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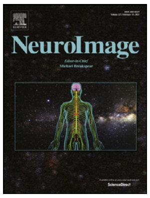

Connectome-based evidence for creative thinking as an emergent property of ordinary cognitive operations

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ABSTRACT

Creative thinking is a hallmark of human cognition, which enables us to generate novel and useful ideas. Nevertheless, its emergence within the macro-scale neurocognitive circuitry remains largely unknown. Using resting-state fMRI data from two large population samples (SWU: $n = 931$; HCP: $n = 1001$) and a novel "travelling pattern prediction analysis", here we identified the modularized functional connectivity patterns linked to creative thinking ability, which concurrently explained individual variability across ordinary cognitive abilities such as episodic memory, working memory and relational processing. Further interrogation of this neural pattern with graph theoretical tools revealed both hub-like brain structures and globally-efficient information transfer paths that together may facilitate higher creative thinking ability through the convergence of distinct cognitive operations. Collectively, our results provide reliable evidence for the hypothesized emergence of creative thinking from core cognitive components through neural integration, and thus allude to a significant theoretical advancement in the study of creativity.

1. Introduction

Creativity can be defined as our ability to generate novel and useful ideas (Beaty et al., 2016). Enabling an unprecedented capacity for problem solving and innovation (Sternberg, 1999), this foundational skill is suggested to constitute a vital component of the adaptive success of our species. In addition to lying at the roots of extraordinary achievements in literature and arts such as poetry composition and musical improvisation, creative thinking enhances productivity by promoting advancements in industrial design and scientific research (Kaufman and Sternberg, 2010). Relying on a complex interaction of biology and environment, emerging findings now highlight the brain-based underpinnings of creative cognition and its central importance in healthy mentation (Jauk, 2019; Khalil et al., 2019). Nevertheless, neural mechanisms that give rise to creative cognition remains a matter of debate, requiring further investigation.

Although creative thinking is distinguishable from ordinary cognitive processes, recent perspectives argue that it does not rely on any special cognitive process, but can rather be viewed as an emergent property that arises from the interaction of a set of ordinary cognitive processes (Abraham and Windmann, 2007; Benedek and Fink, 2019; Ward and Finke, 1995). In line with this view, numerous behavioral studies have now reported that higher-quality creative thought can be attributed to higher performance in cognitive operations such as memory-based processing (e.g., semantic retrieval and association) (Gray et al., 2019; Kenett et al., 2018a), cognitive control (e.g., working memory, inhibition, and cognitive flexibility) (Benedek et al., 2014; Dreu et al., 2011; Dygert and Jarosz, 2020), attention (e.g., focused and flexible attention) (Nusbaum and Silvia, 2011; Zabelina and Robinson, 2010), mental imagery (e,g., mental simulation of perceptual or motor states) (LeBoutillier and Marks, 2003) and reasoning (e.g., analogical reasoning) (Green et al., 2012). Together, this evidence suggests that creative thinking requires the combined function of multiple cognitive processes.

At the neural level, converging evidence from neuroimaging studies illustrate that neural activities in creative thinking are widely distributed across the human brain from unimodal to transmodal areas in

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charge of different cognitive processes (Chen et al., 2020). For example, the brain areas that generally contribute to creative thinking include the supplementary motor area, which may be attributed to the internally-driven free selection of motor sequences, mental imagination, and motor planning; the left dorsolateral prefrontal cortex, which may help maintain and integrate goal-relevant information, as well as other central executive functions such as flexible attention and selection; the angular gyrus, which may allow for the retrieval and integration of information from episodic and semantic memory that are relevant for creative thinking (Chen et al., 2020; Gonen-Yaacovi et al., 2013; Kleibeuker et al., 2016; Wu et al., 2015). Collectively, these brain-based findings allude to the interactive engagement of distinct brain regions with dissociable functions in order to support creative thinking.

The latest perspectives from cognitive neuroscience now suggest that the cognitive processes, supported by specific functional interactions amongst distinct large-scale brain networks, are of vital importance to the emergence of creative thinking (Beaty et al., 2019). Particularly, both task-based and resting-state functional magnetic resonance imaging (fMRI) studies have revealed that enhanced coupling between the default mode and the frontoparietal control networks, comprise a prominent feature of the neural mechanism behind creative thinking (Beaty et al., 2016). Their cooperation may simultaneously support the goal-directed memory retrieval (Madore et al., 2019) and prepotent-response inhibition (Beaty et al., 2017) during the course of creative thinking. In parallel, recent evidence additionally indicate that enhanced integration abilities of distinct brain areas that support sensorimotor processing can also facilitate creative thinking ability (Kenett et al., 2018b). Collectively, these findings suggest that specific functional integration amongst large-scale brain networks may constitute a vital component of our capacity to think in a creative manner. However, how neural integration facilitates the convergence between creative thinking and different cognitive processes remains largely unexplored. Specifically, the set of cognitive units that give rise to high versus low creative thinking ability and their neural instantiations within the topological organization of the intrinsic large-scale brain network interactions have not been previously investigated.

With the aim of addressing this question, we first identified the whole-brain pattern for high versus low creative thinking ability, by linking individuals' creative thinking ability with resting-state functional connectivity (rs-FC) data, through the stability-based feature importance identification (Rondina et al., 2013) in a large sample (n = 931). Creative thinking ability was measured by three divergent thinking tasks that collectively provided valid indicators of real-world creative achievements (Jauk et al., 2014). Next, the identified brain patterns were transferred to the HCP dataset, in which participants were extensively profiled for various ordinary cognitive abilities. Then, a prediction analysis was carried out in order to test the predictive powers of creativity-related neural representation in explaining individual differences across different cognitive abilities. Furthermore, to examine whether the highly creative brain is topologically constructed in a manner that could support information processing across multiple cognitive processes, graph theoretical tools (Guimera and Amaral, 2005) along with a meta-analytic decoding approach (Poldrack et al., 2012) were employed to detect the cognition-specific hubs of the creativity-related brain pattern. Finally, given the theoretical assumptions highlighting the importance of functional integration underlying creative thinking, we also examined the information transfer efficiency (Latora and Marchiori, 2001) based on the wiring rules of this pattern, in order to assess whether highly creative brains possess greater capacity for globally-efficient communication across functional networks. The results of this study not only describe the neural profile associated with creative thinking in relation to multiple cognitive processes, but also provide a mechanistic explanation to creativity as an emergent property from the interactions of different cognitive processes, that could contribute to a crucial theoretical advancement.

2. Methods and materials

2.1. Datasets

2.1.1. Southwest University (SWU) healthy young adult sample

The main SWU sample employed in our study consists of data from two independent research projects, namely the Southwest University Longitudinal Imaging Multimodal (SLIM) project and Gene-Brain-Behavior (GBB) project. With the aim of testing the validity and reliability of our findings, we additionally utilized data from an independent SWU validation sample. All research projects were approved by the Southwest University Brain Imaging Center Institutional Review Board and written informed consent was obtained from each participant in accordance with the relevant guidelines and regulations outlined in the Declaration of Helsinki. The recruitment program and exclusion criteria are detailed in our previous publications (Chen et al., 2019; Liu et al., 2017).

