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The neural signatures of social hierarchy-related learning and interaction: A coordinate- and connectivity-based meta-analysis

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ABSTRACT

Numerous neuroimaging studies have investigated the neural mechanisms of two mutually independent yet closely related cognitive processes aiding humans to navigate complex societies: social hierarchy-related learning (SH-RL) and social hierarchy-related interaction (SH-RI). To integrate these heterogeneous results into a more fine-grained and reliable characterization of the neural basis of social hierarchy, we combined coordinate-based meta-analyses with connectivity and functional decoding analyses to understand the underlying neuropsychological mechanism of SH-RL and SH-RI. We identified the anterior insula and temporoparietal junction (dominance detection), medial prefrontal cortex (information updating and computation), and intraparietal sulcus region, amygdala, and hippocampus (social hierarchy representation) as consistent activated brain regions for SH-RL, but the striatum, amygdala, and hippocampus associated with reward processing for SH-RI. Our results provide an overview of the neural architecture of the neuropsychological processes underlying how we understand, and interact within, social hierarchy.

1. Introduction

Social hierarchies — referring to a coherent and accepted rank of a group of individuals along one or more social dimensions — are ubiquitous in the biological world (Qu et al., 2017). This rank always has a close link with ones' grasp of resources (Berger et al., 1980). Thus, social hierarchy implied valuable information for individual well-being, socializing, and development (Boyce, 2004; Cheng et al., 2013; Sapolsky, 2005). Given its complexity as well as its importance and pervasiveness to human society, the human need to understand social hierarchies around them and use the knowledge to guide their social life. This also gains an advantage for social hierarchical structure and makes it fluent social stimuli that are processed more easily in cognitive processing of seeing, understanding, learning, and remembering, compared with other types of social structures, such as more flat structures (Zitek and Tiedens, 2012). Meanwhile, as a common social organization, social hierarchy provides a strong force to natural selection. Individuals who display a superior ability in understanding social hierarchy and modifying behavior consequently can often be found to gain an edge in terms of survival and development (Gilbert, 2000; Boyce, 2004; Sapolsky, 2005; Cheng et al., 2013; Watanabe and Yamamoto, 2015). Two mutually independent yet closely related cognitive processes play crucial roles in aiding humans to navigate complex societies: (i) the process of social hierarchy learning and (ii) the process of social hierarchy guiding behaviors and social interaction (Chiao et al., 2008; Watanabe and Yamamoto, 2015; Olsson et al., 2020). Numerous studies have used neuroscientific techniques to investigate the neural mechanisms involved in these two forms of social hierarchy-related processes. The goal of the current meta-analysis study was to reveal their neural mechanisms by answering the following two questions: How is social hierarchical knowledge acquired by individuals? How is the social hierarchy used to modulate behaviors and interactions? The following section will elaborate on these two fundamental social hierarchy-related processes — *social hierarchy-related learning* (*SH-RL*) and *social hierarchy-related interaction* (*SH-RI*).

1.1. SH-RL phase

The ability to obtain social hierarchical knowledge enables social species to overcome the pressures of navigating a fast-changing and

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complex society (Insel and Fernald, 2004). One of its primary contributions is in aiding decisions that engage fundamental modes of social interaction such as fight or flight decisions in animals and whether to compete or cooperate in humans. Social hierarchy learning paves the way for subsequent behaviors and social interactions.

Both animals and humans can obtain social hierarchical knowledge to guide their behaviors through dominance cues, dyadic competition, and observational learning (Fernald, 2014; Qu et al., 2017). Detecting social rank by interpreting dominance cues could be regarded as a rapid locating process, which is more automatic, such as forming an initial impression of others' social rank through physical characteristics or appearance. Multiple sources of information such as body size, facial features, emotional expressions, postures, and occupational status contribute to social hierarchy detecting at a glance (Chiao et al., 2008, 2009; Mattan et al., 2017). For instance, owners of luxury sports cars must be rich men, and realizing this fact is not costly. Developmental studies have shown that even infants can derive dominance information from some dominance cues (Cummins, 2000; Boyce, 2004; Brey and Shutts, 2015; Charafeddine et al., 2015). Moreover, an event-related potentials (ERP) brain study has indicated that people can perceive dominance cues from aggression-related emotional expressions in the early temporal stages of information processing and detect social dominance cues from facial expressions later on (Chiao et al., 2008). Another study probed the neural electrophysiological responses of participants to faces accompanied by information of occupational social status and found that faces with high-status occupation elicited a larger late positive potential (LPP) (Breton et al., 2019). Through rapid evaluation, individuals appear to be able to detect the social position of others and rapidly adjust subsequent behaviors.

Since dominant cues are insufficient in understanding complicated hierarchical relationships within intricate human social networks (Todorov et al., 2008; Kumaran et al., 2012), humans also employ a more refined updating process which dynamically constructs social hierarchical structure in their mind through learning the feedback of the binary comparison in a goal-directed manner. Direct (e.g., competition) and indirect (e.g., observational learning) comparisons are two ways in which a precise and explicit social hierarchical map can be formed. Direct competition leads to the emergence of social hierarchy (Fernald, 2014; Qu et al., 2017), with potentially high risk and high loss, which is the only way to inverse or change the inherent hierarchical structure (Paz-y-Miño et al., 2004; Fernald, 2014;). The indirect comparison refers to inferring target information through observation. Many species including nonhuman primates, rats, and birds have abilities to make transitive inferences, and it has also been reported that fish learn hierarchical relationships by observing conflicts around them (McGonigle and Chalmers, 1977; Roberts and Phelps, 1994; Bond et al., 2003; Grosenick et al., 2007).

The brain circuits involved in the process of rapidly locating social hierarchy information and the more refined process of updating social hierarchy information have been well documented in previous research (Qu et al., 2017). The *first process* is rapid and involves the detection of social hierarchy cues and mapping dominance cues to social hierarchical structures. Detection is a major neural function supported by the salience network which may also serve to detect dominance cues for this rapid locating process (Bressler and Menon, 2010; Menon, 2015). One study using a facial judgment task found that, relative to simple perceptual judgments of facial features, judgments of social dominance activated hub regions associated with the salience network and the anterior insula (AI) in particular (Smith et al., 2016).

The *second process* includes dynamic updating which is driven by feedback-based trial-by-trial learning. Those hidden features of updating and computing let researchers link this process to neural computational modeling. Researchers have applied both reinforcement learning (RL) and Bayesian computational models to uncover the neural mechanism for the updating process of social dominance learning (Kumaran et al., 2016; Ligneul et al., 2016). RL models emphasize the process of creating relationships between stimuli and outcomes, which can be applied for social hierarchy learning (Suzuki et al., 2012; Seo and Lee, 2017; Qu et al., 2017). In contrast, Bayesian approaches emphasize decision making via probabilistic representations of the world (Knill and Pouget, 2004; Khalvati et al., 2016; Annis and Palmeri, 2017; Baker et al., 2017), and social hierarchy can be considered as a hidden variable that can be learned through the likelihood of observation (Qu et al., 2017; FeldmanHall and Shenhav, 2019). As a powerful tool to reveal the process of encoding, the neurocomputational approach provided more essential knowledge on this issue. In terms of observational learning, the medial prefrontal cortex (mPFC) is engaged in the learning of rank, computing estimates of the rank of others, and updating knowledge about one's own place in the hierarchy (Kumaran et al., 2016). With regards to dyadic competition, the rostromedial PFC (rmPFC) is thought to represent social rank, while the ventromedial PFC (vmPFC) and striatum encode successes and failures, respectively (Ligneul et al., 2016) — emphasizing the foundational role of the mPFC in dynamic updating.

To establish the social hierarchical structure in one's own social knowledge frame, the hippocampus and intraparietal sulcus region (IPS) are credited respectively for cognitive processes abut structure and magnitude — functions closely linked with mental constructing and representing of social hierarchy (Cohen et al., 2007; Tavares et al., 2015).

Overall, based on previous research, the learning phase of social hierarchy presumably depends on three functions and its corresponding supporting brain regions: (i) detecting (AI); updating (mPFC), and representing (hippocampus and IPS) of social hierarchy information.

1.2. SH-RI phase

In daily life, social hierarchical information serves to guide adaptive behaviors and thus promotes a more harmonious social existence. Behaviors and interactions in society modulated by social hierarchy have been observed in humans (i.e., adults but also children) as well as nonhuman primates. These behaviors and interactions have been found to touch on a wide range of cognitive functions, including attention, socio-emotional functioning, and decision-making (Dugatkin and Alan, 1997; Gianaros et al., 2008; Boksem et al., 2012; Breton et al., 2014; Santamaria-Garcia et al., 2014; Feng et al., 2015; Feng et al., 2016; Hu et al., 2014; Hu et al., 2016).

For example, a study on empathy found that empathic responses to the pain of others are modulated by social hierarchy — showing activities in AI and medial cingulate cortex as a function of social status (Feng et al., 2016). Further, in the ultimatum game, people with high social status are more likely to reject unfair offers — mirrored by activities in the amygdala and thalamus — than those from a lower status (Hu et al., 2016). Moreover, after learning the hierarchical structure of employees from two companies, people were asked to judge which company these persons belong to. Although this simple task did not explicitly require any knowledge about rank, however, activities in the amygdala and anterior hippocampus generated rank-related signals automatically (Kumaran et al., 2016).

