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Original Article

The hyper-brain neural couplings distinguishing high-creative group dynamics: an fNIRS hyperscanning study

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This hyperscanning study aimed to identify a neural coupling profile that distinguishes high-creative group dynamics through functional near infrared spectroscopy. A total of 123 dyads completed one creativity task (alternative uses task, AUT) and contrast task (objective characteristics task). A *K*-means clustering analysis on AUT performance grouped 31/29 dyads into high/low-creative group, respectively. In comparison with the low-creative group, the high-creative group showed: (i) higher collective flexibility and delayed perspective-taking behaviors, but lower immediate perspective-taking behaviors; (ii) enhanced interpersonal brain synchronization (IBS) between the left inferior frontal gyrus (lIFG) and right motor cortex, and nodal *Eloc* at the right superior temporal gyrus (rSTG); (iii) declined intrapersonal functional connectivity between the right angular gyrus (rAG) and rSTG, and IBS between the lIFG and rAG. The enhanced neural couplings positively correlated with group creative performance, whereas a reverse correlation pattern existed in the declined ones. A leave-one-out cross-validation analysis showed these neural couplings reliably predicted group creative performance within the sample. These indicate that high-creative group dynamics are characterized by utilizing partners' shared information when necessary (e.g. encountering idea exhaustion). A neural coupling profile consisting of sophisticated interplays between regions within frontal, temporal, and parietal lobes may underlie high-creative creative dynamics.

Key words: group creativity; hyperscanning; IBS; neural coupling; hyper-brain network.

Introduction

Keith Sawyer (Sawyer 2017) once stated that "Both my research and my real-world experience had led me to the same conclusion: collaboration is the secret to breakthrough creativity." Beyond dispute, group creativity, the capacity of a group to produce novel and useful ideas (Runco and Jaeger 2012), is increasingly indispensable and vital to the survival and development of enterprises, scientific institutions, and even countries. Scientists have repeatedly emphasized the balance between "generating one's own ideas" and "attending to others" to group creative dynamics (Sawyer 2017; Paulus and Kenworthy 2021). That is, an imbalanced group creative dynamic that focusing on generating self-interested ideas and neglecting attending to others, or vice versa, seems to impair group creativity. So, what does a high-creative group dynamic look like? Moreover, despite the rapid progress of behavioral and neuroscientific research on creativity (Beaty et al. 2016; Acar and Runco 2019), this field lacks in exploring the neurocognitive characteristics of group creative dynamics, especially those help distinguish high-creative groups from low-creative groups. Investigating this can certainly help further understand the neurocognitive mechanism that underlies high-creative group dynamics.

Given the importance of balance between "generating one's own ideas" and "attending to others" to group creative dynamics (Paulus and Kenworthy 2021), a high-creative group dynamic should assure an appropriate allocation of resources to both "generating one's own ideas" and "attending to others." Previous research showed the most effective brainstorming process is one that involves a variation in individual and group ideation (Korde and Paulus 2017). Alternating individual and group ideation was more effective than both group ideation and solitary ideation. This may indirectly suggest that group members should not only strive to generate ideas upon their own, but also fully utilize the cognitive stimulation effect of partners' ideas (maybe especially when they temporally encounter idea exhaustion). Accordingly, with respect to the creative performance and collaborative idea convergence (or perspective-taking behaviors), we hypothesized that: (I) high-creative group dynamics will show higher idea

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quality and quantity and involve more time-delayed perspective-taking behaviors (utilizing partners' ideas when necessary) but less immediate perspective-taking behaviors (block one's own idea generation flow and jump into collaborative idea convergence) than low-creative group dynamics. Moreover, while solitary creative process merely requires factors such as cognitive and motivational ones, group creative process requires others such as social factors (Paulus and Brown 2007). We thus suggested the intrapersonal neural coupling would also differ when an individual is involved in a group or not, and thereby examined both intrapersonal and interpersonal neural couplings in this study.

Solitary creative thinking encompasses a series of cognitive processes that evoke intricate interplays among multiple cortical regions such as the inferior frontal gyrus (IFG), superior temporal gyrus (STG), angular gyrus (AG), etc. Research indicated the IFG is responsible for retrieving and selecting relevant remote associations (i.e. loosely related semantic concepts) that assists in generating creative ideas (Abraham et al. 2018; Cogdell-Brooke et al. 2020). The IFG also involves inhibiting prepotent response and exerting top-down control over imaginative processes (Rae et al. 2014; Beaty et al. 2015). Moreover, research showed that evaluating the originality of ideas is associated with a relative activation increase in left IFG, and inhibiting the left IFG can slack idea evaluation and increase idea originality (Kleinmintz et al. 2018). The STG was supposed to be responsible for selectively accessing and integrating conceptual representations, which may help stimulate the novelty of incoming associations (Shen et al. 2017). The right AG serves as a core hub of the default network, which involves the automatic generation of candidate responses during creative thinking (Beaty et al. 2016). Deactivation of the right AG is also critical for efficient automatic retrieval of semantic information (Davey et al. 2015) and divergent thinking (Pick and Lavidor 2019). Moreover, from the network-based perspective, the experiment by Beaty et al. (2016) suggested that creative thought involves interplay between the default network (e.g. posterior cingulate cortex, medial prefrontal cortex, bilateral temporal cortex) involving the generation of candidate responses, and executive control network (e.g. dorsolateral prefrontal cortex, DLPFC) that involves constrain and direct the generation process. Research also revealed that high-creative individuals could be characterized by the ability to simultaneously engage large-scale brain networks comprised of cortical hubs within the executive control, default, and salience networks (Beaty et al. 2018). A further experiment by Beaty et al. (2021) examined the interact between the default network and subnetworks (FPCNa and FPCNb) of the frontoparietal control network (FPCN or executive control network). They observed a positive correlation between the FPCNa and default network, but a negative correlation between the FPCNb and the default network at rest. However, both FPCNa and FPCNb increased their communication with the DN during the divergent thinking task. Accordingly, single-brain research indicates creative thinking closely ties to cortical structures within the frontal, temporal, and parietal lobes.

Recently, social scientists have become increasingly interested in unveiling the neural characteristics of diverse social interaction using the multi-brain neuroscience approach named "hyperscanning" (Gvirts and Perlmutter 2019; Redcay and Schilbach 2019). Similar to synchronous neural oscillations within a single brain, synchronous cross-brain oscillations may also contribute to the fast and accurate information exchange and binding of neural messages from different brain regions or brains. Previous hyperscanning research observed interpersonal brain synchronization (IBS) at the IFG during entailing communication and social learning (Jiang et al. 2012; Pan et al. 2018). IFG not only involves in both production and comprehension of speech (Silbert et al. 2014), but also serves as a vital hub of the "mirror neuron system" that subserves social interaction such as understanding others' actions and intentions (Iacoboni and Dapretto 2006). Silbert et al. (2014) also observed comprehension-production coupling at the STG. The superior temporal cortex (including gyrus and sulcus) also serves as a key region for the mirror system (Iacoboni et al. 1999), and imitation (Iacoboni et al. 2001). A review study also suggested that the superior temporal cortex is associated with the alignment system of the predictive coding framework of alignment (Shamay-Tsoory et al. 2019). Enhanced IBS or activation at the MTG was also observed during online interpersonal mutual gaze (Koike et al. 2016) and three-person collaboration (Xie et al. 2020). The first hyperscanning-based group creativity study by Xue et al. (2018) compared the creative performance of groups consisting of high-creative or low-creative individuals and estimated IBS between group members. Findings indicated that enhanced IBS at the right DLPFC and right angular gyrus (AG) might subserve the creative performance of groups consisting of low-creative individuals. Lu et al. also adopted functional near infrared spectroscopy (fNIRS)-based hyperscanning technique and found that enhanced IBS at the right DLPFC and rAG contributed to the creative performance of groups under cooperation mode (Lu et al. 2019). AG is an important part of the right temporal–parietal junction (rTPJ), which involves in social cognitive processes such as perspective-taking (Santiesteban et al. 2015) and theory of mind (Filmer et al. 2019). Moreover, the experiment by Mayseless et al. (2019) reported that group creative design involved enhanced IBS among cerebral regions pertaining to the executive control, mentalizing and mirror neuro networks (i.e. prefrontal cortex, TPJ, and STG). These multiple-brain research further indicated social interaction and group creativity closely involve cortical regions within the frontal, temporal and parietal lobes.