All neuroimaging data for the above-mentioned projects were collected at the Southwest University Brain Imaging Center with a 3.0-T Siemens Trio MRI scanner (Siemens Medical, Erlangen, Germany), using an eight channel phased array head coil. While the high-resolution 3D T1-weighted structural images were obtained using a Magnetization Prepared Rapid Acquisition Gradient-echo (MPRAGE) sequence (TR/ TE = 1900 ms/ 2.52 ms, FA = 9°, FOV= 256 × 256 mm^2; slices = 176; thickness = 1.0 mm; voxel size = 1 × 1 × 1 mm^3), the resting-state fMRI images were acquired using a Gradient-echo Echo Planar Imaging (GRE-EPI) sequence (TR/ TE = 2000 ms/ 30 ms, FA = 90°, resolution matrix = 64 × 64, FOV = 220 × 220 mm^2, thickness = 3 mm, slices = 32, acquisition voxel size = 3.4 × 3.4 × 4 mm^3, volumes = 242). In the SLIM and GBB projects, participants were instructed to close their eyes and refrain from falling asleep for the duration of the resting-state scanning, whereas participants in the SWU validation sample were instructed to rest with their eyes open, fixating on a crosshair.

Following the exclusion of participants with missing demographic information (e.g., name, gender, and serial number) across different assessments and tasks, abnormal structural images (e.g., enlarged ventricles), poor functional imaging signal intensity, and excessive head motion, we preserved data from 916 participants in SLIM, 764 participants in GBB, and 108 participants in the SWU validation sample. The cohort of 931 participants in the SLIM and GBB projects who fully completed all tasks related to creative thinking ability was labeled as the main SWU sample. The average age for this group was 20.10 years (range = 17 - 27, SD = 1.28) with a 328/603 male to female ratio. The average age for the 108 participants in the SWU validation sample was 20.29 years (range = 18 - 24, SD = 0.75) with a 39/69 male to female ratio.

2.1.2. Human connectome project (HCP) healthy young adult sample

The behavioral assessments and minimally-preprocessed neuroimaging data from the HCP S1200 release was used in this study (Van Essen et al., 2013). Detailed information about this sample is provided in the 1200 Subjects Data Release Reference Manual, which can be found at (https://www.humanconnectome.org/). Briefly, in the HCP sample all imaging data was collected on a customized Siemens Skyra scanner, using a standard 32-channel Siemens receive head coil. Two separate averages of the T1-weighted structural images were acquired using a 3D MPRAGE sequence (TR/ TE = 2400 ms/ 2.14 ms, FA = 8°, FOV= 222 × 224 mm^2; slices = 176; thickness = 0.7 mm; voxel size = 0.7 × 0.7 × 0.7 mm^3). In addition, each participant was scanned during two resting-state fMRI sessions (REST1 & REST2) on two separate days using a GRE-EPI sequence. For each session, there were two separate 14 min 34 s acquisitions in left-to-right (LR) and right-to-left (RL) phase-encoding directions (volumes = 1200, TR/ TE = 720 ms/ 33.1 ms, FA = 52°, resolution matrix = 104 × 90, FOV= 208 × 180 mm^2, thickness = 2 mm, slices = 72, acquisition voxel size = 2 × 2 × 2 mm^3). During the resting-state fMRI sessions, participants were instructed to lie with their eyes open, fixating on a crosshair. In order to achieve consistency with the SWU sample, only the LR runs from both days were utilized in this study. Detailed information on the HCP resting-state fMRI data can be found in the work of Smith et al. (2013). Finally, we employed the maximum number of available data ($n = 1001$) for each of the HCP behavioral measures. The average age for this group was 28.72 years (range = 22 - 37, SD = 3.71) with a 464/ 537 male to female ratio.

2.2. Behavioral tasks

2.2.1. Assessment of creative thinking ability

In this study, individuals creative thinking ability (CTA) was assessed by a set of divergent thinking tasks. Divergent thinking, also known as cognitive creative potential, is widely acknowledged as the key component of creative thinking (Jauk, 2019; Runco and Acar, 2012), and has been regarded as a valid indicator of real-world creative achievements (Jauk et al., 2014). Compared to other aspects of cognitive abilities which are commonly assessed by close-ended problems that always have correct solutions, the divergent thinking task requires participants to generate unusual but meaningful solutions to open-ended questions. In order to obtain generalizable results, we employed three separate divergent thinking tasks that quantified individual differences in creative thinking ability: (1) alternative uses task (AUT), (2) product improvement task (PIT) and (3) figural creativity task (FCT). In the AUT task (2 items, 6 min), subjects were instructed to list as many interesting and unusual uses for objects (can and brick) as possible (Sun et al., 2016). In the PIT task (1 items, 10 min), subjects were instructed to write down as many ideas as possible to improve an elephant toy in order to make it more enjoyable and appealing (Chen et al., 2016). In the FCT task (10 items, 10 min), subjects were instructed to draw up as many uncommon but meaningful sketches as possible on the basis of incomplete figures (Ye and Hong, 1988). All these 3 tasks were carried out via paper and pencil, and participants' responses were assessed by 4 trained raters with a uniform rating manual. More detailed information can be seen in our previous work (Chen et al., 2019). For each test, responses were scored into dimensions of fluency and originality. The former is defined as the number of meaningful and relevant responses, and the latter is defined as the degree of uncommonness for each idea. Given that the assessment process was conducted separately by different raters in SLIM, GBB and the supplementary SWU sample, here, we transformed the scores in every dimension of each test into Z scores within each sample. This aimed to prevent a systematic assessment bias across raters and projects. Finally, we took the weighted mean of originality and fluency from the above 3 tasks as the representative index of individual's creative thinking ability.

2.2.2. Assessment of ordinary cognitive abilities

Participants in the HCP sample underwent various behavioral tests that were part of the NIH Toolbox battery as well as several Non-NIH Toolbox behavioral assessments. In order to unravel neural representations that link creative thinking ability to different ordinary cognitive process, we primarily focused on 13 cognitive factors highlighted in the HCP data dictionary and five extra cognitive factors from the task-based fMRI data (18 in total). The assessments of these cognitive factors include: Episodic Memory; Cognitive Flexibility; Inhibition; Fluid Intelligence; Reading Decoding; Vocabulary Comprehension; Processing Speed; Self-regulation/Impulsivity; Spatial Orientation; Sustained Attention (Sensitivity); Sustained Attention (Specificity); Verbal Episodic Memory; Working Memory; Language Task (Average Difficulty Level in Story Condition); Language Task (Average Difficulty Level in Math Condition); Relational Task Accuracy (Match Blocks); Relational Task Accuracy (Relational Blocks); Working Memory Task Accuracy (2-back). However, with the aim of testing whether the detected correlations were specific to cognitive factors, we also included 24 non-cognitive factors from the HCP data dictionary. Specifically, these belong to the categories of "Alertness", "Emotion", and "Personality". A complete list of the above-mentioned behavioral measures is provided in the Supplementary Table 1. More detailed information related to these measures can be found in the HCP Wiki page (https://wiki.humanconnectome.org/).