Some researchers suggested that the dominance of higher status may be associated with the processing of reward (Zink et al., 2008; Freeman et al., 2009; Ly et al., 2011; Santamaría-García et al., 2015). For example, an association between neural responses to social hierarchy and brain morphology was reported in the caudate nucleus — a region implicated in reward processing — combining ERP with structural MRI (Santamaría-García et al., 2015). Superior rank faces compared with inferior rank faces induced a larger N170 component, implying a higher sensitivity in the striatum to superior social rank. The same pattern of asymmetric value assignment according to social rank can be observed in nonhuman primates. For example, monkeys sacrifice juice rewards to view the faces of high-status monkeys despite being thirsty but require juice payment to view the faces of low-status monkeys (Deaner et al., 2005).

Overall, based on previous evidence, the impacts of social hierarchy on interactions and behaviors are probably mediated by (i) reward processes (e.g., striatum) and additional processes regulating the reward circuit (e.g., amygdala, hippocampus).

1.3. The present study

A plethora of studies in the field of social hierarchy learning and interacting provide the opportunity for deeper exploration. One issue that might arise from various tasks or paradigms that have been employed to investigate social hierarchy is the possibility that unrelated activation mingled in the target neural mechanism in a single study. While in the meantime, the neural patterns produced by these key processes that occur consistently across studies must be characterized in some quantitative way. Another issue that remains open is the underlying psychological functions of brain regions or networks engaged in social hierarchy-related processing. Thus, we implemented a meta-analysis approach that was designed to quantitatively synthesize previous neuroimaging findings regarding the two social hierarchy-related processes: SH-RL and SH-RI. By integrating neuroimaging studies that have investigated these processes, we can gain a more reliable and precise picture of the neural basis of how humans understand and respond to social hierarchy.

In this study, we implemented separate neuroimaging meta-analyses to explore the two neural mechanisms supporting SH-RL and SH-RI. First, we identified the consistent activated brain region associated with two social hierarchy-related processes by conducting coordinate-based meta-analyses using an activation likelihood estimation (ALE) approach (Eickhoff et al., 2009). Second, we investigated the connectivity among brain regions by performing task-based meta-analytic connectivity mapping (MACM) and task-free resting-state functional connectivity (RSFC). Finally, based on a large-scale database, we employed functional decoding (FD) on mental processes associated with identified regions to understand their psychological functions (Bellucci et al., 2020).

2. Methods

2.1. Meta-analysis

2.1.1. Literature search and selection

First, we performed a literature search of online databases including PubMed, ISI Web of Science, and Google Scholar. The following relevant topic items were entered into these databases: social hierarchy, social rank, social status, social standing, social-economic status, and dominance. These were combined with the following terms describing measurement technique terms: fMRI, functional MRI, and PET. In addition, we also searched bibliographies and citation indices in pre-selected papers.

Studies generated from these searches were further assessed according to the following criteria (Fig. 1): (i) research content correlated with social hierarchy; (ii) fMRI or PET was used as the imaging modality; (iii) subjects were free from psychiatric and neurological diagnoses; (iv) whole-brain general-linear-model-based analyses (rather than a region of interest [ROI] analyses) were applied; (v) activation was presented in a standardized stereotaxic space (Talairach or Montreal Neurological Institute, MNI). Using GingerALE software with Brett's mni2tal algorithm, a conversion to the MNI coordinates was employed for studies that reported in Talairach coordinates (Lancaster et al., 2007).

Articles that fulfilled the above criteria were assigned — either to SH-RL or SH-RI — based on the category of cognitive processing induced by experimental tasks. Since some studies included more than one task and explored both modes of processing, experiments of these studies were assigned separately according to the mode of processing (SH-RL vs. SH-RI). We labeled in this study any process of judging or estimating the position of others within a social hierarchy through various forms of information as the process related to SH-RL. SH-RL describes the transition of social hierarchy knowledge from unknown to known or from vagueness to clarity. During this phase, participants often need to produce a judgment, estimation, or choice regarding the social rank of others in the experimental context. As the second process of interest, SH-RI examined or described any process that involved interacting within a social hierarchy environment. SH-RI implies that an individual's activities or behaviors are, in some way, modified by the social hierarchy. For instance, social hierarchy information is the known condition within the experimental setting or has been learned by participants, and the influence of social hierarchy is the primary focus in this process.

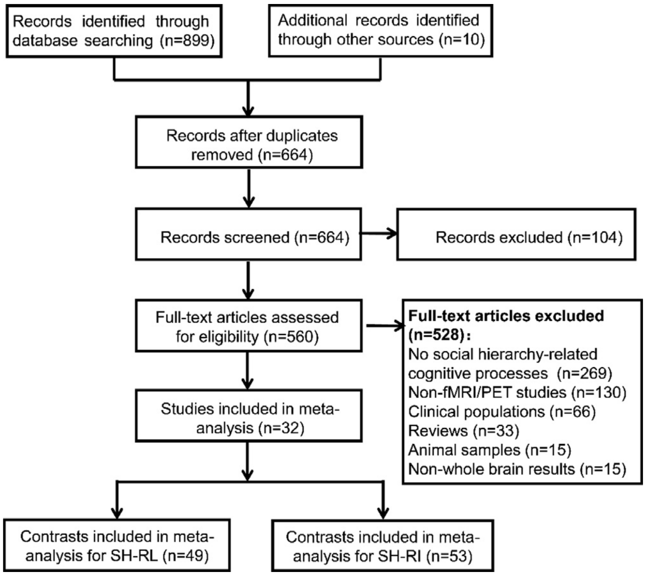

Fig. 1. Flowchart of literature search and selection for meta-analysis. SH-RL, social hierarchy-related learning; SH-RI, social hierarchy-related interaction.

By applying a filter on search results according to the inclusion/exclusion and category criteria, we were left with a total of 32 published studies. Thirteen of these studies examined the process of SH-RL and 22 examined the process of SH-RI (Table 1).

2.1.2. Activation likelihood estimation (ALE) analysis

We conducted a coordinate-based meta-analysis by using the ALE algorithm (GingerALE software, version 3.0.2) (Eickhoff et al., 2009). This algorithm identified areas that showed convergence of foci across different functional or structural experiments to obtain brain regions with a spatial association that was higher than random (Turkeltaub et al., 2002; Laird et al., 2005). This method treats reported foci not as single points, but rather as spatial three-dimensional Gaussian probability distributions. Widths of foci were based on empirical estimates of the spatial uncertainty based on the between-subject and between-template variability of the neuroimaging data (Eickhoff et al., 2009).

Individual modulated activation (MA) map was created firstly by taking the maximum probability associated with any one focus (the closest one) for each voxel within each included experiment (Turkeltaub et al., 2012). This modified ALE algorithm was able to reduce the influence of multiple foci from a single on individual MA value of a single voxel (Turkeltaub et al., 2012). Next, a union of individual MA maps was generated across selected studies by computing it against a null-distribution of random spatial associations between studies using a non-linear histogram integration algorithm (Eickhoff et al., 2012; Turkeltaub et al., 2012). The resulting p value maps were thresholded using the cluster-level family-wise error (cFWE) correction at $p < 0.05$ with a cluster defining threshold of $p < 0.001$ and 10,000 permutations (Eickhoff et al., 2012).

A total of 49 experiments (i.e. contrasts) examined the process of SH-RL (261 foci, 1044 subjects, average of 21.3 subjects per experiment)

Table 1
Summary of studies included for the coordinate-based meta-analysis.

Study	*N*	Task	Contrast
Social hierarchy-related learning			
Ligneul et al. (2016)	28	competitive task	parametric analysis, correlation with positive competitive prediction errors
			parametric analysis, correlation with negative competitive prediction errors
			parametric analysis, correlation with social dominance status
			intermediate opponent win (control failure) > intermediate lose (control success)
Kumaran et al. (2016)	28	transitive inference task	parametric analysis, correlation with the difference in power (test trials)
			parametric analysis, correlation with hierarchy update index (training trials)
			parametric analysis, correlation with hierarchy update index in the self condition (training trials)
			parametric analysis, negative correlation with entropy over item pairs (training trials): main effect self and other
			parametric analysis, positive correlation with entropy over item pairs (training trials): main effect self and other
			parametric analysis, chosen power (training trials): main effect of self and other conditions
			parametric analysis, chosen power in the self condition (training trials)
			parametric analysis, chosen power in the other condition (training trials)
			parametric analysis, chosen power (training trials): self > other condition
Kumaran et al. (2012)	25	transitive inference task	parametric analysis, correlation with the inference score index in the social condition
			parametric analysis, correlation with the inference score index in the social > non-social condition
			parametric analysis, correlation with correct probability in the social condition
			parametric analysis, correlation with correct probability in the social > non-social condition
Kishida et al. (2012)	27	Ranked group IQ task	rank_beginning > rank_end
			parametric analysis, negative correlation with the rank change
			parametric analysis, positive correlation with the rank change
Cloutier and Gyurovski (2014)	13	self-referential social status judgment task	status type by status level interaction
			status type main effect
			status level main effect
Farrow et al. (2011)	22	facial viewing task	social hierarchy > fame, age, gender and ‘number. higher / lower’
Chiao et al. (2008)	7	facial viewing task	dominant > neutral faces
			submissive > neutral faces
Marsh et al. (2009)	30	status poses viewing task	hierarchy cue
			hierarchy cue × stimulus gender
			hierarchy cue × stimulus gender × subject gender
			hierarchy cue × subject gender
Smith et al. (2016)	23	social judgment task	social judgment > perceptual judgment
Freeman et al. (2009)	34	display viewing task	dominant > subordinate
			social hierarchy (dominant, subordination) × culture (Japanese, American)
Chiao et al. (2009)	12	comparison task	uniform comparison
			face comparison
			car comparison
			uniform distance
			face distance
			car distance
			number (close-far) > face (close-far)
			uniform (close-far) > number (close-far)
			face (close-far) > number (close-far)
			face (close-far) > car (close-far)
			car (close-far) > number (close-far)
			car (close-far) > uniform (close-far)
			car (close-far) > face (close-far)
Mason et al. (2014)	19	status judgment task	status judgments > weight judgments
Haaker et al. (2016)	23	observation of confrontations	parametric analysis, correlation with dominance rank
			parametric analysis, correlation with increasing hierarchy knowledge
Social hierarchy-related interaction			
Feng et al. (2016)	22	sensory stimulation viewing	superior > inferior
			inferior > superior
			(inferior_pain–inferior_no pain) > (superior_pain–superior_no pain)
			(inferior_Pain–Inferior_no pain) < (superior_pain–superior_no pain)
Op de Macks et al. (2017)	58	jackpot task	social rank feedback > monetary gain feedback