In the current study, we mainly aimed to address the following question: what is the specific neural coupling profile that distinguishes high-creative group dynamics? Given a group is defined as two or more individuals who are connected by social relationships (Forsyth 2014), the dyadic paradigm was used in this study (Lu et al. 2019; Mayseless et al. 2019). All dyads solved one creativity task (alternative uses task, AUT) and one contrast task (object characteristics task, OCT). Note that the experimental tasks were also the tasks that were used to split the high-creative and low-creative groups. Based on the K-means clustering analysis on group creative performance, 31 high-creative dyads and 29 low-creative dyads from an original sample of 123 dyads were, respectively, grouped into the high-creative group and low-creative group. The fNIRS device has higher tolerance for motor artifacts and ecological validity than electroencephalogram (EEG) or functional magnetic resonance imaging (fMRI), and allows verbal communication, thereby an fNIRS-based hyperscanning device was used to simultaneously record the brain (i.e. bilateral prefrontal cortex, temporal and parietal cortex) activities of the participants in each dyad. We used the cross-correlation to assess intrapersonal functional connectivity (Fc) and IBS, and validate these findings using phase randomization and "nominal groups," respectively. Given solitary creative thinking is associated with communication across regions within the frontal, temporal, and parietal lobes (e.g. IFG, AG, STG), we hypothesized that: (II) a high-creative group dynamic may involve increased intrapersonal neural coupling between these regions. Given the association between regions within the frontal, temporal, and parietal lobes (e.g. IFG, AG, STG) and group communication (including creative communication), we hypothesized that: (III) a high-creative group dynamic may also involve increased interpersonal neural couplings cross regions within the frontal, temporal, and parietal lobes (e.g. IFG, AG, STG). In addition, networks come to be considered as physiological basis of information transfer and mental representation (Strogatz 2001), and graph theoretical approaches provide a powerful new way of quantifying brain systems to analyze complex brain networks (Bullmore and Sporns 2009). We thus also attempted to use the graph theoretical approaches to first explore the characteristics of the hyper-brain network comprising of intrapersonal Fc and IBS of the high-creative group dynamics without specific hypothesis.

Of particular note is that several previous studies have preliminary investigated the association between interpersonal neural couplings and group creative performance using hyperscanning technique (Xue et al. 2018; Lu et al. 2019; Mayseless et al. 2019; Lu et al. 2021). However, these studies had not directly treated the level of group creative dynamics as an independent variable, described what a high-creative group dynamic looks like, and revealed a neural coupling profile that distinguishes high-creative group dynamics. This study will provide intriguing and meaningful findings to these issues, and discuss the implications of these findings to improve the low-creative group dynamics.

Materials and methods

Participants

A total of 246 college students (187 females, age: 21.28 ± 2.03 years) were randomly assigned as 123 dyads. All participants provided written informed consent. Procedures were approved by the University Committee on Human Research Protection of East China Normal University. We used AUT scores to measure the group creative performance. In order to divide these dyads into the high-creative group (HCG) or low-creative group (LCG), the *K*-means clustering approach was conducted on the composite standard *Z*-scores of AUT fluency and originality. *K*-means clustering can group objects into meaningful subclasses so that the objects from the same cluster are quite similar, and the objects from different clusters are quite different from each other. The number of clusters was set as 3 (i.e. high-creative, middle-creative, and low-creative groups). The squared Euclidean distance was used during the *K*-means clustering (100 iterations). Accordingly, 31 dyads from the top 25% and 29 dyads from the bottom 24% were, respectively, divided into the HCG and LCG (Fig. 1). This study mainly focused on comparing these two groups. Additionally, relative analysis on the whole sample was presented in the Supplementary Material as supplementary analysis (Supplementary Material results, S2–S4).

The HCG consisted of 7 female–male, 3 male–male, and 21 female–female dyads, ages 21.26 ± 1.86. The LCG consisted of 5 female–male, 2 male–male, and 22 female–female dyads, ages 21.00 ± 1.69. Therefore, we suggested that the age and sex compositions were comparable between two groups.

Procedures

Here, we took one dyad as an example. Upon arrival, two participants were asked to sit face-to-face around a table (Fig. 2A) and complete several pre-tests (e.g. individual creative potential; see "Pre- and post-experimental tests"). The experiment procedure consisted of two ∼3-min "rest & instruction" sessions and two 5-min task sessions (Fig. 2B). These two participants remained still with eyes closed and mind-relaxed during the rest sessions and received communication rules (Supplementary Material methods, S1) and task instructions before each task. During two task sessions, they completed a creativity task (i.e. AUT) and a contrast task (i.e. object characteristic task, OCT; it does not demand creativity). During the AUT session, they were explicitly instructed to be creative and generate as many creative uses for an everyday object (i.e. book) as possible (Said-Metwaly et al. 2020). AUT is a well-established divergent thinking task and a reliable predictor of real-world creativity (Runco and Acar 2012) that has been widely used in both behavioral

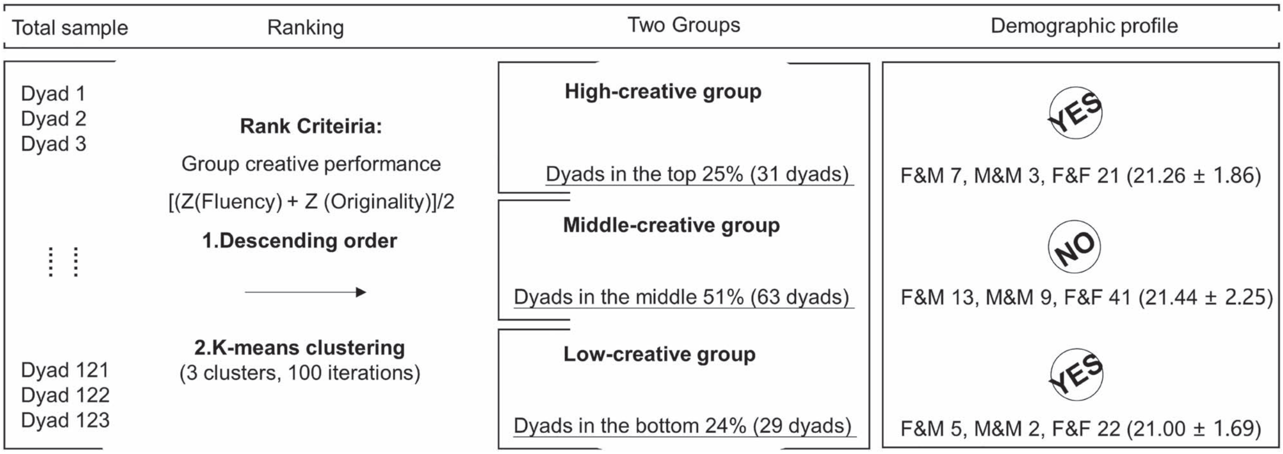

Fig. 1. Grouping procedure and demographic profile. Note that "YES" or "NO" in the circle denotes whether the group contributed to the main analysis.