2.3. Data preprocessing

2.3.1. RS-fMRI data preprocessing

Neuroimaging data from different samples (SWU and HCP samples) were preprocessed independently. The main and validation SWU samples were preprocessed using the Data Processing & Analysis of Brain Imaging toolbox (DPABI; Version 3.1) (Yan et al., 2016) and Statistical Parametric Mapping (SPM; Version 8.0) software package, based on the MATLAB platform (Version 18a). First 10 functional volumes were discarded to suppress equilibration effects. Remaining 232 vol. were corrected for slice-timing via sinc interpolation and adjusted for head motion using rigid-body transformation with 6 degrees of freedom (3 translations and 3 rotations). Data from participants whose mean frame-wise displacement was greater than 0.2 mm was excluded from further processing (Jenkinson et al., 2002). The functional volumes were then spatially normalized to the Montreal Neurological Institute (MNI) coordinate space using the unified segmentation-normalization approach (Ashburner and Friston, 2005). Here, the temporal signal-to-noise ratio (tSNR) was calculated as the voxel-wise mean of the MRI signal over time divided by the standard deviation of the time series. Participants with mean tSNR under 2 standard deviations were excluded from further analysis. We subsequently applied the Friston 24-parameter model (Friston et al., 1996) to regress out head motion effects from the realigned data (6 motion parameters, 6 temporal derivatives, and their squares) based on recent findings highlighting that higher-order models demonstrate additional benefits in removing head motion-related artifacts (Yan et al., 2013). Next, the cerebrospinal fluid signal and white matter signal was regressed out to reduce respiratory and cardiac effects. Moreover, given latest reports which indicate that global signal regression can spuriously increase the association between functional connectivity and behavior (Li et al., 2019), the whole brain signal was also regressed out. The nuisance regressors also included linear and quadratic trends to remove low-frequency drifts. Finally, bandpass filtering (0.01–0.1 Hz) and spatial smoothing (4 mm full width at half maximum in each direction) were performed.

For the HCP sample, we utilized the minimally-preprocessed neuroimaging data using the C-PAC pipeline. Detailed information on the minimal-preprocessing steps can be found in the work of Glasser et al. (2013) and 1200 Subjects Data Release Reference Manual. To ensure relatively consistent preprocessing procedures between the HCP and SWU datasets, several additional steps were subsequently carried out in the following order: (i) regression of nuisance covariates; (ii) bandpass filtering; (iii) spatial smoothing. All parameters for the above-mentioned procedures were consistent with other datasets we used in this study.

2.3.2. Functional network construction

For both datasets, functional connectivity matrices were constructed using the GRETNA toolbox (Wang et al., 2015). First, the automated anatomical labeling (AAL) template (Tzourio-Mazoyer et al., 2002) was randomly parcellated into 1024 regions with equal volume size (AAL-1024 template) using the method developed by Zalesky et al. (2010). Next, these 1024 ROIs were used as nodes from which to extract average BOLD time series. For each participant, Pearson correlations were calculated between the time series of all nodes included in the parcellation scheme. The correlation coefficients were then converted to Fisher's z-values, which characterized the edges in the functional connectivity matrix. We retained only positive correlations for further analysis. Note that, because HCP dataset includes two separate runs, the functional connectivity matrices from these two runs were averaged in order to obtain a mean connectivity matrix. Finally, covariates of sex, age as well as project membership (i.e. SLIM or GBB) were regressed out from

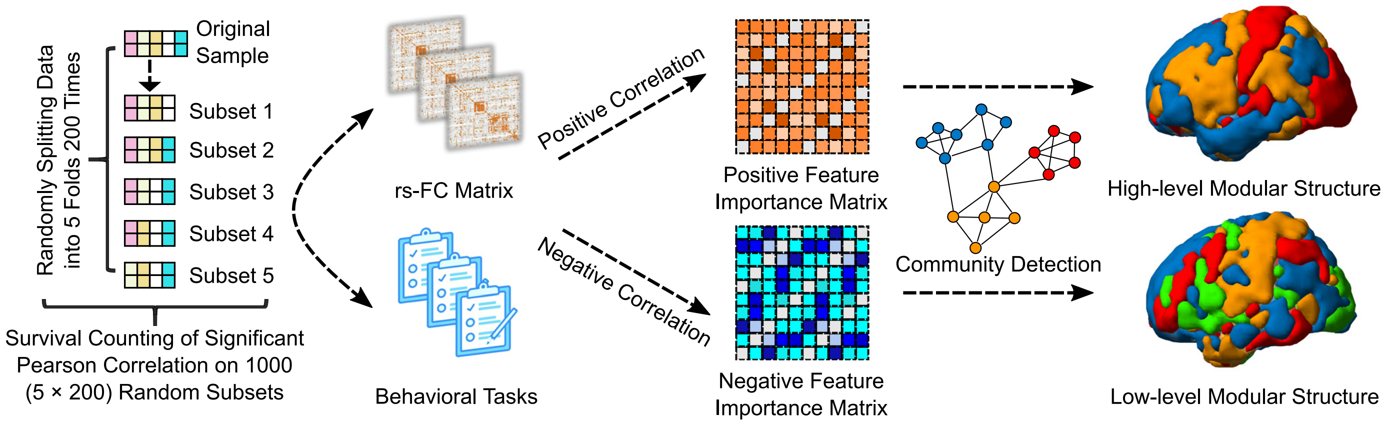

Fig. 1. Schematic diagram for the construction of whole-brain connectivity patterns related to creative thinking ability. In order to build robust relationships between rs-FC and creative thinking ability (CTA), a resampling strategy (survival counting on random subsamples) was applied to construct the CTA-related feature importance matrices. Given the correlation direction, the positive and negative feature importance matrices were identified as high and low-creative brain patterns. The edge value in these feature importance matrices range from 0 to 1, indicating the importance of a given rs-FC to high and low-creative brain patterns. Higher values in these matrices represented larger importance of a given rs-FC feature. In addition, to detect the global topological organization of both matrices, a Louvain algorithm was applied to decompose the matrices into distinct modules.

every participants' functional connectivity matrix. In addition, the 7-network parcellation from Yeo et al. (2011) was applied to label the ROIs according to their maximal spatial overlap (i.e. largest number of voxel-wise overlap) with known large-scale brain networks. The Yeo7-parcellation divides the cortex into seven specific functional networks: visual, somatomotor, dorsal attention, salience, ventral attention, limbic, frontoparietal control and default mode networks. Together with subcortical regions identified by the AAL template, we finally assigned all AAL-1024 regions into eight functional networks.

2.4. The construction of whole-brain connectivity patterns

The schematic diagram of whole-brain connectivity pattern construction can be seen in Fig. 1. In detail, to build robust brain patterns based on rs-FC data that were associated with creative thinking ability, a simplified stability-based feature importance identification approach (i.e. survival counting on random subsamples) (Rondina et al., 2013) was applied in the present study. First, we applied jackknife resampling to randomly group the original sample into five folds. This procedure was repeated 200 times, generating 1000 (5 × 200) subsets. Second, we calculated the Pearson correlation coefficient between each rs-FC (edge) and the composite divergent thinking score in every sample set and measured the number of times (n) a specific brain-behavior link survived at a given significance level. In line with our prior studies, here we set the significance level as $p < 0.005$ (Liu et al., 2018). The ratio of significant edges to number of permutations (n/1000) was then taken as the weight of a given edge, with values ranging from 0 to 1. Repeating this procedure across all edges generated two 1024 × 1024 matrices, in which edge values reflected the significance of a given edge's positive or negative relation to creative thinking ability. In other words, higher values in these matrices represented larger importance of a given feature, which were thus labeled as positive and negative feature importance matrices. These matrices constitute the high and low-creative brain patterns in this study. In addition, the feature importance matrices for different ordinary cognitive abilities were also built using the same procedure as mentioned above.