(*continued on next page*)

Table 1 (*continued*)

Study	*N*	Task	Contrast
			social rank feedback > monetary loss feedback
			social rank play > monetary play
Kim et al. (2016)	28	infant cry paradigm	socioeconomic status effect
Kim et al. (2015)	40	infant cry paradigm	socioeconomic status × gender in (baby cry–white noise)
Zheng et al. (2017)	72	allocate money task	low rank (unfair–fair)– high rank (unfair–fair)
			unfair low rank (reject–accept)–unfair high rank (reject–accept)
			unfair high rank (reject–accept)–unfair Low rank (reject–accept)
Muscatell et al. (2018)	23	face observation task	correlation with subjective social status in black faces observe > white faces observe
			correlation with subjective social status in black faces observe > baseline
			correlation with subjective social status in white faces observe > baseline
Kumaran et al. (2016)	28	categorization task	correlation with person rank
Zink et al. (2008)	24	reaction time task	superior player > inferior player
Zink et al. (2008)	24	visual discrimination task	superior player > inferior player
			subject lost and inferior won > subject lost and inferior lost
			subject won and superior lost > subject won and superior won
Ligneul et al. (2017)	28	passive presentation task	superior faces > inferior faces
Kumaran et al. (2012)	25	bid task	parametric analysis, correlation with person rank
Hu et al. (2016)	23	ultimatum game	(low status unfair > low status fair) > (high status unfair > high status fair)
			high status unfair > low status unfair
Erk et al. (2002)	12	attractiveness rating task	sports cars> small cars
			sports cars> limousines
			limousines > sports cars
			limousines> small cars
Cloutier et al. (2014)	20	impression formation task	status type × status level
			status type main effect
			status level main effect
Sheridan et al. (2012)	18	stimulus response learning task	high socioeconomic status (novel rule> familiar rule) > low socioeconomic status (novel rule> familiar rule) (all trial)
			low socioeconomic status (novel rule> familiar rule) > high socioeconomic status (novel rule> familiar rule) (all trial)
			high socioeconomic status (novel rule> familiar rule) > low socioeconomic status (novel rule> familiar rule) (early trial)
			low socioeconomic status (novel rule> familiar rule) > high socioeconomic status (novel rule> familiar rule) (early trial)
Mattan et al. (2018)	60	face viewing task	perceived status main effect (negative correlation with external motivation, with internal motivation covariate)
			perceived status main effect (negative correlation with external motivation, without internal motivation covariate)
			perceived status main effect (negative correlation with internal motivation, with external motivation covariate)
			perceived status main effect (negative correlation with internal motivation, with external motivation covariate)
			race × status
Kim et al. (2013)	49	emotion regulatory task	positive correlation with the family income-to-needs ratio in the reappraise–maintain
Noble et al. (2006)	38	letter string one-back task	socioeconomic status × phonological awareness
Muscatell et al. (2016)	31	social stress task	negative correlation with subjective social status
			positive correlation with subjective social status
Cloutier et al. (2012)	19	impression formation task	high>low morale status
			low>high financial status
			low>high financial status
Quirin et al. (2013)	17	movie watching task	power motive viewing
Haaker et al. (2016)	23	confrontation task	fear acquisition with dominant face > no fear acquisition with intermediate face (categorial)
			fear acquisition with subordinate face > no fear acquisition with intermediate face (categorial)
			fear acquisition dominant face > no fear acquisition with intermediate face (change over time)
			fear extinction dominant face > fear extinction subordinate face
			fear acquisition with dominant face > fear acquisition with subordinate face (reinstatement)

N, number of participants.

and a total of 53 experiments examined the process of SH-RI (282 foci, 1656 subjects, average of 31.2 per experiment).

2.1.3. Conjunction and contrast analyses

To explore convergences and differences between the meta-analytic findings of SH-RL and SH-RI, we conducted conjunction and contrast analyses. The conjunction analysis was performed by applying the minimum conjunction of ALE results of SH-RL and SH-RI with a cFWE < 0.05 and a voxelwise, cluster-forming threshold of $p < 0.001$ (Nichols et al., 2005).

Next, contrast analyses were conducted to identify the statistically significant differences in the convergence between SH-RL and SH-RI. Contrast analyses were based on voxelwise differences of ALE maps of SH-RL and SH-RI. To test its statistical significance, permutation tests were conducted as follows. All foci contributing to these two ALE maps were pooled and randomly divided into two groups of the same size as the original data sets (Eickhoff et al., 2011). Based on each new data set, an ALE image was created, then subtracted from the other and compared with the original data. After 25,000 times permutations, a null-distribution of difference in the ALE values between two SH-RL and SH-RI was created. Then the true difference in the ALE values was examined against the voxel-wise null-distribution, yielding a p value for the difference at each voxel under label exchangeability. The resulting p values were thresholded at a posterior probability of $p > 95\%$ for true differences and with an additional cluster extent threshold of cluster size > 200 mm^3.

2.2. Functional connectivity analyses

2.2.1. Task-based connectivity: meta-analytic connectivity modeling (MACM) analyses

MACM analyses were performed to examine functional co-activation patterns of pre-defined ROIs involved in SH-RL and SH-RI (Note that we extracted brain regions of the meta-analytic clusters as ROIs.) (Robinson et al., 2010; Eickhoff et al., 2011; Langner et al., 2014). To do this analysis, whole-brain peak coordinates from all eligible studies, i.e. whole-brain neuroimaging studies reporting activation in standard stereotaxic space in a healthy population, were downloaded from BrainMap (http://www.brainmap.org/) if at least one focus of activation within each ROI was reported. Studies that investigated effects on age, sex, handedness, and interventions (e.g., pharmacological or training-based), as well as clinical populations, were excluded. Coordinates were then analyzed using the ALE algorithm to detect areas of convergence of co-activation with each seed. Finally, the ALE maps were thresholded using a cFWE correction ($p < 0.05$) with a cluster-forming threshold of $p < 0.001$ using 10,000 permutations for correcting multiple comparisons.

Information of MACM analyses — i.e., ROI, the number of experiments, subjects, and foci that the functional co-activation pattern produced for each ROI — were included as follows: ROIs related to SH-RL consisted of left amygdala/hippocampus cluster (L amygdala/hippocampus) (338 experiments, 5112 subjects, 4099 foci), right amygdala/hippocampus cluster (R amygdala/hippocampus) (316 experiments, 4900 subjects, 3712 foci), medial prefrontal cortex (mPFC) (143 experiments, 2173 subjects, 1766 foci), left anterior insula (LAI) (581 experiments, 8661 subjects, 8803 foci), right anterior insula (RAI) (406 experiments, 6140 subjects, 5924 foci), left intraparietal sulcus region (LIPS) (407 experiments, 5940 subjects, 5878 foci), right intraparietal sulcus region (RIPS) (250 experiments, 3789 subjects, 3643 foci) and right temporo-parietal junction (RTPJ) (96 experiments, 1389 subjects, 1412 foci). ROIs related to the SH-RI consisted of L amygdale/hippocampus (212 experiments, 3340 subjects, 2550 foci), R amygdale/hippocampus (280 experiments, 4394 subjects, 3391 foci), left fusiform gyrus (LFG) (194 experiments, 2676 subjects, 2884 foci) and striatum (214 experiments, 3635 subjects, 2994 foci).

2.2.2. Task-free connectivity: resting-state functional connectivity (RSFC) analyses

RSFC analyses were run separately using the same ROIs as for the MACM analyses as seed regions. These analyses were based on resting-state fMRI images of 192 healthy volunteers obtained from the enhanced Nathan Kline Institute-Rockland Sample (NKI-RS: http://fcon_1000.projects.nitrc.org /indi/enhanced/) (Nooner et al., 2012). The sample of enhanced NKI-RS is representative of the general population across age, ethnicity, and socioeconomic status (Horn and Blankenburg, 2016). The enhanced NKI-RS dataset has been widely used by many meta-analysis studies and made numerous contributions to RSFC analyses (Krall et al., 2015; Gu et al., 2019; Wong et al., 2019). Functional images were acquired by a Siemens TimTrio 3 T scanner using a gradient-echo, echo-planar imaging (EPI) pulse sequence with repetition time = 1.4 s, echo time = 30 ms, flip angle = 65, voxel size = $2.0 \times 2.0 \times 2.0$ mm; number of slices = 64.

Using FIX (FMRIB's ICA-based Xnoiseifer, version 1.061 as implemented in FSL 5.0.9) (Griffanti et al., 2014; Salimi-Khorshidi et al., 2014), physiological and movement artifacts were removed from the resting-state data by decomposing the data into independent components and identifies noise components employing a large number of distinct spatial and temporal features via pattern classification. Unique variance related to the artefactual independent components was regressed from the data together with 24 movement parameters (including derivatives and second-order effects as previously described and evaluated; cf. Satterthwaite et al. 2013). Using SPM8 (Wellcome Trust center for Neuroimaging, London) and in-house Matlab scripts, images were then further preprocessed as following described. The first four scans were excluded before further analyses, the remaining images were corrected for head movement using a two-pass (alignment to the initial volume followed by alignment to the mean after the first pass) affine registration. For each subject, the mean image was spatially normalized to the ICBM-152 reference space using the "unified segmentation" approach (Ashburner and Friston, 2005).