and neuroscience studies on creativity (Fink et al. 2009; Acar and Runco 2019). During the OCT session, two participants were asked to report characteristics of an everyday object (i.e. fishing pole) (Fink et al. 2009). OCT is broadly a memory-retrieval task that demands no creativity but involves direct stimulus-related information (Binder et al. 2009; Fink et al. 2009, 2010). In previous studies, participants were only asked to present typical characteristics for the target object during the OCT (Fink et al. 2009). However, the task duration was 5 min in the study, much longer than those in previous studies. Therefore, participants were allowed to report all relevant characteristics for the target object. Both task sequence and reporting sequence were counterbalanced across dyads.

Note that researchers usually reveal neural substrates specific to creative cognition by comparing neural responses during AUT to those during OCT (Fink et al. 2009; Sun et al. 2016; Beaty et al. 2018). While participants generate alternative uses of everyday objects during AUT, they name attributes of everyday objects during OCT. Here, we also used OCT as the contrast task to reveal neural substrates specific to group creative cognition. Immediately after the experiment, participants completed several post-tests (e.g. task depletion, task enjoyment, etc.).

Behavioral assessments

Group AUT performances were assessed by scoring idea fluency, originality, and uniqueness (Guilford 1967; Runco and Acar 2012). AUT fluency was assessed using the total number of non-redundant responses reported by each dyad. AUT originality was assessed using a subjective method. Five trained raters independently scored the originality of each idea on a 5-point Likert scale (1 = not original at all, 5 = highly original). The inter-rater agreement of this method was satisfactory (internal consistency coefficient [ICC] = 0.72). The score of each idea was obtained by averaging raters' ratings. The final AUT originality of each dyad was obtained by averaging the originality scores of all responses from that dyad (i.e. Sum [AUT originality]/AUT fluency). Similar with AUT originality, AUT uniqueness is also an index for idea quality but typically assessed using an objective scoring method. Reponses from all dyads were first collated into a comprehensive lexicon. Next, synonyms were identified and responses collapsed accordingly. If a response was statistically infrequent (i.e. the response was reported by only 5% or fewer participants in the sample), it was scored "1." All other responses were scored "0." The final AUT uniqueness of each dyad was the amount of ideas scoring "1."

To evaluate the extent to which each dyad explored responses from different categories during AUT, three trained raters discussed and assessed the collective flexibility for each dyad together (Lu et al. 2020). For instance, "using the book to kill mosquitos" and "kill the flies" belong to the same category, whereas "using it to kill mosquitos" and "light a fire" belong to two different categories. The final collective flexibility of each dyad was the amounts of categories.

Additionally, the index of convergence (IOC) was calculated to assess perspective-taking behavior during AUT (Larey and Paulus 1999; Lu et al. 2020). Redundant/equal responses were excluded from the response pool before this analysis. The IOC was scored as follows: (i) the responses of the two participants were listed in chronological order; (ii) from the first idea to the last, when a response pertained to the same category (identified in the collective flexibility scoring) as the previous response, it scored "1," and the number of ideas that scored "1" was counted (i.e. if there were 3 ideas that scored "1," the sum would be "3," which indicates that there were 3 ideas pertaining to the same category as the previous response); (iii) the IOC for each dyad was obtained using the following equation: IOC = Sum/[fluency—Sum]. Here, fluency indicates AUT fluency of the dyad. Note that perspective-taking behaviors can be either immediate or delayed. For instance, some drew on the partner's ideas immediately

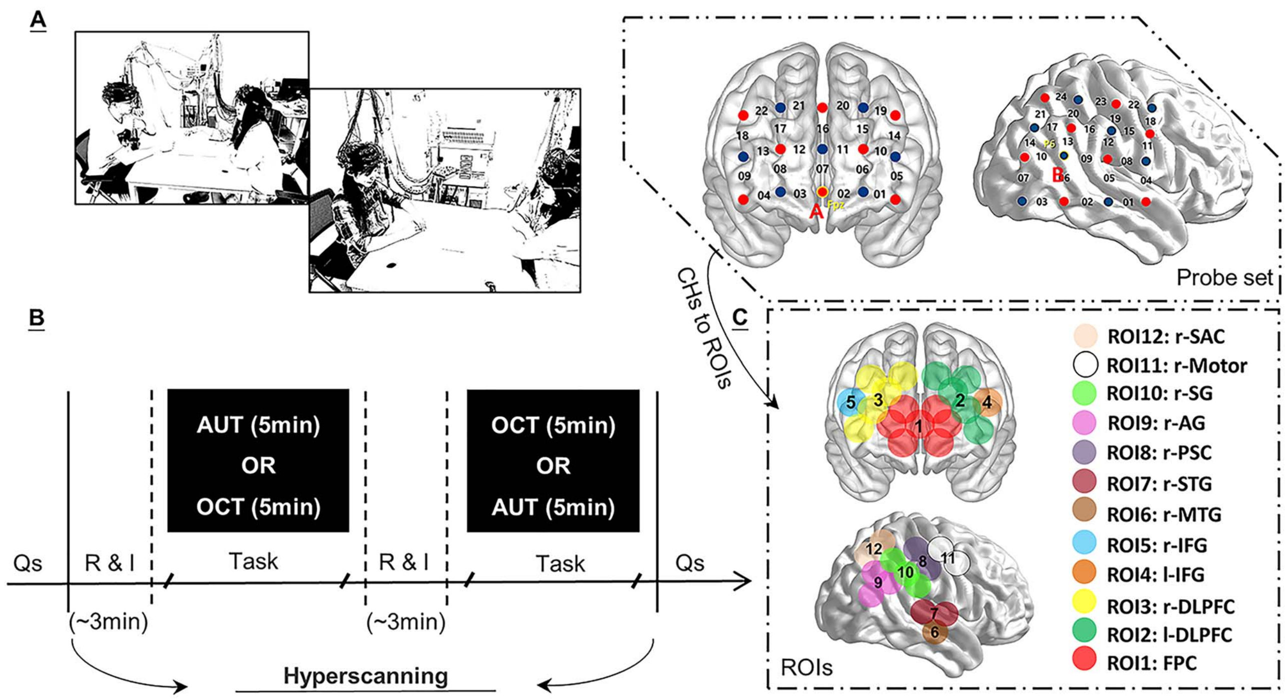

Fig. 2. Experimental and hyperscanning design. A) Experimental setup. B) Hyperscanning procedure. Qs: pre-tests/post-tests. R&I: ~3 min resting and instruction session. Task: 5-min AUT or OCT session, sequence of the two tasks was counterbalanced. C) Optode probe set on the bilateral prefrontal cortex and right temporal and parietal regions. A total of 12 regions of interest (ROIs) were created based on shared source localizations according to the Montreal Neurological Institute coordinates of the CHs.

after they were presented, whereas some would like to use others' ideas after they exhausted their own ideas. Therefore, we respectively scored the immediate IOC (abovementioned) and delayed IOC for each dyad. These two IOCs only differ in whether an idea was utilized immediately after it was presented (Details are presented in Supplementary Material methods, S2.).