Moreover, with the aim of characterizing the topological organization of the identified patterns of creative thinking ability, we applied a Louvain-like greedy algorithm (Blondel et al., 2008; Jutla et al., 2011) that decomposed the two feature importance matrices of creative thinking ability into separate communities or modules. The Louvain community detection method aims to maximize the modularity index Q defined as (Fortunato, 2010; Porter et al., 2009):

$$Q = \frac{1}{2m}\sum_{ij}\left[A_{ij} - \gamma\frac{k_i k_j}{2m}\right]\delta\left(c_i c_j\right)$$

where A_{ij} means the edge weight between nodes i and j; k_i and k_j represent the sum of the edge weights attached to nodes i and j, separately; $2m$ mean the sum of all of the edge weights; c_i and c_j are the communities nodes are belong to; $\delta(c_i c_j)$ is equal to 1 if $c_i = c_j$, and is equal to 0 otherwise; γ is a structural resolution parameter, which can tune the relative number of modules (higher value leads to smaller modules).

In the initialization of Louvain-like locally greedy algorithm, there are N modules (N is the number of nodes in the graph), resulting in the modularity index $Q = 0$. The algorithm proceeds by iteratively assigning nodes to modules until no appreciable increases in index Q can be observed. Here, we set the structural resolution parameter γ to the default value 1. Given the stochastic nature of the modularity maximization algorithm, the performance of algorithm was repeated for 100 times, and then a single consensus partition from the agreement matrix was identified (Lancichinetti and Fortunato, 2012). The choice of γ was important to the present study, because it could directly tune the modular structure of the underlying organizational pattern of feature importance matrices of creative thinking. Here, we varied the γ within a range of 0.6 to 1.5 in increments of 0.01, in order to test the stability of community detection results across 100 repetition. We then applied the average of the variation of information (VI) (Meilă, 2007) between any pair of 100 community detection results to quantify the stability of the uncovered modules. The higher the VI value is, the lower the stability is. Let C and C' be two different partition of same nodes set, and $C = \{C_1, C_2, \ldots, C_k\}$, $C' = \{C'_1, C'_2, \ldots, C'_{k'}\}$. Meanwhile, the subsets in C and C' are mutually disjoint. Let the number of nodes in C and in subset C_k be n and n_k; in C' and in subset $C'_{k'}$ be n and $n_{k'}$. The entropy of C (or C') can be identified as:

$$H(C) = -\sum_{k=1}^{k}\frac{n_k}{n}\cdot\log\frac{n_k}{n}$$

The mutual information between C and C' can be identified as:

$$I\left(C, C'\right) = \sum_{k=1}^{k}\sum_{k'=1}^{k'}\frac{\left|C_k \cap C'_{k'}\right|}{n}\cdot\log\frac{\frac{\left|C_k \cap C'_{k'}\right|}{n}}{\frac{n_k}{n}\cdot\frac{n_{k'}}{n}}$$

Then, VI can be defined as:

$$VI\left(C, C'\right) = H(C) + H\left(C'\right) - 2I\left(C, C'\right)$$

After implementing the community detection for both high and low-creative brain patterns, the architectural differences in the module affiliations of these two brain patterns were visualized using alluvial plots as implemented in the ggalluvial package in R (https://cran.r-project.org/web/packages/ggalluvial/index.html).

2.5. The validation of whole-brain connectivity patterns

A machine learning framework was applied here to test the validation of whole-brain connectivity patterns underlying creative thinking ability. First, we conducted a feature extraction procedure for edges related to individual's creative thinking ability, that is, we took the feature importance matrices as "filters" to extract edges based on their values in the feature importance matrices of creative thinking ability. Specifically, every edge in the individual's original rs-FC matrix was separately multiplied by the corresponding edge value in the positive or negative feature importance matrices (feature extraction). After that, a feature reduction procedure was applied to the extracted edges. In detail, we first used the principal component analysis (PCA) to save 80% variations of features (extracted edges), then used an autoencoder to encode the reserved principal components into 10 dimensions. Note that, this feature reduction procedure was carried out separately within (or between) different modules. So, every module had the same dimension of features and a total number of 90 features were reserved for each pattern (40 for high-creative pattern; 50 for low-creative pattern). For internal validation, a ridge regression (Hoerl and Kennard, 1970) with 5-fold cross-validation (5F-CV) was applied in the main sample to test whether the extracted features could reliably predict the individuals' CTA scores. Ridge regression is a model that minimizes the sum of the squared prediction error in the training data and the sum of the squares of regression coefficients. This technique can shrink the regression coefficients β, resulting in better generalizability for predicting unseen samples. Its object function can be defined as:

$$\min_{\beta} \sum_{i=1}^{N} \left(f\left(x_i\right) - y_k \right)^2 + \lambda \sum_{j=1}^{P} \|\beta_j\|^2$$

were a regularization parameter λ is used to control the trade-off between the prediction error of the training data and L2-norm regularization. A large λ corresponds to more penalties on variance (Zou and Hastie, 2005). Within each loop of the outer 5F-CV, an inner 5F-CV was also added to determine the optimal parameter λ from [2^{-5}, 2^{-4},…2^{9}, 2^{10}] (Cui and Gong, 2018). For each loop, the mean absolute error (MAE) were generated for each λ value. The λ value with smallest MAE was then chosen as the optimal parameter. The statistical significance of the cross-validation procedure was assessed using permutation testing. Briefly, for each permutation, we randomized the behavior scores, and repeated the prediction processes to acquire the random prediction accuracy. An empirical cumulative distribution of the prediction accuracy was then obtained with 5000 permutations. Furthermore, a "lesioning" strategy was used to determine the predictive powers of different modules in explaining behavioral data. For each of the outer 5F-CV, we selectively omitted all features within (or between) different modules, observing to what a degree the predictive performances (Pearson correlation between true and predicted values) could be influenced by missing a given part of the feature set. Then, the difference of predictive performance between the complete and perturbed feature sets was identified as the predictive powers of omitted features. In addition, an external validation was carried to test the model's generalizability. That is, the prediction model as well as feature reduction parameters trained in the main SWU sample was applied to the SWU validation sample. Then, the model's generalizability was identified by the correlation strength between predicted and true values of creative thinking ability in the supplementary sample.

2.6. Travelling pattern prediction analysis

Next, in order to test the links between the neural correlates of creative thinking and multiple ordinary cognitive abilities, we employed a travelling pattern prediction analysis in which creativity-related brain patterns (i.e. the feature importance matrices) as well as the prediction models trained in the SWU sample were transferred to the HCP sample. A similar practice from a prior study indicated that even across two heterogeneous samples the prediction model built through the functional connectivity data can reliably reveal the intrinsic correlation between different cognitive measures (e.g., working memory and fluid intelligence) (Bertolero and Bassett, 2020). Specifically, first, the same feature extraction and reduction procedures in Section 2.5 were applied to extract the features related to creative thinking ability in the HCP rs-FC data. To distinguish the predictive performance of different modules in the creative brain patterns, the extracted rs-FC features were further divided into different parts according to their module affiliations. Second, for different modules, we separately built the ridge regression models to predict creative thinking ability in the SWU sample. Then, the same prediction models along with the same feature selection procedures were transferred to the HCP sample to test whether models built for predicting creative thinking ability could also significantly predict different aspects of cognitive abilities measured in the HCP sample. The predictive performance for different modules and cognitive factors were identified by the Pearson correlations between true values and predicted values. The multiple comparisons were corrected using the false discovery rate (FDR) with threshold at a p value of $p < 0.05$. Beyond that, although non-cognitive factors from the HCP data dictionary (e.g., measures of emotion and personality) were not the main focus of the present study, they were also included in the same analysis to test the specificity of relationships between creative thinking and ordinary cognitive abilities. Note that although the difference of scanning parameters between SWU and HCP samples could affect the consistency of resting-state fMRI data, our main objective here was to test the correlation between creative thinking and different ordinary cognitive abilities, through the traveling pattern prediction analysis. Thus, we assumed that if the neural representation of different psychological variables could be established with sufficient stability and validity, the intrinsic connections should be revealed even across heterogeneous samples (Bertolero and Bassett, 2020).

