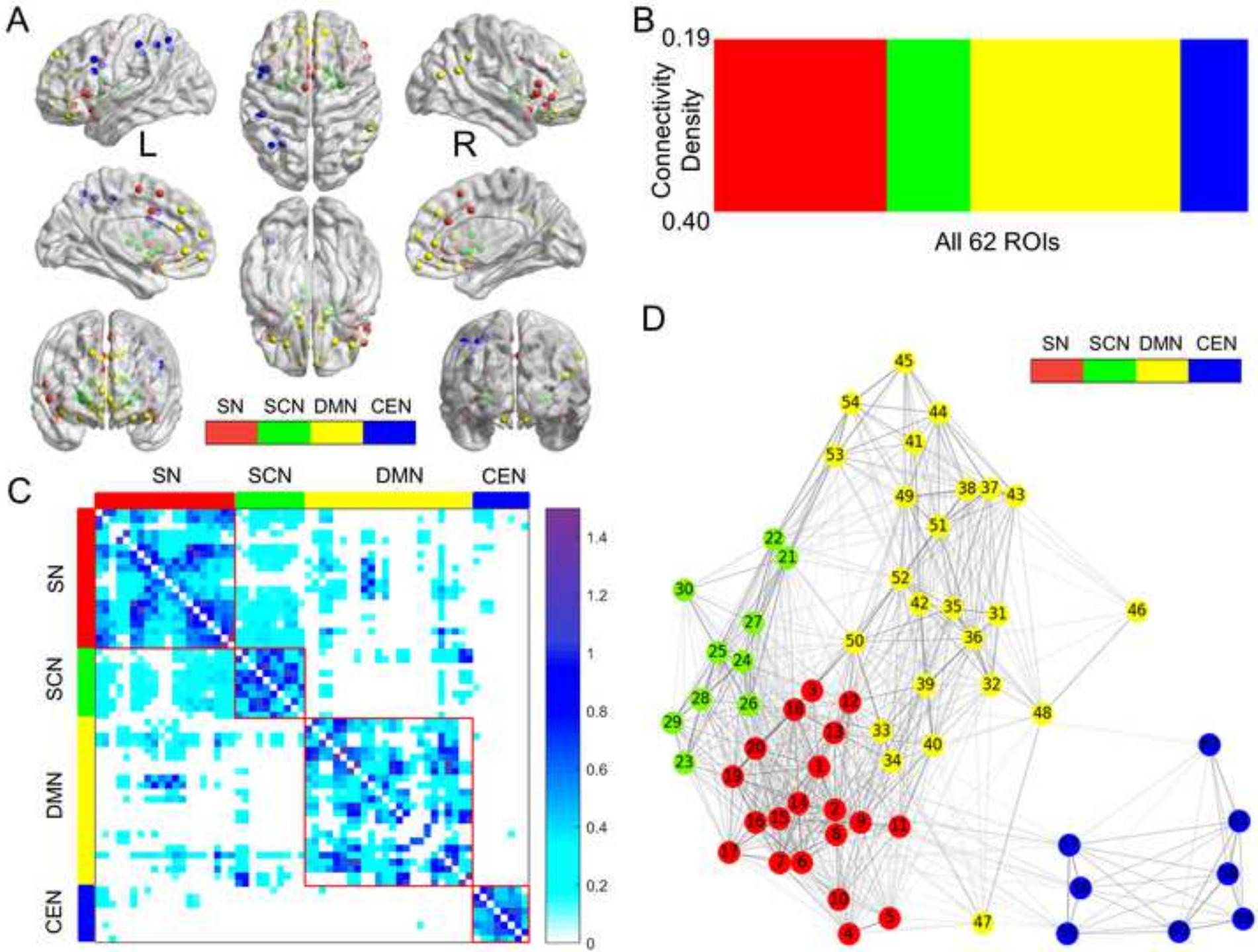

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