As we stated, OCT merely served as a contrast task to reveal neural substrates specific to group creation here, thereby we didn't invest much time on analyzing OCT performance. Group OCT performance was merely evaluated using the fluency score, as explained previously. Such analysis protocol is also widely accepted in creativity research (Fink et al. 2009; Sun et al. 2016; Beaty et al. 2018; Lu et al. 2019).

fNIRS data acquisition and preprocessing

An NIRS system (ETG-7100; Hitachi Medical Corporation) was used to simultaneously record the oxyhemoglobin and deoxyhemoglobin concentrations of participants in each dyad. Each participant was scanned with one 3×5 optode probe set on the bilateral prefrontal cortex and one 4×4 optode probe set on the right temporal and parietal regions (Fig. 2C and Supplementary Material methods, S3).

We used a principal component spatial filter algorithm to remove the global components (Xian et al. 2016) and a correlation-based signal improvement (CBSI) method to correct motion artifacts (Cui et al. 2010) in the raw fNIRS data. The CBSI-corrected deoxyhemoglobin is solely the corrected oxyhemoglobin multiplied by a negative coefficient (Cui et al. 2010) (Supplementary Fig. S1), thereby neural data analyses mainly focused on oxyhemoglobin signals.

Next, a total of 12 regions of interest (ROIs) were created based on shared source localizations according to the Montreal Neurological Institute coordinates of the CHs. ROIs included frontopolar cortex (FPC), left inferior frontal gyrus (lIFG), right middle temporal gyrus (rMTG), right superior temporal gyrus (rSTG), right angular gyrus (rAG), right motor cortex (rMotor), etc. (Supplementary Material methods, S3). This study mainly focused on the ROI-wise analyses.

Neural coupling analysis

We used cross-correlations between oxyhemoglobin time-series within each participant to assess the intrapersonal Fc and those across participants in each dyad to assess the IBS (Silbert et al. 2014; Liu et al. 2021). Cross-correlation is particularly suited to assessing how two signals move together over time.

We respectively calculated 12×12 Fc matrices of the AUT session and OCT session for each participant. The Fc matrix of one dyad was calculated by averaging the Fc matrices of the two participants in that dyad. Similarly, 12×12 IBS matrices of AUT session and OCT session were also calculated for each dyad respectively. The IBS between same ROI pairings were then averaged. For instance, the IBS between FPC (participant 1) and lIFG (participant 2) was averaged with the IBS between FPC (participant 2) and lIFG (participant 1). This resulted in a total of 66 intrapersonal (Fc) and 78 interpersonal connections (i.e. IBS) for each dyad. Fisher's *r*-to-z transformation was used to increase normality of the distribution of Fc and IBS values before further statistical analyses (Chang and Glover 2010). To assess the Fc and IBS specific to group creative dynamic, we subtracted the time-averaged Fc and IBS of OCT session from that of AUT session. See the neural coupling analysis pipeline in Supplementary Fig. S1. The group-averaged intrapersonal Fc and IBS correlation matrices of the HCG and LCG were also presented (Supplementary Fig. S3).

Hyper-brain network analysis

The 24 × 24 hyper-brain neural coupling matrices (including IBS and Fc) obtained using cross-correlation (untransformed using Fisher's *r*-to-z) were further analyzed using graph-based analysis to explore the organization among these ROIs (Supplementary Material methods, S4). We implemented network analyses in MATLAB using GRETNA (Wang et al. 2015) and calculated two typical network measure parameters (including global and nodal), namely local efficiency (E_{loc}) and global efficiency (E_{glob}).

Regarding the nodal parameters, the parameters of the same node were also averaged as stated in the IBS analysis. For instance, the E_{loc} of rSTG (participant 1) and E_{loc} of rSTG (participant 2) were averaged. To assess the hyper-brain network specific to group creation, we subtracted the nodal network parameters of OCT session from that of AUT session and entered them into further analyses. See the network analysis pipeline in Supplementary Fig. S2.

Statistical analysis

Independent-sample *t*-tests using GROUP as the between-subject factor were performed on group behavioral indices during AUT (the originality scores of the best/-worst ideas were also compared between the two groups), neural couplings, and hyper-brain network parameters. The resulting *P*-values from intrapersonal Fc, IBS, and network analyses were respectively corrected using the false discovery rate method ($P < 0.05$). We additionally performed one-sample *t*-tests (test value "0") on the intrapersonal Fc and IBS (Supplementary Material methods, S1; Fig. S4). Bivariate Pearson's correlations were calculated to reveal brain-behavior relationship for significant neural indices. The resulting *P*-values were also FDR corrected.

Moreover, in order to examine whether the significant neural couplings and hyper-brain network parameters can reliably predict group creative performance, a leave-one-out cross-validation analysis was conducted (Beaty et al. 2018). A linear regression model was first specified to estimate the relationship between the observed creative score and model predicted creative score. Note that we mainly focus on four creative performance indices (i.e. fluency, uniqueness, originality, and composite Z-scores). Next, the model was applied to new participants in a leave-one-out cross-validation process. The model was trained on $N-1$ participants' significant neural coupling and creative scores and tested on the left-out participant. The predictive power is reflected in the magnitude and statistical significance of the Pearson correlation between the observed and model predicted creative scores. This cross-validation process was respectively conducted for each significant neural coupling or hyper-brain network parameter.

Validation analysis on neural couplings

Given the presence of long-range temporal autocorrelation in the blood oxygen level-dependent (BOLD) signal, the statistical likelihood of each significant Fc was assessed using a bootstrapping procedure (Simony et al. 2016; Piazza et al. 2019). (i) The surrogate data were generated using phase randomization, which preserves the mean and autocorrelation of the original signal but randomizes the phases after applying a Fast Fourier Transform. (ii) Similar Fc analyses were then conducted for the surrogate data of each dyad. This permutation process was repeated 1000 times.

To examine whether significant IBS were specific to the interacting participants (actual groups), we performed a validation test (Jiang et al. 2015; Reindl et al. 2018). (i) The pre-processed oxyhaemoglobin time series of all participants were randomly re-paired. We named these re-paired groups as "nominal groups." (ii) Similar IBS analyses were then conducted for the nominal groups. This permutation process was repeated 1000 times.

Pre- and post-experimental tests

Prior to the experiment, individual creative potential was measured using Runco Ideational Behavior Scale (RIBS) (Runco et al. 2016). It contains 19 items that are scored on a 5-point Likert scale ranging from 0 (never) to 4 (just about every day). RBIS focuses on ideation that may occur in daily life (e.g. "How often do you have ideas for rearranging the furniture in your home"?). Participants' preference for teamwork was measured using Group Preference Scale (GPS) (Larey and Paulus 1999). GPS contains 10 items that are scored on a 5-point Likert scale ranging from 1 (not at all) to 5 (very much). For example, "I try to look at everybody's side of a disagreement before I make a decision." Furthermore, participants completed Perspective-Taking Scale (PTS), which assesses individual perspective-taking tendency (Davis 1983). It contains 7 items (e.g. whether individuals like to take the perspectives of others into consideration while deciding) that are scored on a 5-point Likert-type scale ranging from 0 ("does not describe me well") to 4 ("describes me very well"). The internal consistency reliabilities of RIBS (Cronbach's $\alpha = 0.85$), GPS (Cronbach's $\alpha = 0.86$), PTS (Cronbach's $\alpha = 0.74$) were satisfactory in this study.