2.7. Decoding the cognitive relevance of hubs in the whole-brain connectivity patterns

Moreover, to identify the hubs of brain patterns related to creative thinking ability, the within-module degree z-score (Guimera and Amaral, 2005) was measured on the creativity-related brain patterns, which identified regional importance in a given module. The within-module degree z-score was defined as:

$$Z_i = \frac{k_i - \overline{k_{S_i}}}{\sigma_{K_{s_i}}}$$

where Z_i refers to the within-module degree z-score; k_i is the strength of the connections of region i to other regions in its affiliated module S_i; $\overline{k_{S_i}}$ is the average of k over all the regions in S_i; and $\sigma_{K_{s_i}}$ is the standard deviation of k in S_i. Regions with within-module degree z-score located on the right side of 1.5 median-absolute-deviation (MAD) were classified as hubs in a specific module and the remaining regions were classified as non-hubs. The regional importance map was visualized via BrainNet Viewer (Xia et al., 2013).

In order to determine the dominant cognitive abilities associated with creativity-linked brain patterns, we next used a topic-based meta-analytic decoding approach (Poldrack et al., 2012) through Neurosynth. In brief, for each module, we decoded hub regions' within-module degree z-score map by assessing their similarity to the reverse inference meta-analysis maps generated for various cognitive topics. Then, we rank-ordered the calculated similarities and selected topics with highest similarity value (top 10) as the dominant psychological feature for a specific module. Here, a 200-topic version (v4-topics-200) from the NeuroSynth repository was applied, and topics that were not explicitly related to psychological constructs were excluded. The identified topics are provided in Table S2. Detailed information on these topics can be found in http://neurosynth.org/analyses/topics/v4-topics-200/.

2.8. Identifying the information transfer efficiencies for whole-brain connectivity patterns

Moreover, we then attempted to examine whether the highly creative brain could support integration across different cognitive processes through the specific wiring rules embedded within its topological organization. For that purpose, we investigated the reciprocal of shortest path length, which assessed information transfer efficiency at the network level over functional connectivity paths marked by brain patterns linked to high versus low creative thinking ability. The pairwise information transfer efficiency E can be defined as $d(i,j)^{-1}$, where $d(i,j)$ denotes the normalized Euclidean distance (*ED*) between node i and j (Latora and Marchiori, 2001) in MNI space. Then, we summarized the pairwise information transfer efficiencies within or between different networks to obtain a network level representation of them. Meanwhile, to highlight the specificity of creative brain patterns, the other 18 brain patterns linked to different ordinary cognitive abilities were also included in the same analysis. In order to make different patterns comparable to each other under equivalent wiring cost, here, we first binarized all patterns across a series of thresholds (across 0.1–2% edge densities; [0.001: 0.001: 0.01]). The network level information transfer efficiencies of all the patterns were then calculated at every threshold. However, for network level comparison, the statistical analyses were carried out at a given threshold, whose network level metrics exhibited the highest average correlation to metrics at other thresholds.

Note that, in order to test whether different brain patterns displayed topological properties to a greater extent than expected by chance under the null hypothesis, different brain patterns were compared to 100 null models. The null models were generated by keeping the same numbers of nodes and edges while randomly distributing edge links.

2.9. Validation analysis

2.9.1. The validation for modular structure of creative brain patterns

The validation analysis was first carried out to the modular structure characteristics. We hypothesized that if the modular structure could offer valuable information independently, individuals whose functional network organization were maximally similar to the high-creative brain pattern, or dissimilar to the low-creative pattern may have higher level of creative thinking ability. Here, we applied VI index quantifying to what degree individual's modular structure feature is similar to the modular structure feature of high-creative pattern (VI_{pos}), and low-creative pattern (VI_{neg}). The higher the VI value is, the lower the similarity is. In addition, an aggregate indicator (VI_{neg}/VI_{pos}), the VI-based positive tendency coefficient (VI-PTC), was applied to make a comprehensive description of these two different trends. The higher the VI-PTC is, the more an individual's modular structure approaches to the high-creative pattern, and simultaneously diverges away from the low-creative pattern. The schematic diagram can be seen in Fig. S6a.

In addition, to further detect brain regions whose change of module affiliation affect creative thinking ability the most, a region level metric of modular variability (MV) (Steen et al., 2011) was applied to calculate the positive tendency coefficient (MV-PTC). For a given region k, we evaluated its module affiliation variability between an individual's modular structure X and CTA-related modular structure Y through a metric of modular variability (MV). The MV can be identified as:

$$MV_k = 1 - \frac{|X_k \cap Y_k|}{X_k} \cdot \frac{|X_k \cap Y_k|}{Y_k}$$

where $|X_k|$ and $|Y_k|$ denote the number of regions having the same module affiliation with region k (including k itself) in X and Y, respectively; $|X_k \cap Y_k|$ represents the number of regions in the common node set of X and Y. As such, a small overlap between X_k and Y_k is associated with a large module affiliation variability of region k.

2.9.2. The validation for feature importance matrix

Since the following analyses were largely based on the feature importance matrix, it was necessary to test whether this kind of brain representation could reliably build a relationship between the rs-FC data and different psychological variates. Moreover, given that the construction of the feature importance matrices required a priori threshold, it was reasonable to test whether the threshold used in this study ($p < 0.005$) was appropriate. Based on the above considerations, the HCP REST1 and REST2 data with psychological variates were employed here to carry out supplementary validation steps for the feature importance matrix. The reliability of patterns was tested in two different strategies: the prediction strategy (Rosenberg et al., 2016) and pattern identification strategy (Finn et al., 2015). The schematic diagram can be seen in Fig. S7a.

In detail, we first constructed the feature importance matrices underlying every psychological variate separately in HCP REST1 data and REST2 data to generate a pair of brain patterns (i.e., the feature importance matrixes). In the prediction strategy, through the feature extraction procedure mentioned in Section 2.4, we simply summed up reserved edge values to generate a single predicted value for each subject. Then the unitary linear regression model was built for each psychological variate separately in both scan sessions. Given the pattern types (positive & negative) and scan sessions (REST1 & REST2), for each psychological variate, there would be four linear regression models built. After that, we applied the models built in REST1 date to REST2 date, and vice versa, in order to test if these models could survive under the cross validation. The reliability of single pattern in this strategy was defined as the mean value of two (REST1 & REST2) correlation coefficients between predicted values and true values. The general reliability of all patterns was then defined as the average value of single pattern's reliability values. In the pattern identification strategy, we first performed the identification from REST1 data to REST2 data. That is, one pattern constructed in REST1 data was compared against each of the 42 patterns constructed in REST2 data to find its counterpart constructed by the same psychological variate. The similarity was defined as the Pearson correlation coefficient between edge values taken from the REST1 pattern and each of the REST2 patterns. For a single pattern (n-1), the identification effect was then quantified as its counterpart (n-2)'s percentile in the similarity ranking. For instance, if n-2 is maximally similar to n-1, the identification effect would be 1 (42/42). If n-2 is secondly similar to n-1, the identification effect would be 0.98 (41/42). The same process was then carried out from REST2 data to REST1 data. Similar to the prediction strategy, the reliability of single pattern was defined as the mean value of two (REST1 & REST2) identification effect values. The general reliability of all patterns was defined as the ratio of how many patterns can be fully identified (identification effect = 1). Note that, for both of these two strategies, the feature importance matrices were constructed under the thresholds from 0.05 to 0.0001 in increments of 0.05. Then the reliability of patterns was compared in different thresholds to find out the optimal threshold value.