Applying resulting deformation parameters, the individual functional images were subsequently smoothed with a 5-mm full width at half maximum Gaussian kernel to improve the signal-to-noise ratio and compensate for residual anatomic variations. The time-course of each seed was extracted by computing the first eigenvariate of the time-series of all voxels within 5 mm of the seed coordinates. Variance explained by the mean white matter and cerebral spinal fluid signal were removed from the time series to reduce spurious correlations, which was subsequently band-pass filtered preserving frequencies between 0.01 and 0.08 Hz. The functional connectivity map of each seed was correlated with the time-series of all other gray-matter voxels across the brain using Pearson correlation. Correlation coefficients were transformed into Fisher's z-scores, which were entered in a second-level ANOVA for group analysis, including age and sex as covariates of no interest. Statistical significance was assessed by non-parametric permutation-based inference and cluster-level thresholded at $p < 0.05$ to correct for multiple comparisons.

2.2.3. Consensus connectivity maps

The following analyses were performed to explore the functional connectivity networks by identifying the brain regions that are strongly connected to multiple brain regions as defined by ALE analyses. It is defined as brain areas that showed robust connectivity with multiple consensus functional connectivity maps generated by conjunction analyses of MACM and RSFC for each ROI. Specifically, based on MACM and RSFC analyses, task-dependent and task-independent whole-brain functional connectivity maps were generated for each ROI for SH-RL and SH-RI separately. For each ROI, the conjunction map between MACM and RSF was generated by using the minimum statistic approach (Nichols et al., al.,2005) — leading to eight connectivity maps for SH-RL and four for SH-RI, showing the brain areas consistently interacting with each ROI across rest and task states (cf. Clos et al., 2014; Hardwick et al., 2015). Finally, functional connectivity networks involved in processes of SH-RL and SH-RI delineated by identifying all regions that were significantly connected with multiple ROIs, specifically the brain regions in which overlapped with the consensus connectivity maps of at least half of the ROIs with an additional extent-threshold of 10 continuous voxels (Camilleri et al., 2018; Amft et al., 2014).

2.3. *Functional decoding (FD) analysis*

Functional decoding was run for the same ROIs that were identified in ALE analyses. The function profile of each ROI of SH-RL and SH-RI were characterized based on behavioral domain meta-data categories in the BrainMap database (http://brainmap.org/scribe/). These categories describe the experimental properties of each study stored in the database according to different mental processes, such as action, emotion, cognition, perception, and interoception (Turner and Laird, 2012). The individual functional profile corresponding to each ROI was determined by using the forward inference approach —providing information about the probability of identifying activity in a brain region given previous knowledge of a psychological process. Specifically, forward inference tested whether the conditional probability of activation given a particular behavioral domain i.e. P(Activation|Behavioral domain) was higher than the baseline probability i.e. P(Activation). Significance was determined by a binomial test with a standard $\alpha = 0.05$, corrected for multiple comparisons using the false discovery rate (FDR) method.

2.4. *Anatomical labeling and data visualization*

The SPM Anatomy toolbox (www.fz-juelich.de/ime/spm_anatomy_toolbox, v.2.2b, Eickhoff et al. 2007) and MRIcron (http://people.cas.sc.edu/rorden/mricron/install.html/) were used for anatomical labeling. MRIcroGL (https://www.mccauslandcenter.sc.edu/mricrogl/home/) was used for brain visualizations.

3. Result

Results for the meta-analyze are reported separately for the social hierarchy-related learning and interaction phase.

3.1. *Results for SH-RL phase*

3.1.1. *Results for ALE analysis*

The ALE analysis for SH-RL revealed significant convergence of activation in the following regions: mPFC, L amygdala/hippocampus, R amygdala/hippocampus, LIPS, RIPS, LAI, RAI, and RTPJ (Fig. 2a, Table 2).

3.1.2. *Results for consensus connectivity maps*

Results from MACM and RSFC analyses and their conjunctions for each ROI are displayed in Fig. S1. For mPFC, the connectivity results were consistent with the activation patterns of the default network. With regards to bilateral AI — the core region of the salience network — we found a clear similarity between its functional connectivity pattern and that of the salience network. L amygdala/hippocampus and R amygdala/hippocampus revealed similar functional connectivity patterns with mPFC, posterior cingulate, bilateral inferior frontal gyrus, striatum, bilateral fusiform gyrus. LIPS and RIPS both showed a pattern of connectivity with bilateral middle frontal gyrus, bilateral dorsal anterior cingulate cortex, bilateral middle occipital gyrus, bilateral middle temporal gyrus, bilateral inferior temporal gyrus. For RTPJ, it showed a pattern of connectivity with bilateral middle frontal gyrus, bilateral middle temporal gyrus, and middle cingulate cortex.

Next, regions supporting SH-RL were identified that were robustly connected with multiple seed regions: bilateral AI, bilateral anterior cingulate cortex (ACC), bilateral dorsolateral prefrontal cortex (DLPFC), posterior parietal cortex (PCC), bilateral middle frontal gyrus, and bilateral fusiform gyrus (FG) (Fig. 3).

3.1.3. *Results for FD analysis*

Functional decoding analyses were performed to gain insights about the psychological functions of the identified regions (Fig. 4a). With the hypothesis of the main cognitive function involved in SH-RL, how closely related the three main functions (detection, updating and computation, and construction and representation) and brain regions were brought into focus. Results revealed that LAI, RAI, and RTPJ had a close link with observation in the action domain as well as vision and audition in the perception domain, the behavioral domains that related to detection. The mPFC was functionally associated with processes of high-order cognition including social cognition and reasoning in the cognition domain, which was in accord with the assumption that mPFC supports social hierarchical information updating and computation in SH-RL. L amygdala/hippocampus, LIPS, RIPS had close associations with the visuospatial cognition, i.e., spatial in the cognition domain, which had a close link to the mental operation of integrating scattered social hierarchy knowledge to the social hierarchy structure in one's mind. All results that survived after correction (FDR$<$ 0.05) are reported in Fig. S2.

3.2. *Results for social hierarchy-related interaction phase*

3.2.1. *Results for ALE analysis*

For the ALE analysis, significant convergence of activation was observed in L amygdala/hippocampus, R amygdala/hippocampus, LGF, and striatum (Fig. 2b, Table 2).

3.2.2. *Results for consensus connectivity maps*

Results of MACM and RSFC and their conjunctions for each ROI can be found in Fig. 4. Striatum produced functional connectivity patterns with the thalamus, midbrain, bilateral inferior frontal gyrus, bilateral medial frontal gyrus, and middle cingulate cortex. For LFG, it is found that the patterns of connectivity with bilateral inferior occipital gyrus and bilateral superior parietal lobule. Bilateral amygdala/hippocampus clusters revealed functional connectivity with mPFC, posterior cingulate, bilateral inferior frontal gyrus, striatum, and bilateral fusiform gyrus.

Next, the brain network supported SH-RI was identified by searching brain regions that were robustly connected with multiple seed regions. It is found that many brain regions of overlapped consensus connectivity map located in the reward circuit, including the striatum, medial orbitofrontal cortex (mOPC) which implied the close link between SH-RI and reward circuit. Results of overlapping two and three consensus connectivity maps were illustrated in Fig. 5. No brain regions survived after the number of consensus connectivity maps overlapped increase to four.

3.2.3. *Results for FD analysis*

To explore the underlying psychological function of meta-analytic brain regions engaged in SH-RI, the likelihood ratios of some main behavioral domains in each ROI were determined (Fig. 4b). In a broad sense, many psychological functions, such as action, cognition, and emotion can be influenced by social hierarchy. To characterize the functional profile of the meta-analytic clusters in SH-RI, some basic domains received attention including execution and preparation in the action domain, attention and social cognition in the cognition domain, and positive, negative, reward/gain, and punishment/loss in the emotion domain. High likelihood ratios of some psychological domains in multiple ROIs illustrate the importance and consistency of their roles in SH-RI. Results showed that among these basic psychological domains, striatum and bilateral amygdala/hippocampus clusters were closely related to the domains of reward/gain as well as punishment/loss which implied the close links between reward-related psychological functions with SH-RI.

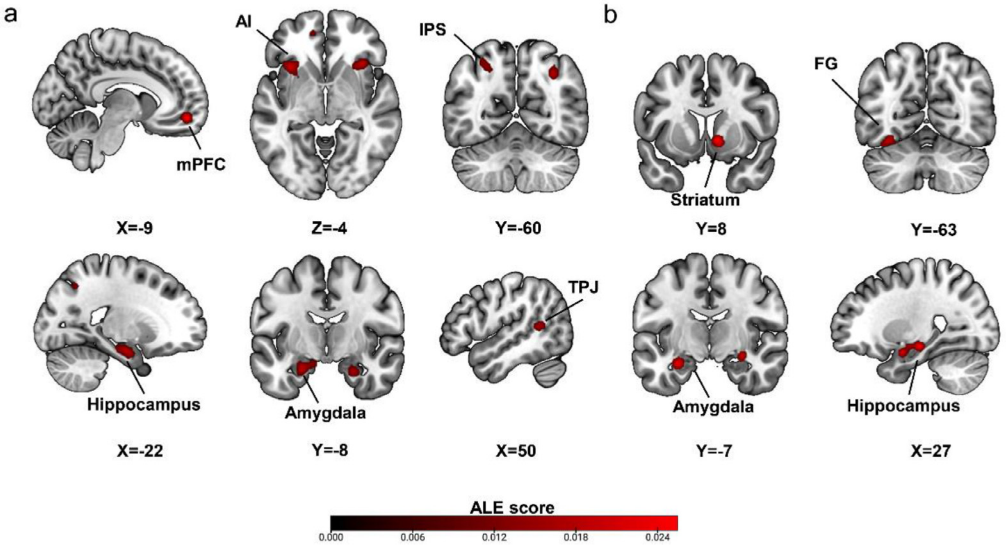

Fig. 2. Social hierarchy-related brain regions.
ALE meta-analysis results showing brain regions consistently engaged for (A) social hierarchy-related learning and (B) social hierarchy-related interaction. Results were cluster-level familywise-error corrected for multiple comparisons (cFWE < 0.05 with a cluster defining threshold of $p < 0.001$ and 10,000 permutations). L, left; R, right; mPFC, medial prefrontal cortex; AI, anterior insula; IPS, intraparietal sulcus; TPJ, temporo-parietal junction; LFG, left fusiform gyrus.