Table 1. Full statistical reports for behavioral performance ($M \pm SD$).

Variables	HCG (31)	LCG (29)	t	P	Cohen's d
AUT Fluency	33.79 ± 6.99	18.68 ± 3.57	10.44***	<0.001	2.72
Uniqueness	6.24 ± 2.75	1.04 ± 0.73	10.15***	<0.001	2.58
Originality	2.20 ± 0.10	1.92 ± 0.06	13.83***	<0.001	3.40
Z-scores	2.05 ± 0.84	−2.04 ± 0.64	21.19***	<0.001	5.48
Flexibility	21.03 ± 4.33	12.85 ± 1.68	9.76***	<0.001	2.49
Immediate IOC	0.07 ± 0.02	0.12 ± 0.02	−11.00***	<0.001	2.50
Delayed IOC	0.19 ± 0.08	0.13 ± 0.11	2.15*	0.035	0.62
Best	3.56 ± 0.24	2.70 ± 0.31	12.05***	<0.001	3.10
Worst	1.45 ± 0.19	1.39 ± 0.19	1.34	0.19	0.32
OCT fluency	34.10 ± 8.91	24.17 ± 6.78	4.83***	<0.001	1.25

Notes: Z-score indicates the composite Z-scores of creative performance (composite standard Z-scores of idea fluency and originality). Flexibility indicates collective flexibility. Best/Worst indicates the originality score of the best/worst idea. $^{*}P < 0.05$, $^{***}P < 0.001$.

Immediately after the experiment, participants rated the task depletion, task enjoyment and their tendency to perspective taking (i.e. we tended to complete the task by taking each other's perspectives), during tasks using a 5-point Likert-type scale ranging from 1 ("not at all") to 5 ("very much").

Results

Behavioral performance

Independent-sample *t*-tests using GROUP as the between-subject factor were performed on the scores of RIBS, PTS, GPS, as well as task depletion, task enjoyment and tendency to perspective-taking during AUT or OCT. Results showed no significant difference ($Ps > 0.05$).

Moreover, the HCG showed significantly higher AUT fluency, originality, uniqueness, composite Z-scores of creative performance, collective flexibility, delayed IOC, originality of the best idea and OCT fluency, but significantly lower immediate IOC than the LCG did ($Ps < 0.01$; See statistical details in Table 1).

Intrapersonal Fc

Independent-sample *t*-tests (corrected by false discovery rate method, FDR) showed that the intrapersonal Fc between the rSTG and rAG (i.e. Fc of rSTG-rAG) were lower in the HCG ($M = -0.15$, $SD = 0.33$) than in the LCG ($M = 0.18$, $SD = 0.33$), [$t\ (58) = -3.91$, $P = 0.0002$, $P_{fdr} = 0.016$, Cohen's $d = 1.03$] (Fig. 3A and B).

IBS

Independent-sample *t*-tests showed that the IBS between the lIFG and rAG was lower in the HCG ($M = -0.13$, $SD = 0.23$) than in the LCG ($M = 0.13$, $SD = 0.29$), [$t(58) = -3.92$, $P = 0.0002$, $P_{fdr} = 0.019$, Cohen's $d = 1.03$]. However, the IBS between the lIFG and rMotor was higher in the HCG ($M = 0.28$, $SD = 0.40$) than in the LCG ($M = -0.12$, $SD = 0.43$), [$t(58) = 3.80$, $P = 0.0003$, $P_{fdr} = 0.013$, Cohen's $d = 1.00$] (Fig. 3D, E, G).

Neural coupling validation

Regarding intrapersonal Fc, the analyses on surrogate data confirmed that the observed effects on the Fc of rSTG-rAG were in the top 1% of the permutation distribution (Fig. 3C).

Regarding IBS, the analyses on nominal groups confirmed that the observed effects on the IBS of lIFG-rAG, and lIFG-rMotor were in the top 1% of the permutation distribution (Fig. 3F and H).

Hyper-brain network specific to group creation

Regarding global network parameters, independent-sample *t*-tests showed that two groups did not differ in E_{loc} or E_{glob} ($Ps > 0.1$).

Regarding nodal network parameters, independent-sample *t*-tests showed that the HCG ($M = 0.01$, $SD = 0.04$) had significantly higher nodal E_{loc} at the rSTG than the LCG ($M = -0.03$, $SD = 0.04$) [$t(58) = 3.64$, $P = 0.0006$, $P_{fdr} = 0.007$, Cohen's $d = 1.00$]. However, no significant group difference was observed for the nodal E_{glob} ($P_{fdr}s > 0.1$; Fig. 4).

Brain-behavior relationships

Regarding the Fc of rSTG-rAG, bivariate Pearson correlations showed that it negatively correlated with creative performance (i.e. AUT fluency, uniqueness, originality and composite Z-scores), and collective flexibility, but positively correlated with immediate IOC (Fig. 5A). Cross-validation analysis showed significant positive correlations between the model-predicted and observed fluency, uniqueness, originality, and Z-scores ($Ps < 0.05$; Supplementary Fig. S8A).

Regarding the IBS of lIFG-rAG, bivariate Pearson correlations showed that it negatively correlated with creative performance, collective flexibility, and delayed IOC, but positively correlated with immediate IOC (Fig. 5B). In addition, the IBS of lIFG-rMotor positively correlated with creative performance, and collective flexibility, but negatively correlated with immediate IOC (Fig. 5C). Cross-validation analysis showed significant positive correlations between the model-predicted and observed fluency, originality, and Z-scores ($Ps < 0.05$; Supplementary Fig. S8B and C).

Regarding the nodal E_{loc} of rSTG, bivariate Pearson correlations showed that it positively correlated