2.10. Data and code availability

All analysis code used in this study is openly available on https://github.com/Zhuang2KX/MANA/tree/master/Project/CTA. Due to restrictions imposed by the administering institution, the SWU dataset is only available from the authors upon request. Sharing and reuse of this dataset require a formal data sharing agreement, as well as approval from the relevant Institutional Review Boards. The HCP

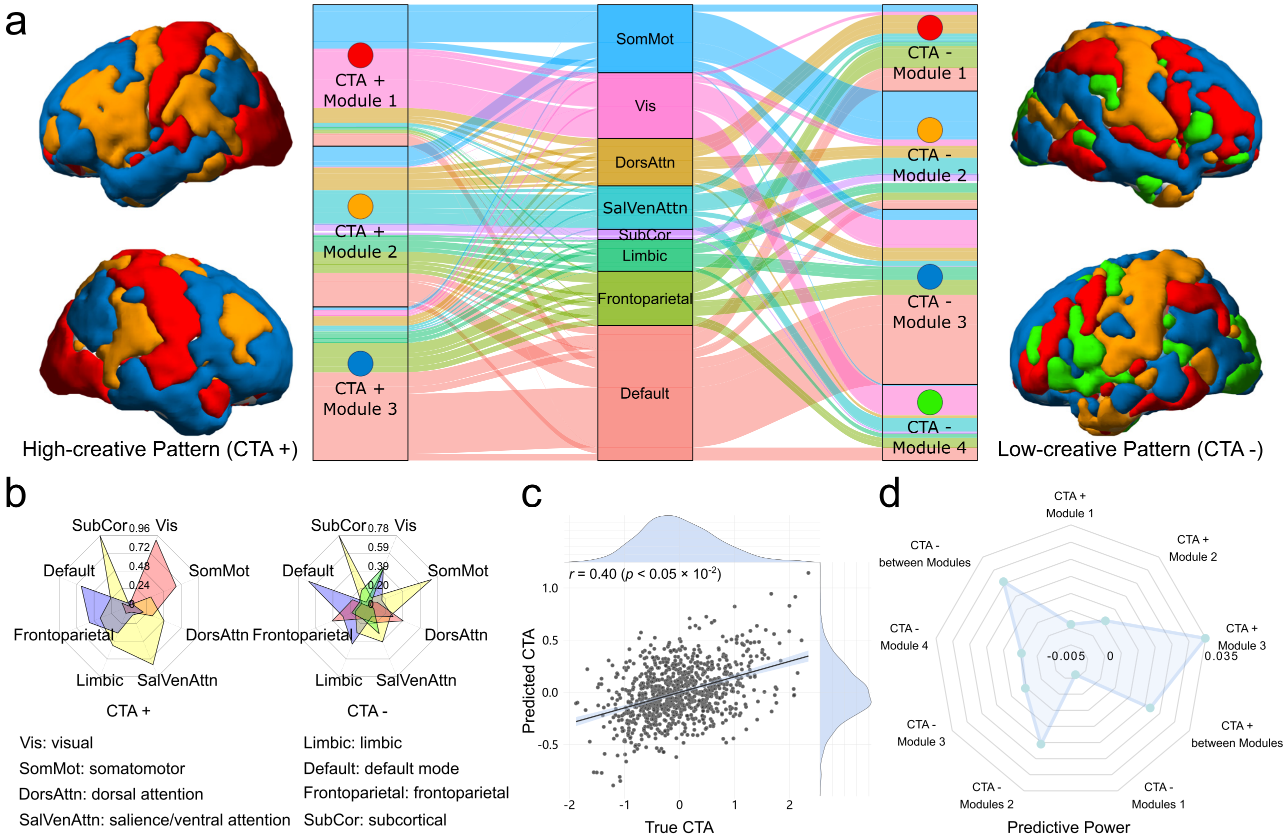

Fig. 2. Brain patterns associated with high versus low creative thinking ability. **(a)** The global topological organizations of high-creative (CTA+) and low-creative (CTA-) brain patterns. The areas of different colors indicate different modules in high versus low creative brain patterns, in which cortical areas are labeled based on the Yeo et al. 7-network parcellation scheme. Vis: visual network; SomMot: somatomotor network; DorsAttn: dorsal attention network; SalVenAttn: salience/ ventral attention network; Limbic: limbic network; frontoparietal: frontoparietal control network; Default: default mode network; SubCor: subcortical network. **(b)** The network affiliation of brain regions within specific modules across both high and low-creative brain patterns. The values of the radar plot indicate the proportion of modules in different networks. **(c)** The correlation between true CTA and predicted CTA scores in main SWU sample. **(d)** The predictive powers of rs-FC features identified through "lesioning" strategy across different modules. Module 1–4 indicate rs-FC features within different modules in high and low-creative brain patterns; inter-module indicates rs-FC features between different modules in these brain patterns.

Open Access Data is publicly available on the ConnectomeDB database (https://db.humanconnectome.org).

3. Results

3.1. Whole-brain connectivity patterns of creative thinking ability

Our initial aim was to deduce patterns of functional interactions amongst large-scale brain networks that were associated with high versus low creative thinking ability. Utilizing a feature importance representation approach based on resampling strategy, we built positive and negative rs-FC feature importance matrices to separately represent brain patterns associated with both high and low creative thinking ability (high-creative and low-creative brain patterns). Then following the community detection procedure, the global topological organizations of these patterns were characterized (Fig. 1). The high-creative brain pattern revealed three modules (Fig. 2a-left and Fig. 2b). The first module encompassed large parts of the visual and somatomotor networks, the regions of which are suggested to engage in the neural coding and transformation of perceptual and action-based modalities in the human brain (Sepulcre et al., 2012). The second module on the other hand, largely included the dorsal and ventral attention networks, limbic network as well as subcortical areas, which are critical for context-dependent attention (Farrant and Uddin, 2015; Kim, 2014). Finally, the third module combined parts of the default mode and frontoparietal control networks, whose regions together contribute to the memory-based cognitive processing (Murphy et al., 2018; Smallwood et al., 2012). In contrast, However, we found that this neural structure was perturbed in the low-creative brain pattern with decreased modularity (Fig. 2a-right and Fig. 2b). Notably, the integration across transmodal areas was largely broken down with a segregated topology that included modules across both transmodal and unimodal regions. For example, instead of forming a module with the somatomotor network, the visual network was functionally integrated with the default mode network. Supplementary analysis supported the robustness of these modular structures, that they remained stable across different structural resolution parameters (around $\gamma = 1$) in the community detection algorithm (Fig. S1).