Table 2
ALE meta-analysis results for social hierarchy-related learning and interaction.

Brain Region Labels	Anatomical location	BA	MNI Coordinates			*Z* score*	Cluster Size (mm^3)
			x	*y*	*z*		
Social hierarchy-related learning							
L Amygdala/ Hippocampus	Amygdala/ Hippocampus	34/28	−24	−12	−20	4.90	2152
R Amygdala/ Hippocampus	Amygdala/ Hippocampus	34/28	24	−10	−26	4.46	1944
mPFC	Medial frontal gyrus	32/10	−10	52	−10	5.85	1400
LAI	Insula	13	−34	20	−2	5.76	1392
RAI	Insula	13	34	22	−6	4.86	888
LIPS	Superior parietal lobule	7	−30	−58	52	4.07	1024
RIPS	Superior parietal lobule	7	32	−62	42	4.76	872
RTPJ	Superior temporal gyrus	39	48	−50	10	4.40	832
Social hierarchy-related interaction							
L Amygdala/ Hippocampus	Amygdala/ Hippocampus	28/34	−28	−8	−20	4.97	1632
R Amygdala/ Hippocampus	Amygdala/ Hippocampus	/	−26	−20	−14	4.97	1032
LFG	Fusiform gyrus	37/19	−32	−66	−14	4.08	952
Striatum	Caudate/Putamen	/	10	8	−4	5.11	792
Contrast: SH-RL>SH-RI							
LIPS	Superior parietal lobule	7	−20	−63	45	2.64	960
LAI	Insula	13	−28	22	0	2.71	840
RAI	Insula	/	28	24	−6	2.10	352
mPFC	Medial frontal gyrus	32/10	−10	48	−14	2.42	592
L Hippocampus	Hippocampus	28/34/35	−20	−18	−20	2.41	424
L Amygdala	Amygdala	34/28	−14	−2	−22	2.35	336
R Amygdala	Amygdala	34	18	4	−16	2.10	232
RTPJ	Superior temporal gyrus	22	52	−46	10	2.00	288
Contrast: SH-RI>SH-RL							
R Amygdala/ Hippocampus	Amygdala/ Hippocampus	28	30	−14	−12	2.39	840
Striatum	Caudate/Putamen	/	6	6	−2	2.18	704
LFG	Fusiform gyrus	19	−28	−64	−18	2.45	312
Conjunction						ALE ($\times 10^{-2}$)	
L Amygdala/ Hippocampus	Amygdala/ Hippocampus	/	−24	−8	−20	1.86	288
R Amygdala/ Hippocampus	Amygdala/ Hippocampus	34/28	22	−4	−20	1.65	176

ALE, activation likelihood estimation; MNI, Montreal Neurological Institute; L, left; R, right; mPFC, medial prefrontal cortex; LAI, left anterior insula; RAI, right anterior insula; L Amygdala/ Hippocampus, left Amygdala/ Hippocampus cluster; R Amygdala/ Hippocampus, left Amygdala/ Hippocampus cluster; LIPS, left intraparietal sulcus; RIPS, right intraparietal sulcus; LFG, Fusiform Gyrus; RTPJ, right temporo-parietal junction; SH-RL, social hierarchy-related learning; SH-RI, social hierarchy-related interaction. * Cluster-level family-wise error (FWE) correction ($p < 0.05$) with cluster-forming threshold of $p < 0.001$ using 10,000 permutations.

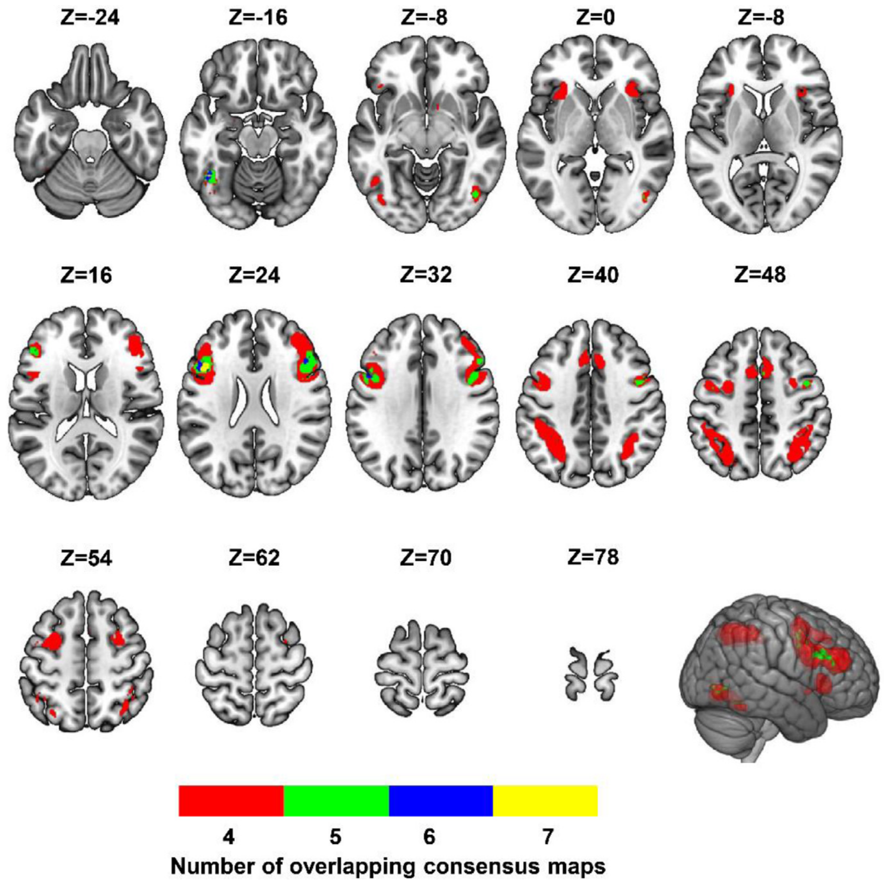

Fig. 3. Consensus connectivity maps of social hierarchy-related learning.
Consensus connectivity maps identified by overlapping task-free (RSFC) and task-based (MACM) connectivity maps in the process of social hierarchy-related learning.

All results that survived after correction (FDR< 0.05) are reported in Fig.S1.

3.3. *Results for contrast and conjunction analyses*

For the contrast analyses, LIPS, bilateral AI, mPFC, left amygdale/hippocampus clusters and RTPJ were more consistently activated in SH-RL compared to SH-RI, whereas striatum, LFG, and right hippocampus were more consistently activated in SH-RI compared to SH-RL (Fig. 6a, Table 1). The conjunction analysis showed a common activation maximum in the bilateral amygdala/hippocampus clusters (Fig. 6b, Table 2).

4. Discussion

The role of social hierarchy cannot be overstated in its importance. In addition to acting as a guide to social interactions and improving the survival prospects of individuals within it, social hierarchy also contributes greatly to stability and harmony within societies. Given the significance of social hierarchy, there is much to be gained by endeavoring to understand more about how humans create and work within them. The pace of this quest has increased since the advancement of functional neuroimaging techniques and has allowed us to develop insights into the neural underpinnings of how humans understand and interact with social hierarchies. However, the wide variety of experimental tasks that have been employed by these studies means that results are somewhat heterogeneous. As a consequence, in the absence of any systematic framework of analysis, it is not possible to identify the core neural mechanisms which remain significant even if specific experimental situations change.

To synthesize previous findings, we divided paradigms into two distinct domains: those that examine the process of SH-RL (i.e. social hierarchy-related learning) and those that examine the process of SH-RI (i.e. social hierarchy-related interaction). Further, we used quantitative meta-analyses to reveal the neural mechanisms that support these two processes. Using the ALE method, we identified brain regions that were consistently engaged by these cognitive processes and examined their underlying functional connectivity networks as generated by task-based co-activation (i.e., MACM) and task-free connectivity analyses (i.e., RSFC). Then we conducted functional decoding analyses which provided us with a sound basis for speculation regarding the functional roles of these regions.

In general, we made the following observations. For SH-RL we found that AI and TPJ were associated with the detection of dominance cues and that the mPFC plays an important role in updating and computing dynamic social hierarchy information. These regions may be used to construct a social hierarchy structure with the support of IPS, amygdala, and hippocampus. With regards to SH-RI, we found that the modulation of the social hierarchy may have strong associations with the reward network. Supports in regulating behaviors could be traced to the striatum, amygdala, and hippocampus. With the framework of analysis described, we will discuss the results within the context of the two above processes and their relationship based on conjunction and contrast analyses.