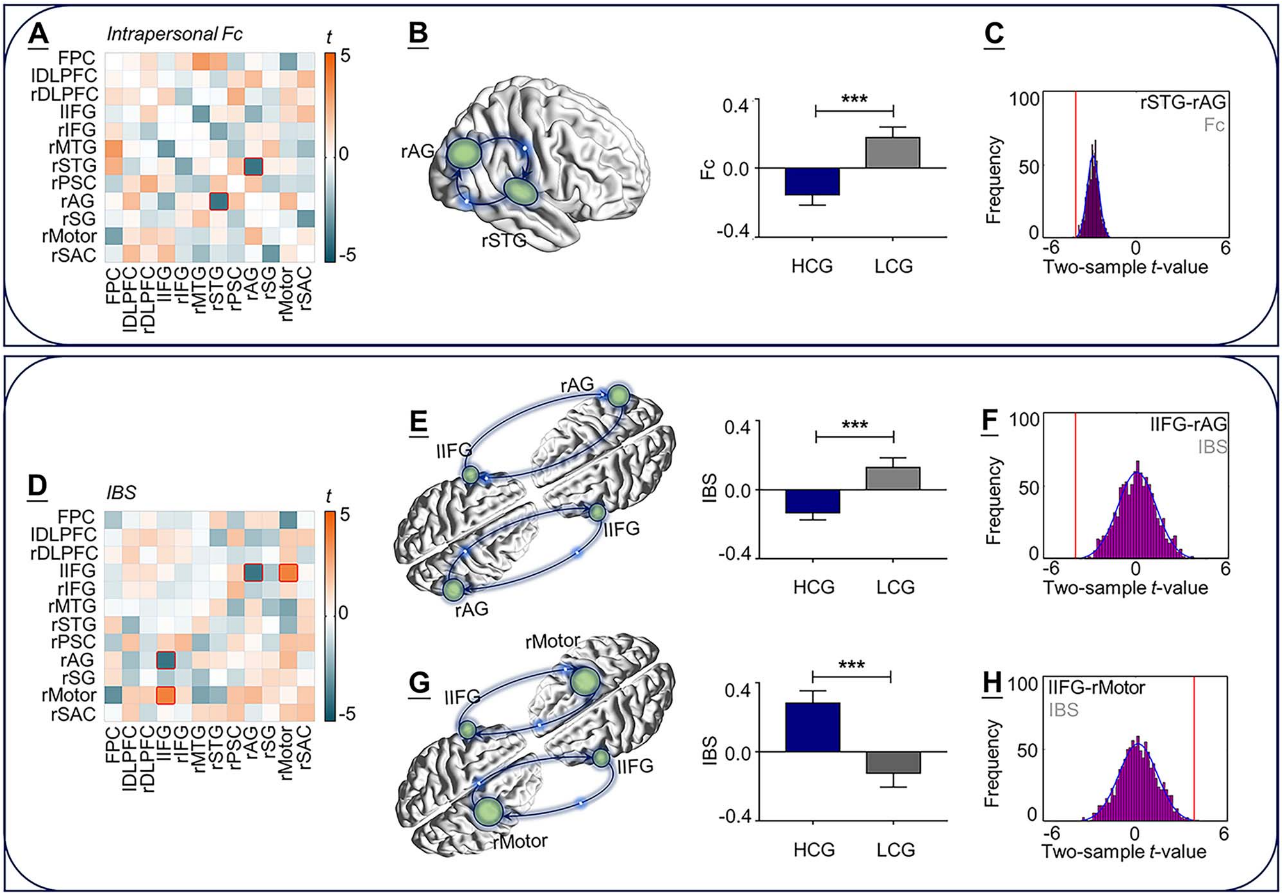

Fig. 3. Intrapersonal Fc and IBS. A/D) The heatmap of the t-values for independent-samples t-tests using GROUP as the between-subject factor on the intrapersonal Fc/IBS across all ROIs. The color bar denotes the t-values. The vertical/horizontal axis denotes ROIs. The red rectangles indicate the GROUP effect survived the false discovery rate correction. B/E/G) The locations of the intrapersonal Fc of rAG-rSTG/IBS of lIFG-rAG/IBS of lIFG-rMotor on the cerebral cortex and the amplitudes of these three neural couplings. Error bars indicate standard errors of the mean. $^{***}P_{\text{uncorrected}} < 0.001$. C) The distribution of t-values from validation analyses on the surrogate data (phase randomization). F/H) The distribution of t-values from validation analyses on the nominal groups. The vertical axis denotes the occurrence frequency of the corresponding t-value. The red line denotes the position of the t-value from the original data/actual group which is in the 1% areas. lIFG, left inferior frontal gyrus; rSTG, right superior temporal gyrus; rAG, right angular gyrus; rMotor, right motor cortex.

with creative performance, and collective flexibility, but negatively correlated with immediate IOC (Fig. 4D). FDR-corrected *P*-values were presented in Supplementary Table S2. Cross-validation analysis showed significant positive correlations between the model-predicted and observed fluency, uniqueness, originality, and Z-scores ($Ps < 0.05$;Supplementary Fig. S8D).

Discussion

This study first used fNIRS-based hyperscanning to directly compare creative-specific hyper-brain neural couplings between the high-creative and low-creative groups, portrayed what a high-creative group dynamic looked like, and revealed a hyper-brain neural coupling profile that distinguished high-creative group dynamics. Although the HCG and LCG showed similarities in creativity potential and perspective-taking tendency in the pre-tests, the HCG exhibited higher creative performance, collective flexibility and delayed perspective-taking behaviors, but lower immediate perspective-taking behaviors than the LCG. Moreover, results showed that the IBS of lIFG-rMotor and nodal E_{loc} of the rSTG were higher in the HCG than in the LCG, and positively correlated with group creative performance and collective flexibility, but negatively correlated with immediate perspective-taking behaviors. However, the intrapersonal Fc of rSTG-rAG and IBS of lIFG-rAG were lower in the HCG than in the LCG, and negatively correlated with group creative performance and collective flexibility, but positively correlated with immediate perspective-taking behaviors. A leave-one-out cross-validation analysis further showed these neural couplings can reliably predict group creative performance within the sample.

Specifically, while the HCG and LCG showed similarities in creativity potential and perspective-taking tendency in the pre-tests, the HCG exhibited higher creative performance than the low-creative group. This indicated that the observed difference was attributed to group creative dynamics rather than static group creativity. The HCG also showed higher collective flexibility and

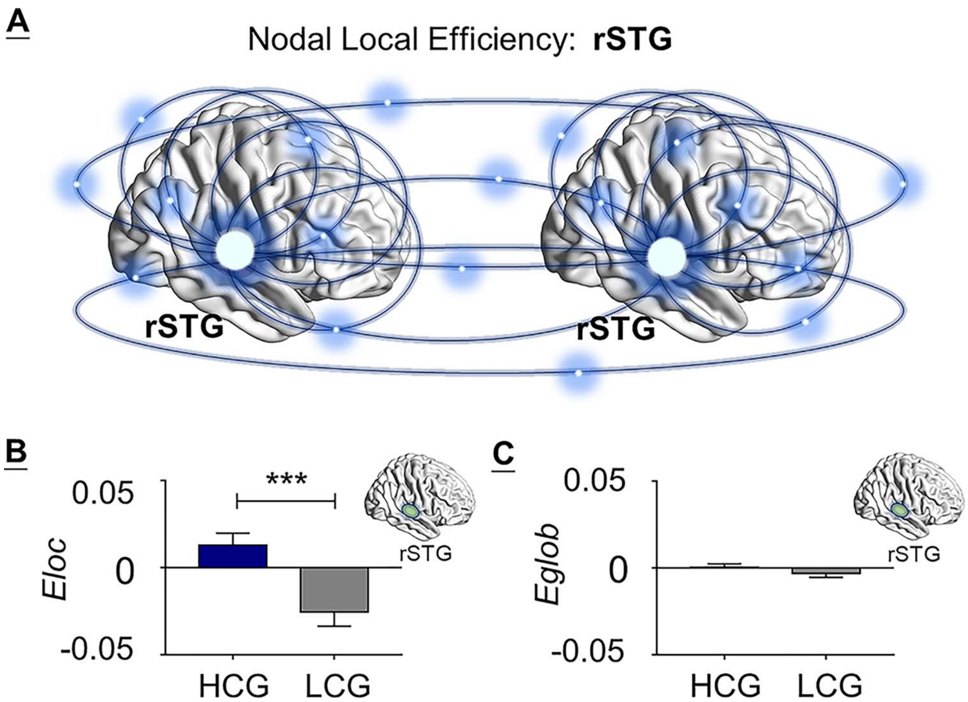

Fig. 4. Hyper-brain network parameters. A) The hyper-brain network. Note that the figure was merely generated to conceptually visualize the hyper-brain network which consists of intrapersonal Fc and IBS. Except for the location of the right superior temporal gyrus (rSTG), it has no statistical meaning. B/C) The amplitudes of the nodal E_{loc} (local efficiency)/E_{glob} (global efficiency) at the rSTG. Error bars indicate standard errors of the mean. $^{***}P_{\text{uncorrected}} < 0.01$.