To assess the validity of the identified brain patterns related to creative thinking ability across analytical procedures, the ridge regression with cross-validation procedures were carried out. The results supported the validity of the identified brain patterns (cross-validation in main SWU sample: $r = 0.40$, p (permutation test, $n = 5000$) $< 0.05 \times 10^{-2}$ (two-tails), 95% confidence interval (CI) = 0.35–0.46, Fig. 2c). In addition, the generalizability of the creativity-related brain patterns was also tested by an independent sample (external validation in SWU validation sample: $r = 0.24$, $p < 0.05$ (two-tails), 95% CI = 0.06–0.41, Fig. S2). Further, a "lesioning" strategy was applied to determine the predictive power of different rs-FC features in explaining individual variability

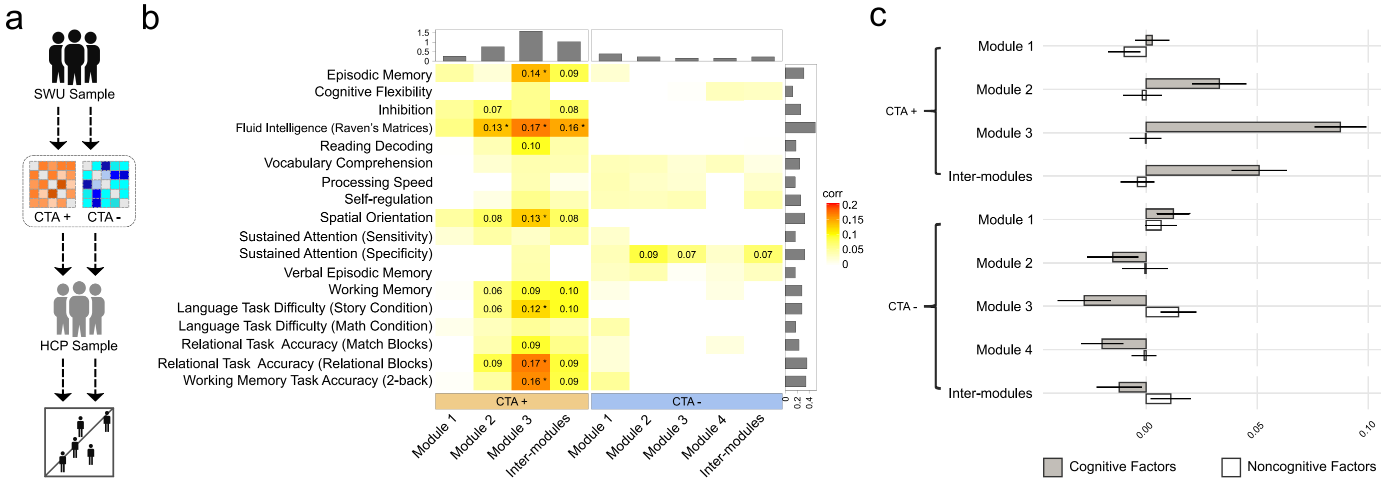

Fig. 3. Shared neural representations between creative thinking and multiple ordinary cognitive abilities. **(a)** A simplified schematic representation of the "traveling pattern prediction analysis". Briefly, the creativity-related brain patterns as well as the prediction models trained in the SWU sample were transferred to the HCP sample, in order to test if prediction models built for predicting creative thinking ability could also significantly predict different HCP cognitive factors. The analyses were separately carried out in different modules of high-creative (CTA +) and low-creative (CTA -) brain patterns. **(b)** The predictive powers (Pearson correlations between true and predicted values) of different modules. The predictive powers less than zero are set to be zero in the heat map. The labeled factors in the heat map indicate ordinary cognitive abilities that were significantly predicted by creativity-related features at a *p*-value of $p < 0.05$ (uncorrected). * represents factors whose FDR adjusted *p*-values are less than 0.05. The bar charts indicate the row and column sums of predictive powers. **(c)** The distinguished predictive performances (Pearson correlations between true and predicted values) between cognitive factor and non-cognitive factors, as well as among different modules of high-creative (CTA +) and low-creative (CTA -) brain patterns.

in creative thinking ability. The results indicated that most of the identified rs-FC feature sets can offer valuable information to the prediction model, with their predictive powers noted as greater than 0. Notably, the feature set involving functional integration amongst the default mode and frontoparietal control networks (Module 3 of high-creative pattern) displayed the greatest importance (Fig. 2d).

3.2. Brain pattern of higher creative thinking ability encodes important features for multiple ordinary cognitive abilities

We next tested whether the brain patterns related to creative thinking ability also contained vital rs-FC features related to different ordinary cognitive abilities. For that purpose, we applied a traveling pattern prediction analysis to test if prediction models built for predicting creative thinking ability could also significantly predict different aspects of cognitive abilities measured in the HCP sample (Fig. 3a). To distinguish the predictive powers in modules of the creativity-related brain patterns, the analyses were separately carried out in these modules. The results indicated that cognitive factors that could be successfully predicted by creativity-related rs-FC features (uncorrected, $p < 0.05$) included episodic memory; fluid intelligence (Raven's Matrices); reading decoding; spatial orientation; Sustained Attention (specificity); working memory; language task difficulty (story condition); relational task accuracy (math blocks); relational task accuracy (relational blocks); and working memory task accuracy (2-back). Moreover, rs-FC features within modules 2 and 3, as well as between different modules (especially within the combined areas of default mode and frontoparietal control networks, i.e., Module 3) of high-creative pattern exhibited higher predictive performance than other areas (Fig. 3b and c). However, none of the creativity-related features could significantly predict non-cognitive factors (Fig. S4), with evidently lower predictive performances in different feature sets than cognitive factors (Fig. 3c). These results together indicated that brain patterns of creative thinking ability specifically encode important features for a wide range of ordinary cognitive abilities. Particularly, the higher predictive performances exhibited in the high-creative brain pattern, suggest the creativity-related rs-FC features can be robustly embedded within different sets of this pattern.

3.3. Brain pattern of higher creative thinking ability is dominated by hubs recruited by distinct cognitive functions

Furthermore, we next aimed to explore whether the identified brain patterns linked to higher creative thinking ability was topologically constructed in a manner that could support different cognitive processes. To address this, we first applied within-module degree z-score on creative brain patterns to characterize brain regions' importance within their own modules. The regional importance in all of the modules exhibited right skewed distribution, suggesting that different brain regions played unequal roles within the identified modules (Fig. S4). To identify the most important regions in high versus low-creative brain patterns and their dominant cognitive functions, we set regions whose regional importance were located on the right side of 1.5 median-absolute-deviation (MAD) as hubs in their subordinate module, and the remaining regions as non-hubs. Then, a topic-based meta-analytic decoding via Neurosynth database was used to determine which psychological functions were preferentially related to the hub regions within different modules. Results revealed that the regional importance of hubs between high and low-creative brain patterns exhibited a strong negative relationship ($r = -0.45$, $p < 0.05 \times 10$–11 (two-tails), 95% CI = −0.54–−0.34), whereas there was no significant correlation in non-hub regions ($r = 0.03$, $p = 0.43$ (two-tails), 95% CI = −0.04–0.10, Fig. 4a). Such results indicate that these two antagonistic brain patterns are largely dominated by dissociable hubs.