4.1. *SH-RL phase*

We found that the process of SH-RL elicited consistent activation patterns in the following brain regions: mPFC, RTPJ, and amygdala, hippocampus, IPS, and AI. Based on the results of MACM, RSFC, and

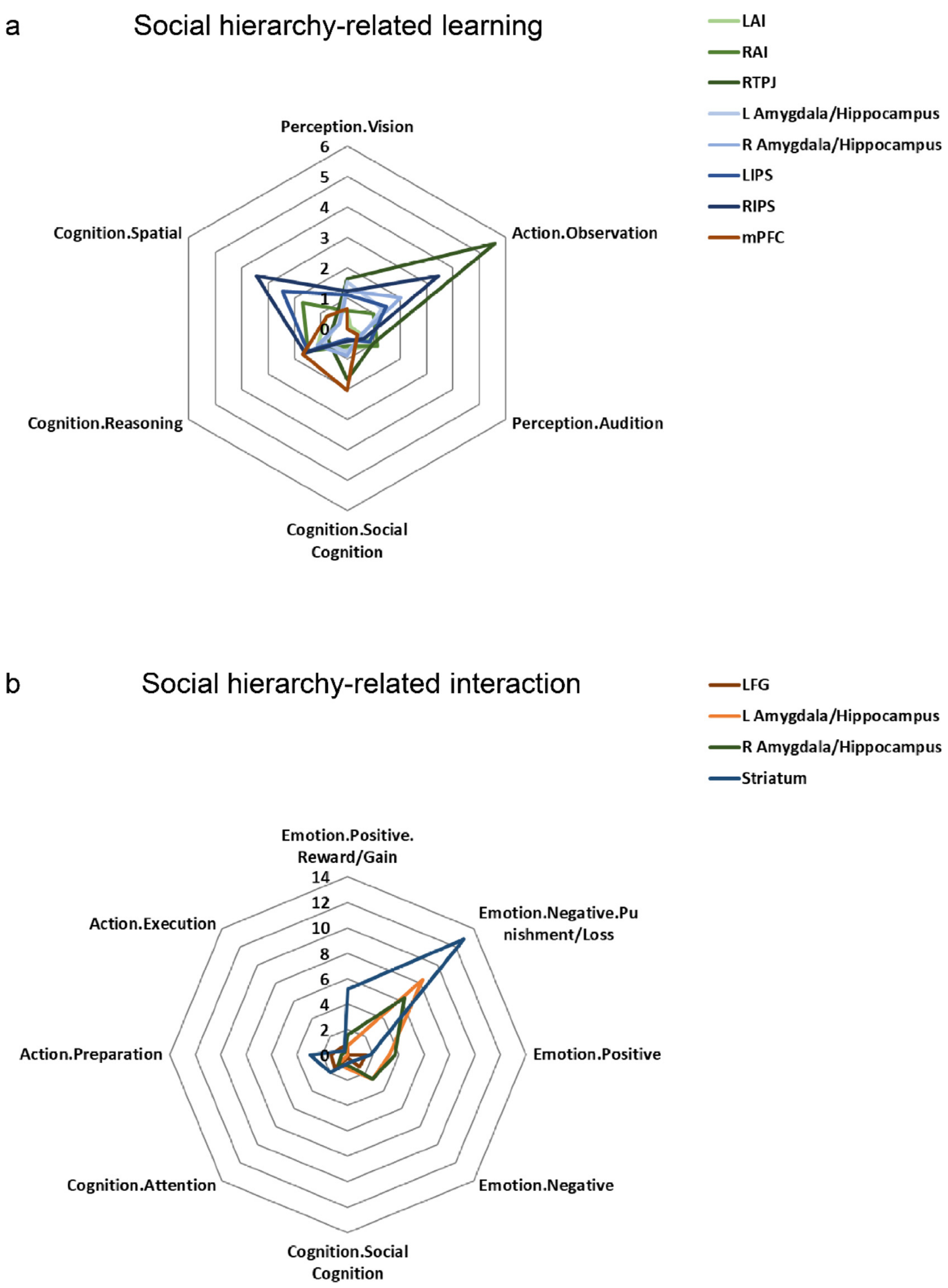

Fig. 4. Functional decoding (FD) analyses to characterize the functional roles of meta-analytic clusters consistently involved in the processing of social hierarchy-related learning (SH-RL) and social hierarchy-related interaction (SH-RI).

(A) For SH-RL, the value of likelihood ratios in FD depicted the weight of each brain region on three main functions involved in SH-RL: detection (perception.vision; action.observation; perception.audition), updating, and computation (cognition. social cognition; cognition. reasoning), construction and representation (cognition. spatial). (B) For SH-RI, the value of likelihood ratios in FD depicted the weight of each brain region on some basic behavioral domains involved in SH-RI, i.e. action (execution; preparation), cognition (attention; social cognition), and emotion (positive; negative; positive. reward/gain; negative. punishment/ loss). L Amygdala/ Hippocampus, left amygdala/hippocampus cluster; R Amygdala/Hippocampus, right amygdala/hippocampus cluster; mPFC, medial prefrontal cortex; LAI, left anterior insula; RAI, right anterior insula; LIPS, left intraparietal sulcus region; RIPS right intraparietal sulcus region; RTPJ, right temporo-parietal junction; LFG, left fusiform gyrus.

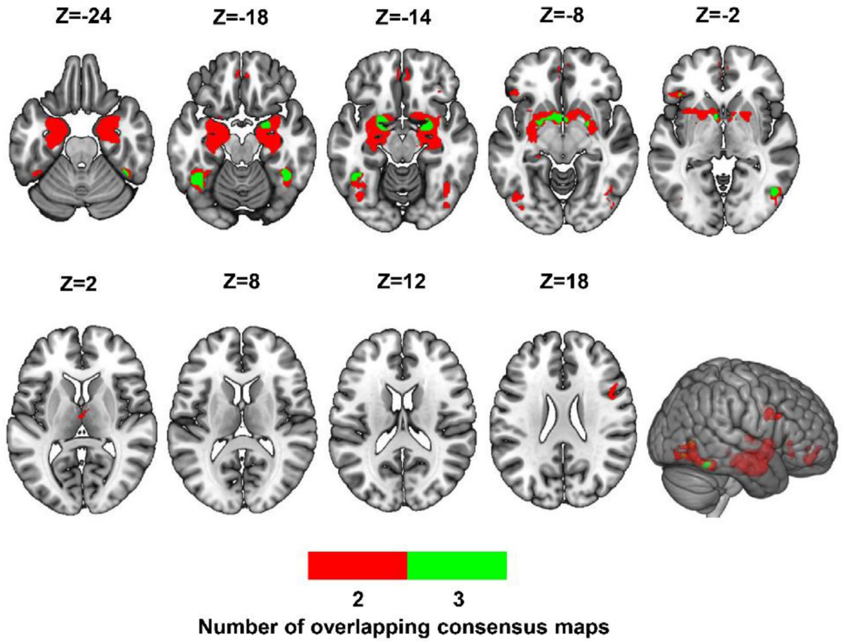

Fig. 5. Consensus connectivity maps of social hierarchy-related interaction.
Consensus connectivity maps identified by overlapping task-free (RSFC) and task-based (MACM) connectivity in the process of social hierarchy-related interaction.

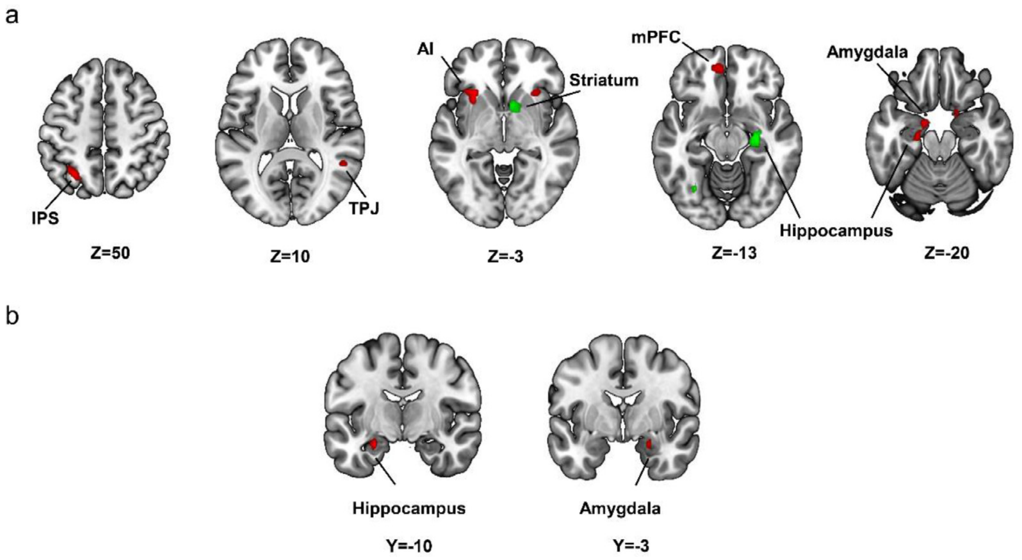

Fig. 6. Significant clusters from conjunction and contrast analyses.
Results of contrast analysis (A) and conjunction analysis (B). Brain regions showing higher consistent activation in the social hierarchy-related learning are illustrated in red, whereas regions showing higher consistent activation in the social hierarchy-related interaction are illustrated in green. L, left; R, right; mPFC, medial prefrontal cortex; AI, anterior insula; IPS, intraparietal sulcus; TPJ, temporo-parietal junction; LFG, left fusiform gyrus (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

FD, we will discuss how these brain regions relate to SH-RL within the context of three main functions: detection, updating and computation, and construction and representation.