delayed perspective-taking behaviors, but lower immediate perspective-taking behaviors than the LCG. Hypothesis I was supported. This reflected that apparent different strategies in perspective-taking behaviors was employed by the HCG and LCG. Individuals in the HCG not only strived to generate ideas upon their own and kept the idea generation flow, but also utilized the partners' ideas (maybe especially when they temporally encountered idea exhaustion). However, although those in the LCG also strived to generate ideas, they tended to block their own idea generation flow and jump into collaborative idea convergence. Research showed that alternating solitary and group ideation was more effective than both group ideation and solitary ideation (Korde and Paulus 2017). It seemed that the HCG carried out a similar "alternating solitary and group ideation" strategy, alternating "generating their own ideas" (solitary ideation) and "utilizing partners' ideas" (group ideation). Such a strategy may assure the smooth flow of idea sharing, the occurrence of necessary collaborative idea convergence, and eventually a high-creative group dynamic. Moreover, research showed that presenting examples in the later task stage could stimulate higher individual creative performance than presenting them in the early task stage (Yuan et al. 2021). This might be explained by the idea exhaustion after thinking about the task for a period of time (Yuan et al. 2022), and idea exhaustion may augment the beneficial effects of examples (or cognitive stimulation) on creative thinking. In this case, the delayed perspective-taking strategy by the HCG seems more appropriate. This may also offer some implications to improve the low-creative group dynamics: (i) keep on sharing ideas that have already come to your mind; (ii) attending to your partners' shared information at the same time; and (iii) utilizing your partners' shared information without a hesitation when you temporally encounter exhaustion.

The HCG showed a significant decrease in intrapersonal Fc between the rSTG and rAG (rSTG-rAG) in comparison to the LCG. Hypothesis (II) was not supported. Deactivation of the rAG is critical for efficient automatic retrieval of semantic information (Davey et al. 2015), and divergent thinking (Pick and Lavidor 2019). The rAG also serves as a core hub of the default network, which involves the automatic generation of candidate responses during creative thinking (Beaty et al. 2016). Meanwhile, the rSTG is responsible for selectively accessing and integrating conceptual representations (Shen et al. 2017). Accordingly, the decrease in intrapersonal Fc between the rSTG and rAG might reflect the selection and integration processes over the automatically generated candidate responses, which may help stimulate the novelty of the generated responses. This can be supported by the negative correlation between the group creative performance and Fc of rSTG-rAG. Moreover, previous research used the innovative neurofeedback training (NFT) procedure to enhance alpha and beta EEG oscillations over the right parietal region (Agnoli et al. 2018). Increases in both AUT originality and fluency emerged as a consequence of the rapid beta NFT (especially for individuals with a low level of creative achievement). Such a beta activity over the parietal region is associated

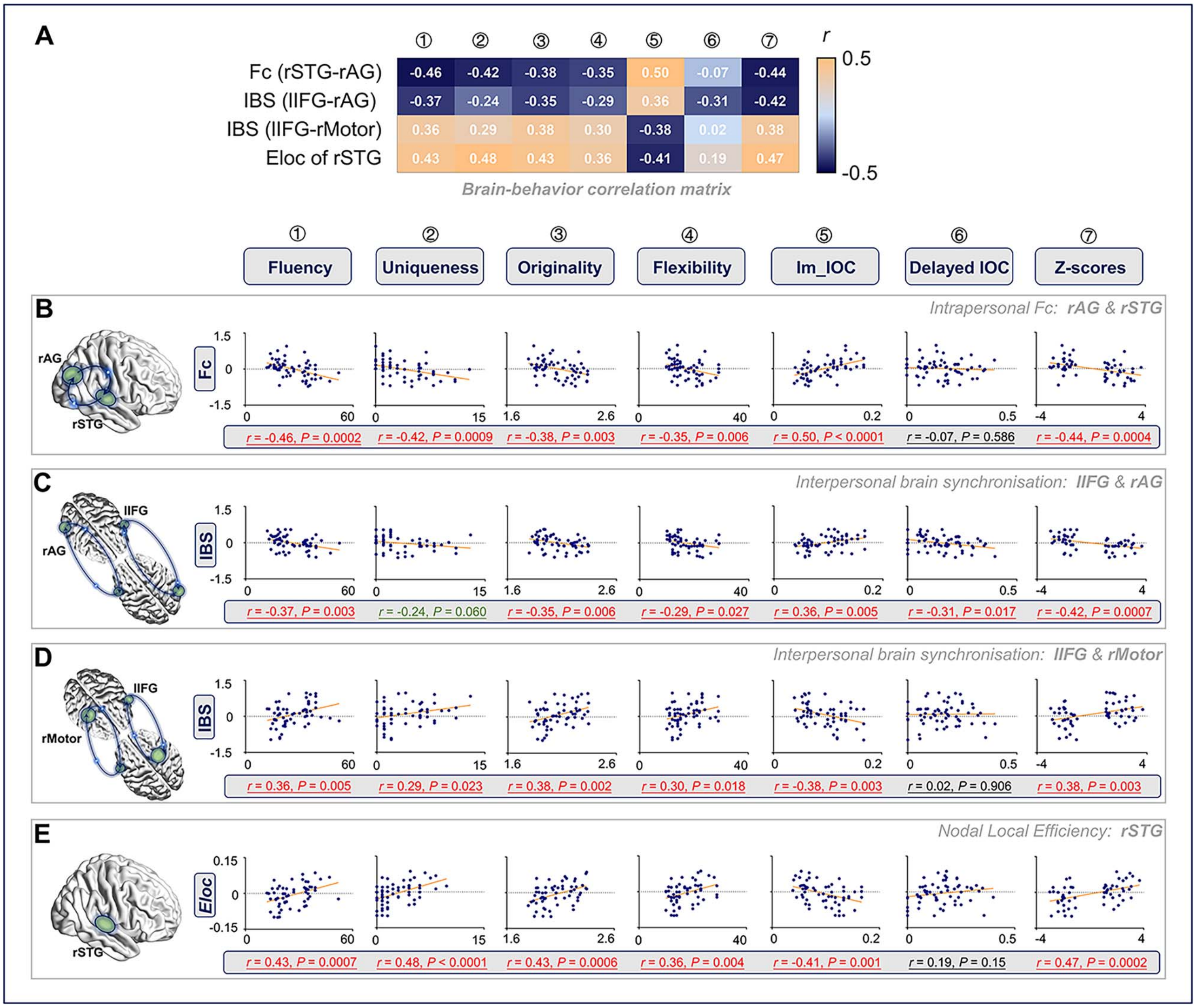

Fig. 5. Brain-behavior correlations. A) The brain-behavior correlation matrix. B) The correlations between the intrapersonal Fc of rSTG-rAG and behavioral performance. C/D) The correlations between the IBS of lIFG-rAG/lIFG-rMotor and behavioral performance. E) The correlations between the E_{loc} of rSTG and behavioral performance. The presenting P-values were uncorrected. The red/green fonts denote the correlation survived/marginally survived the false discovery rate correction. lIFG, left inferior frontal gyrus; rSTG, right superior temporal gyrus; rAG, right angular gyrus; rMotor, right motor cortex; Z-scores, the composite standard Z-scores of idea fluency and originality; Im_IOC, immediate IOC. Note that scatter plots in each column have the identical X-axis name which is presented above the column (e.g. fluency). Additionally, the Y-axis intervals were equal across plots in each row.

with enhancement in attentiveness and binding capacity (Bhattacharya and Petsche 2005; Razumnikova 2007). The rAG is also strongly associated with social cognition such as perspective taking and theory of mind (Santiesteban et al. 2015; Schurz et al. 2017; Filmer et al. 2019). In this case, such a decrease might also reflect that individuals in the HCG orderly alternated processing/integrating self-generating ideas and taking partners' perspective into consideration. However, those in the LCG might tend to parallel these two processes and block their own idea generation flow. This can be supported by the finding of higher immediate IOC in the LCG than in the HCG, as well as the negative/positive correlation between the group creative performance/immediate IOC and Fc of rSTG-rAG.

Moreover, the LCG showed a significant increase in IBS of lIFG-rAG in comparison with the HCG. The work by Chrysikou et al. (2018) reviewed evidence from developmental and cognitive neuroscience studies, and highlighted the importance of hypofrontality for certain aspects during creative thinking such as accessing bottom-up input, and iterative switching between controlled and spontaneous processes. The lIFG involves inhibiting pre-potent response and exerting top-down control over imaginative processes (Rae et al. 2014; Beaty et al. 2015). Research showed that reducing lIFG activity and enhancing rIFG reduces cognitive control, thus allowing for more creative idea production (Mayseless and Shamay-Tsoory 2015). The activation of the lIFG is associated with evaluating the idea originality, and inhibiting the left IFG can slack idea evaluation and increase idea originality (Kleinmintz et al. 2018). The 2-fold model of creativity also emphasized the important role of lIFG in evaluating idea originality (Kleinmintz et al. 2019). Relying on this, the relative increase in the IBS of lIFG-rAG (in the LCG) might reflect that individuals in the LCG were more strictly evaluating partners' shared ideas during perspective-taking process than those in the HCG. Such a strict evaluation process might impair group creative performance. This can also be supported by the observed negative correlation between the group creative performance and IBS of lIFG-rAG. Alternatively, such an IBS increase might reflect that individuals in the LCG allocated more resources to idea evaluation. Given they carried out an immediate perspective-taking strategy, they certainly devoted more efforts (in comparison to the HCG) to timely evaluate partners' shared ideas so that they could timely determine which ideas to combine or improve. This can also be supported by the observed positive correlation between the immediate IOC and IBS of lIFG-rAG.

In addition, the HCG showed a significant increase in IBS of lIFG-rMotor in comparison with the LCG, which covaried with group creative performance, but negatively correlated with immediate IOC. The lIFG not only involves in both production and comprehension of speech (Silbert et al. 2014), but also serves as a vital hub of the "mirror neuron system" which also includes the rMotor (Iacoboni and Dapretto 2006). The mirror neuron system subserves social interaction such as understanding others' actions and intentions (Iacoboni and Dapretto 2006). When generating alternative uses for the target object, individuals usually need to represent this object (construct an image) and operate it in their mind. We suggest that such an IBS increase (in the HCG) might reflect when individuals in the HCG were considering partners' ideas, they imitated the object operation according to the shared ideas from partners in their own mind.

Strikingly, the hyper-brain network analysis showed that the nodal E_{loc} of rSTG, which was suggested as a part of the mirror region system (Iacoboni et al. 1999), was significantly higher in the HCG than in the LCG, and covariated with group creative performance but negatively correlated with immediate IOC. The experiment by Silbert et al. (2014) observed comprehension-production coupling at the rSTG. Also, as abovementioned, the rSTG is responsible for selectively accessing and integrating conceptual representations (Shen et al. 2017). Accordingly, we suggest that the rSTG might be responsible for not only information comprehension, but also selectively accessing and integrating information from self-generating idea flow and shared ideas from partners during high-creative group dynamics. However, the precise meaning behind this finding should be further examined.

Previous hyperscanning research on group creativity emphasized the importance of interpersonal neural couplings at cortical structures such as DLPFC and AG to group creation (Xue et al. 2018; Lu et al. 2019; Mayseless et al. 2019). The present findings showed no group difference in neural coupling associated with DLPFC. This may indicate that the neural responses at the DLPFC do not differ much between the HCG and LCG. Nevertheless, we observed significant disparity in rAG-related neural couplings between the HCG and LCG, which confirmed the importance of rAG to group creation. Moreover, the findings further extend the previous findings by showing that the functional dissociation between the rAG and regions such as lIFG, rSTG underlies the high-creative group dynamics.

In addition, from the network-based perspective, the hyper-brain network emerging during the group creative process involves the interplay between regions from multiple networks (i.e. executive control network, default network, and mirror neuron network). Based on the findings, the neural couplings that underlie high-creative group dynamics seems to involve three facets: (i) enhanced neural couplings between regions within the executive control system and areas associated with mirror neuron network (an increase in IBS of lIFG-rMotor), (ii) the functional dissociation between the default network and mirror neuron system (i.e. a decrease in Fc of rAG-rSTG and IBS of lIFG-rAG), and (iii) increased nodal E_{loc} of rSTG in the hyper-brain network.

Several limitations should be noted in the present study. First, due to the device limitation, fNIRS merely covered the bilateral prefrontal cortex and right temporal and parietal areas and left the other cortical regions unexplored. Second, fNIRS cannot sense neural responses occurring in the subcortical structures. These two limitations suggest that the present findings were just a tip of the iceberg of the hyper-brain neural substrates that underlie the high-creative group dynamics. Future studies can adopt optode probes with larger coverage or even incorporate multimodal neuroimaging devices such as fNIRS, EEG, and fMRI to unveil the underlying neural substrates of high-creative group dynamics.

In summary, this study found that a high-creative group dynamic is characterized by two facets: (i) members keep on sharing ideas that have already come to their mind, and attend to partners' shared information at the same time; (ii) members utilize partners' shared information when temporally encounter exhaustion (or when necessary) rather than block their own idea generating flow as soon as partners shared an idea. This study also identified a neural coupling profile associated with high-creative group dynamics comprised of interplays between regions from various brain networks such as executive control, mirror neuron, and default networks (i.e. lIFG, rAG, rSTG, and rMotor). Cross-validation analysis showed these neural couplings reliably predicted group creative performance within the sample. These findings enrich the field of creativity by not only confirming the importance of "the interplays of the executive control network and default network" to creativity (Beaty et al. 2018), but also extending previous findings by emphasizing the importance of mirror neuron network in-group creative dynamics.

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Supplementary material

Supplementary material is available at *Cerebral Cortex* Journal online.

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Author contributions

K.L., Z.G., X.W., and N.H. conceived of the project and designed the experiments. K.L., Z. Gao., X.W., Y.H., X.Q., and Y.Z. implemented the experiment and collected data. K. Lu., Z. Gao., X.W., and X.Q. pre-processed the data, performed analyses, and discussed results. K.L., Z.G., X.W., and N.H. wrote the paper.

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