4.1.1. Detection

The ability to detect valid cues carrying social hierarchy information represents an important starting point to the process of obtaining knowledge about social hierarchy. Extrapolating from our findings, we argue that bilateral AI may serve this role for the two following reasons. Based on our task-based co-activation and task-free connectivity analyses, we found that the pattern of its functional connectivity was consistent with that of the salience network. This finding underlined the important link between AI and this network. From a constant stream of incoming sensory inputs, the salience detection mechanism in this network dynamically selects specific stimuli for additional processing (Menon, 2015). As a prominent node of the salience network, a main function of AI in the salience network is the detection of relevant stimuli (Crottaz-Herbette and Menon, 2006; Seeley et al., 2007; Sterzer and Kleinschmidt, 2010). Researchers have found that AI contributes to detection in many tasks examining numerous cognitive domains (Swick et al., 2011; Menon, 2015). Facial features are the most likely candidate to act as valid stimuli for providing information about one's social status. One study used a forced-choice task based on human faces to reveal brain regions engaged in social hierarchy comparison. After controlling for confounding factors, including the age of targets, gender, and fame, activation of AI (Brodmann 47) remained significant for social hierarchy discrimination (Farrow et al., 2011). Based on such evidence combined with our current findings, we confirmed that the detection function of AI acts on a wide spectrum of mental processes including the acquisition of social hierarchy knowledge.

In the process of obtaining social hierarchy knowledge, the role of TPJ seems related to the detection of social dominance cues. Functional profiling of TPJ revealed its role involved in observation and perception. This result is consistent with previous research. Meta-analysis studies found that TPJ has an influential role in the detection of extraneous stimuli and reorienting of attention (Decety and Lamm, 2007; Krall et al., 2015). Therefore, we suggest that TPJ serves to detect relevant information about social hierarchy when individuals attempt to clarify hierarchical relationships.

4.1.2. *Updating and computation*

Obtaining social hierarchy knowledge through dominance cues represents only one component of what is required to navigate the human social landscape. Sometimes these clues are fuzzy or even contrived (Kumaran et al., 2012). It seems that almost all creatures, whether human or animal, are born knowing how to camouflage themselves behind external characteristics. Thus, a more refined process is necessary to build a more precise model of social hierarchy structures. Competition and observational learning are ways in which more precise information about the positions of others within social hierarchies can be obtained. Successful learning supported by these two modes requires outcome to be tracked and knowledge of one's social rank to be updated. The core factor underlying this ability is that of internal updating and computation. Our functional connectivity and functional decoding analyses gave us a clear indicator of the importance of mPFC in this role. Function profiles revealed its role associated with computation and updating, such as social cognition and reasoning. Thus, we argue that the ability to compute and update information about social hierarchies can be attributed to mPFC.

In many studies, mPFC is credited with internal computation. A model-based fMRI study found that mPFC tracked and updated the rank of opponents (Ligneul et al., 2016). Moreover, mPFC is the only brain region that has been found to encode prediction errors, a cognitive component that promotes information updating, implying mPFC contribution to updating variations between predictive outcome and reality (Ligneul et al., 2016). Although a different task and model framework was used, another study supports this function in mPFC. Based on Bayesian approaches, when participants compared the ranks of strangers through observation and inference, mPFC was engaged in computing estimates of their power and updating information about one's own rank within the hierarchy (Kumaran et al., 2016).

The internal updating and computation function of mPFC is not restricted to the domain of social hierarchy. It has been found to make similar contributions across numerous studies examing social domains including those examining social norms (Xiang et al., 2013), learning about ownership (Lockwood et al., 2018), tracking of expertise or ability (Boorman et al., 2013; Wittmann et al., 2016), and mentalizing (Hampton et al., 2008). In general, based on neural computations, many studies have found that internal computing signals are correlated with activation in mPFC, highlighting its function in information updating and computation.

4.1.3. *Construction and representation*

The ultimate purpose of the process of SH-RL is to accurately construct or represent social hierarchical relationships in one's own mind. Brain regions involved in this function are thought to reflect the degree of social hierarchy by activation level characteristics. That is, social hierarchical stimuli should induce regular activation in these brain regions as opposed to an irregular signal. This regularity should be correlated with the rank within the social hierarchy of an object. Based on our results and previous findings, this process may recruit several brain regions including the hippocampus, IPS, and amygdala.

Combined with previous findings and our functional decoding analysis, it is found that the role of IPS and the hippocampus have a close link with visuospatial cognition. In addition to physical space, these two areas are also sensitive to the encoding of social space (Parkinson et al., 2014; Montagrin et al., 2017). Moreover, previous studies have found that their cortical activity is a function of rank within the social hierarchy (Chiao et al., 2009; Kumaran et al., 2012; Kumaran, 2016; Haaker et al., 2016).

The hippocampus represents a kind of neural navigation system which helps us to map not just spatial dimensions but also abstract concepts and social relationships (Tavares et al., 2015; Constantinescu et al., 2016; Schafer and Schiller, 2018;). To investigate how the brain responds to ongoing changes in social relationships such as modulations across affiliation and dominance dimensions, one fMRI study recorded neural activity while participants interacted with other roles. They found that perception of social navigation was closely related to the hippocampus (Tavares et al., 2015). This finding of the hippocampus provided a possible explanation for questions about why the hippocampus working prominently in some studies about social hierarchy (Kumaran et al., 2012; Zink et al., 2008). Social hierarchy learning is processing like building social relationship structure in mind constantly where may the role of hippocampus comes into play. This is one possible reason for the phenomenon that the hippocampus parametrically tracked the degree of the rank of target stimuli.

IPS also appears to play a significant role in the construction and representation of relationships within the social hierarchy. It has been found that activation levels in IPS correlate with the social status of targets when performing a self-referential status judgment task (Cloutier and Gyurovski, 2013). Moreover, literature exploring how IPS encodes social space has provided clues as to how it may construct models of social structure. One study used multivoxel pattern analysis to reveal the neural mechanism underlying how distance is processed across spatial, temporal, and social domains. This study found that IPS was engaged across all distance domains at an above-chance level (Parkinson et al., 2014). This finding illustrated the functional integration capability of IPS in processing features of dimension across both physical and social space. Social hierarchy is, conceptually, a kind of ordering or ranking based on one social dimension or combined social values. In this way, the IPS may play a role in processing information to determine superiority/inferiority of rank, a process that requires the computation of magnitude judgments or encoding of relationships in social space.

Amygdala has also been found to be associated with the representation of the social hierarchy. Activation in the amygdala appears to scale linearly with the rank within a social hierarchy (Kumaran et al., 2016; Haaker et al., 2016). For example, in one study, participants were required to learn the rank of others through observation of confrontation. This study revealed that the gradual acquisition of social hierarchy knowledge was negatively associated with amygdala responsivity. That is, increasing rank discrimination predicted decreasing levels of activation in the amygdala (Haaker et al., 2016). In contrast to the representation of hierarchical relationships by IPS and hippocampus, the amygdala only showed sensitivity to social space and not to physical space (Kumaran et al., 2012; Kumaran, 2016). The representation of social hierarchy in amygdala may stem from the sensitivity to different levels of emotion and motivation which is related to social rank. For example, research on non-human primates showed that surgical lesions on amygdalae resulted in diminished social status and increased submissiveness (Rosvold et al., 1954). The role of amygdala in motivation and emotion may not only support learning about social hierarchy but may also offer to play a role in maintaining status (Rosvold et al., 1954; Kumaran et al., 2012; Watanabe and Yamamoto, 2015).

4.2. *SH-RI phase*

Cognitive processes related to social hierarchy involve obtaining information and subsequently this information guiding or impacting behaviors and social interactions. On the basis of acquired knowledge about social hierarchy, behaviors can be modified in ways consciously and unconsciously. Our findings revealed roles for striatum, amygdala, hippocampus, and LFG in this process of social hierarchy-related interaction.

4.2.1. Overlap with the reward circuit

According to our functional connectivity results, we found many brain regions of overlapped consensus connectivity maps located in the reward circuit. Moreover, for three main regions, bilateral amygdala/hippocampus cluster and striatum, functional decoding indicated an association of their function with reward and punishment. These findings suggest that modulation of SH-RI may not be independent of reward processing. Furthermore, these results could not be explained by the presence of financial incentives that were offered by experimenters to increase engagement in participants. Experimental tasks in most previous studies were not directly relevant to monetary reward (Freeman et al., 2009; Haaker et al., 2016; Feng et al., 2016). Thus, the inducing factor of reward processing should be hidden in social hierarchical information itself. Exploring the effects of social hierarchy on behavior and social interaction from a reward processing perspective would be helpful in furthering our understanding.

Previous studies demonstrated that the striatum is one of the key structures in the reward network and that amygdala, hippocampus are key components in regulating this network (Haber and Knutson, 2009). The significant role of the striatum in rewarding processing cannot be isolated from the synergy of other structures. The convergent fibers from the cortex within the striatum along with hippocampal, amygdalostriatal, and other projections make striatum a key entry port for processing emotional and motivational signals and thus driving action output in the basal ganglia (Russchen et al., 1985; Fudge and Haber, 2001; Friedman et al., 2002; McFarland and Haber, 2002 Haber and Knutson, 2009). A variety of aspects of reward processing can be mediated by this complex neural network formed by connectivity between these brain regions.

Striatum, which can represent primary reinforcers is also sensitive to higher-order rewards including social comparisons, social hierarchy, and reputation (Kedia et al., 2014; Christopoulos et al., 2017). For example, when participants viewed players who ranked by stars, their striatum responded to the higher one with a greater degree of activation compared with the lower one (Zink et al., 2008). This can help individuals to interact with others from different ranks in an appropriate way.

The functions of brain regions can sometimes be express through their interaction. The role of amygdala in regulating reward processing has been demonstrated in numerous studies, in part through observations of critical interactions between it and striatum in forming stimulus-reward associations (Baxter and Murray, 2002). Hippocampal input to the shell of the nucleus accumbens is important for driving nucleus accumbens activity. Moreover, activity-dependent modulation of the strength of this input may be involved in the regulation of goal-directed behaviors (Legates et al., 2018). Communication among these brain regions mentioned above in both function and structure plays an integral role in reward processing and may explain a variety of phenomena.

4.2.2. Impacts of social hierarchy guided by social reward

As a basic principle of behavior, rewards are crucial for many activities including incentive learning, comparing social information, forming appropriate responses to stimuli, and developing goal-directed behaviors (Haber and Knutson, 2009; Kedia et al., 2014; Fareri and Delgado, 2014). Although the effect of social hierarchy is numerous and complicated, with the principle of reward guiding, we can summarize the intricate situations as follows: those of superior rank attract more cognitive resources and gain more positive feedbacks compared with those of a relatively inferior rank (Dalmaso et al., 2011; Khalvati et al., 2016). For example, interviewers can obtain information about the social class of candidates and make inferences about the fit, competence, starting salary, and signing bonus in ways that bias the process in favor of applicants of higher social class (Kraus et al., 2019). In a competition task, participants strategically adjusted themselves by improving their performance when facing strong opponents (Ligneul et al., 2016). Many studies have observed parallel effects in the neural system. By using a competitive reaction time task within the context of both stable and unstable social hierarchy structures, many brain regions such as the striatum, occipital gyrus, parahippocampal gyres showed stronger activation when faced with opponents of a high rank (Zink et al., 2008). It is reasonable to assume that, compared with those of an inferior rank, individuals of superior rank have a greater social influence. Such superiority often implies a higher threat in competition or higher benefit in cooperation, thus mobilizing more cognitive resources to interact with them carefully is adaptable.

With evidence from another direction, we become more convinced that rewarding guide the influence of social hierarchy on behaviors and interactions: if the reward behind the social rank change, the effect of social rank change accordingly. Western culture tends to reinforce dominant behaviors, whereas Eastern culture tends to reinforce subordinate behavior (Freeman et al., 2009). This well-established cross-cultural difference in behavior has been verified by self-reports of participants (Freeman et al., 2009). The different reward signal underlying this characteristic behavior of social hierarchy between cultures was expressed on a neural level by the mesolimbic reward system (Freeman et al., 2009). In participants from the USA, dominant stimuli selectively engaged the caudate nucleus and mPFC, whereas these same regions were selectively engaged by subordinate stimuli in participants from Japan (Freeman et al., 2009). In a social status task, the results didn't show a significant status-relative value assignment in the striatum but reflect an interaction between agent's status and subject's own status: subjects with high social status had a higher degree of activation for high-status agents which is opposite to low-status subjects, they have a higher activation to low-status agents in striatum (Ly et al., 2011). In other words, subjects showed an equal rank preference. In nonhuman primates, one study also found a similar pattern of preference for equal rank. Specifically, high-status monkeys preferentially attended to others with high-status, whereas low-status monkeys attend to other low-status monkeys (Shepherd et al., 2006). Such an equal rank preference can be interpreted by the in-group effect. Similar ones can provide lessons and reference for one's own behavior which increases the value of equal rank ones. In this way, although this social class preference is not fixed, the reward signal underlying social status is always a key motivation in social hierarchy interaction. These close correlations between social hierarchy and reward processing allow us to understand the process of social hierarchy-related interaction from a more general perspective. That is the link between social hierarchy stimuli — reward implied in the social hierarchy information — valuation response.

4.3. Information transfer and sharing: from SH-RL to SH-RI

Although we view SH-RL and SH-RI as two independent processes in analyses to obtain clearer results, these two psychological processes are clearly complementary (Qu et al., 2017). In daily life, these two processes may be evoked in a cyclical manner. Knowledge of the social hierarchy would allow an appropriate adjustment of behaviors for the subsequent interaction phase. This adjustment can then be enhanced by the feedbacks of the environment or others post-interaction which can be used to update information regarding the other individual (Santamaria-Garcia et al., 2014; Wittmann et al., 2016). Or even learn others' social hierarchy via interaction somehow, and interaction process includes an updating of social hierarchy. In this way, these two processes are not parallel but rather connected and interactive. This connection implied a requirement of a bridge for communication between these two processes that can transfer information about social hierarchy from the SH-RL to SH-RI.

We found two regions, the amygdala, and hippocampus may contribute to this role. First, if some brain regions are involved in both processes, the possibility that they contribute to the join points would be higher than other brain areas. This assumption is fully backed by the results of conjunction analysis, suggesting amygdala and hippocampus are overlappings between SH-RL and SH-RI. Second, in the successive cognitive process of SH-RL, the action scope of the join points is more likely to be located at the end of this overall cognitive stream. In other words, in terms of cognitive functions involved in SH-RL, it is more reasonable that brain regions engaged in the construction and representation of information are more likely involved in the transfer of this information to SH-RI, rather than engaged in the initial detection or computation stages. The third reason relates to what we previously discussed about the notion that the influence asymmetry of social hierarchy is generated by differences in social value as a function of social rank. Therefore, brain regions involved in connecting both processes should also be implicated in processing reward. This function can be used to carry information about social hierarchy to regulate rewarding processing. In this view, it is persuasive that the amygdala and hippocampus serve as join points between SH-RL and SH-RI. Besides this finding in data analyses, this viewpoint can be supported by experimental evidence from previous studies. In an fMRI study, participants learned some persons' and galaxies' ranks by observational learning, then they were required to use their knowledge about the person and galaxy hierarchies to decide how much in real monetary terms to pay for potential projects on offer in the later interaction phase (Kumaran et al., 2012). Their fMRI results indicated that the activation of the hippocampus as a function of person rank and galaxy rank (Kumaran et al., 2012). As to the amygdala, they found a significant linear correlation between its neural activity and person rank, but not galaxy rank (Kumaran et al., 2012). Another study that investigated both the learning phase and the interaction phase observed domain-general coding of rank in the amygdala and hippocampus, even when the interaction task was just required to categorize other persons according to the company to which they belonged and not require the knowledge about their social hierarchy (Kumaran et al., 2016). These experimental findings confirmed the role of the amygdala and hippocampus in information transfer and sharing between SH-RL and SH-RI processes.

4.4. Limitations

The limitation related to the method should be discussed first. ALE meta-analysis utilizes partial information of fMRI study, including the peak coordinates of brain activation and the number of participants. Some other factors such as cluster size, effect size, scanning parameters are not taken into account which also have their impacts on results and potential publication bias based on these factors can not be obtained. Then, our study includes a couple of main limitations that should be addressed in future studies. First, we treated SH-RL and SH-RI as two mutually independent yet closely related cognitive processes in our current analyses. However, in some situations such as when the social rank of another individual can not be assessed accurately at a time, these two processes may invoke circularly and frequently. In this closed cognitive loop, the information transfer from SH-RL to SH-RI is important. Based on our meta-analyses results, we proposed that the amygdala and hippocampus may play a crucial role in transferring information from SH-RL to SH-RI. However, this deduction is derived from data-driven analyses but lacks direct experimental evidence and needs further investigations in the future.

Second, social hierarchy-related information exists in a dynamic social context, i.e., everyone can be a sender or a receiver of the social hierarchical signal. Thus, investigating interpersonal interactions by adopting a hyper-scanning approach that records signals from two or more participants simultaneously is a meaningful research direction (Pinti et al., 2020). Since this proposed paradigm needs further exploration, our identified brain regions could be used as regions of interest for future studies employing, for example, functional near-infrared spectroscopy (fNIRS) based hyper-scanning studies. Despite these limitations, we were able to gain valuable insight into the neural mechanism of two key stages related to social hierarchy by combining a quantitative meta-analytical method with a qualitative perspective.

5. Conclusion

In daily life, SH-RL and SH-RI are both essential to the efficient navigation of our social world. In this study, we applied multiple meta-analytical methods to reveal the relevant neural mechanisms of these processes. For SH-RL, we identified that AI and TPJ are likely implicated in detecting dominance cues that carry information about social hierarchy; mPFC probably contributes to internal updating and computing dynamic feedbacks; and that amygdala, hippocampus; and IPS possibly serve to construct and represent a model of social hierarchy structure. For SH-RI, we found that this process recruited the amygdala, hippocampus, striatum, and fusiform gyrus. Evidence of activation pattern and function decoding revealed close links between SH-RI and reward processing, suggesting the possibility that guidance by the reward processing network is the root mechanism underlying the modulation of behavior in relation to social hierarchy. These results provide insights into the neural signatures of social hierarchy-related learning and interaction. Considering social hierarchy as a basic rule of society, these findings shed light on the understanding in interaction between social organization and social cognition as well as some application for social adaptation in a neuropsychological way.

CRediT authorship contribution statement

Siying Li: Conceptualization, Methodology, Formal analysis, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Frank Krueger:** Methodology, Writing – review & editing. **Julia A. Camilleri:** Methodology, Software, Formal analysis, Resources. **Simon B. Eickhoff:** Methodology, Software, Resources. **Chen Qu:** Conceptualization, Writing – review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare no competing interests.

Credit authorship contribution statement

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Ethics statement

The current work was a meta-analysis of existing data and there were no ethical considerations.

Data and code availability statements

The data that support the findings of this study is publicly available from https://osf.io/ygbq7/. Meta-analyses that we used in this study were achieved via the open-source software, GingerALE (http://www.brainmap.org/ale/).

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2021.118731.

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