Along with the meta-analytic decoding, the results also revealed that the modules in high-creative brain pattern (CTA +) were systematically driven by hub regions with distinct cognitive functions. Notably, the first module included hubs involved in sensorimotor processing (e.g., motion and visual processing) in visual and sensorimotor networks; the second module covered hubs related to general executive functions (e.g., working memory, inhibition and switching) mainly in the frontoparietal network; the third module included hubs related to memory-based cognitive processing (e.g., language, reasoning and memory) in the default mode and frontoparietal control networks (Fig. 4b). Taken together, these results suggest that the identified modules in high-creative brain pattern may serve as higher-order cognitive systems that recruit different cognitive processes in order to facilitate creative thinking. In con-

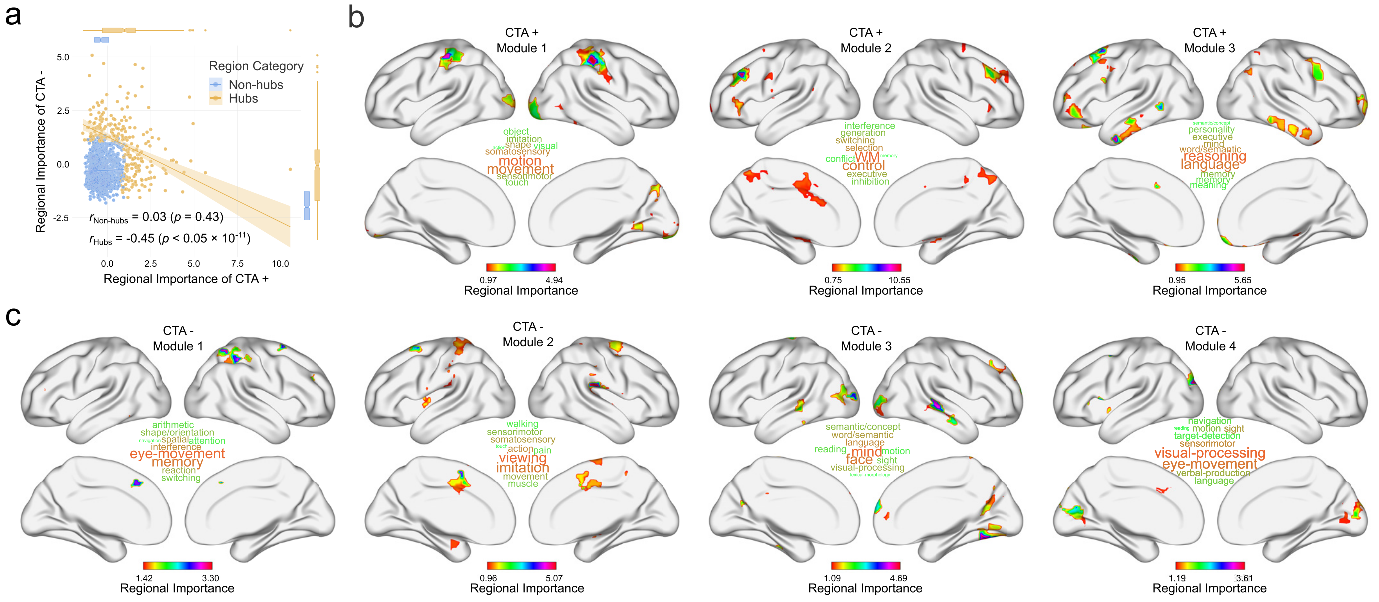

Fig. 4. Hub regions and their dominant cognitive functions in high versus low-creative brain patterns. **(a)** The correlation of regional feature importance (identified by within-module degree z-score) between high-creative (CTA +) and low-creative (CTA -) brain patterns, in which only hub regions exhibited a strong negative relationship. In the scatter plots, shaded areas represent 95% CIs. Hub regions and their corresponding top 10 Neurosynth topics across different modules of **(b)** high-creative and **(c)** low-creative brain patterns.

trast, modules in the low-creative brain pattern were mainly driven by visual and sensorimotor networks relating to functions involved in motor and visual processes (Fig. 4c). The top 10 Neurosynth topics related to hub regions can be seen in Table S1.

3.4. *Brain pattern of higher creative thinking ability facilitates specific functional integration among brain networks*

In our final attempt to understand how high-creative brain can specifically support the interplay of multiple cognitive processes, we investigated the network level information transfer efficiencies over functional connectivity paths marked by brain patterns linked to high versus low creative thinking ability. Meanwhile, to highlight the specificity of creativity-related brain patterns, the other 18 brain patterns linked to different ordinary cognitive abilities were also included in the same analysis (Fig. 5a). In order to compare these patterns under the equivalent wiring cost, all patterns were first binarized across a series of thresholds (across 0.1–2% edge densities). In each threshold, different brain patterns were also compared to 100 null models, in order to test whether they displayed topological properties to a greater extent than expected by chance under the null hypothesis (Fig. 5b). While, given the similar network property ($0.87 < r < 0.98$) uncovered across different edge densities, the statistical analyses were carried out at a chosen edge density (1%), whose network level metrics exhibited the highest average correlation ($r = 0.98$) to metrics at other densities (Fig. 5c and d).

The results revealed that across both creative thinking ability and ordinary cognitive abilities, the high-level brain patterns surpassed the low-level ones in both within-network information transfer efficiency (paired samples t-test for high vs. low (two-tails), $t = 5.52$, $p < 0.001$, Cohen's $d = 1.26$, 95% CI = 1.12×10^4 – 2.49×10^4) and between-network information transfer efficiency (paired samples t-test for high vs. low (two-tails), $t = 2.52$, $p < 0.05$, Cohen's $d = 0.58$, 95% CI = 0.45×10^4 – 4.98×10^4). Meanwhile, these metrics also showed significant differences between empirical data and null models (independent samples t-test for high-level pattern vs. null model (two-tails): within-network efficiency, $t = 3.12$, $p < 0.005$, Cohen's $d = 0.78$, 95% CI = 0.83×10^3 – 3.73×10^3; between-network efficiency, $t = -21.69$, $p < 0.005$, Cohen's $d = -5.43$, 95% CI = -9.92×10^4 – -8.26×10^4; independent samples t-test for low-creative pattern vs. null model (two-tails): within-network efficiency, $t = -15.5$, $p < 0.001$, Cohen's $d = -3.87$, 95% CI = -1.78×10^4 – -1.37×10^4; between-network efficiency, $t = -25.3$, $p < 0.005$, Cohen's $d = -12.72$, 95% CI = -12.72×10^4 – -10.88×10^4). Taken together, these results suggest that the high-level brain patterns behind different aspects of cognitive factors can universally offer optimized information transfer routes for both within-network and between-network communications. However, the information transfer paths of high-level brain patterns were largely constrained by the organization of functional networks, given the higher within-network efficiency and lower between-network efficiency relative to null modules. Furthermore, the results also highlighted that, compared to brain patterns of ordinary cognitive abilities, the high-creative brain pattern displayed particularly enhanced between-network information transfer efficiency (one sample t-test (two-tails), $t = -2.41$, $p < 0.05$, Cohen's $d = -0.57$, 95% CI = -11.03×10^3 – -0.73×10^3), while allowing the roughly equivalent information transfer within networks (one sample t-test (two-tails), $t = -1.09$, $p = 0.29$, Cohen's $d = -0.26$, 95% CI = -5.53×10^3 – 1.75×10^3). This suggested that the higher capacity for global information integration is one of the most prominent features of high-creative brain pattern (Figs. 5c and S5).

To extend this finding, additional analyses were also carried out among the interactions of any pair of networks (Fig. 5d). The result indicated that high-creative brain pattern can widely enhance the interaction among almost all transmodal brain networks, in that their between-network information transfer efficiency was significantly higher than null models (one sample t-test (right-tail), corrected by FDR, $p < 0.05$). On the other hand, the low-creative brain pattern mainly enhanced the information transfer efficiency in regard to somatomotor network (one sample t-test (right-tail), corrected by FDR, $p < 0.05$). Similar results can also be found in the brain patters of various ordinary cognitive abilities (independent sample t-test (right-tail), corrected by FDR, $p < 0.05$). However, in the group level analysis, high-level patterns of ordinary cognitive abilities merely significantly enhanced the information transfer efficiencies in regard to the default mode and frontoparietal control networks; and their low-level patterns enhanced the within-network efficiency of somatomotor network. Taken together, results revealed that, transmodal areas (especially the default mode and fron-

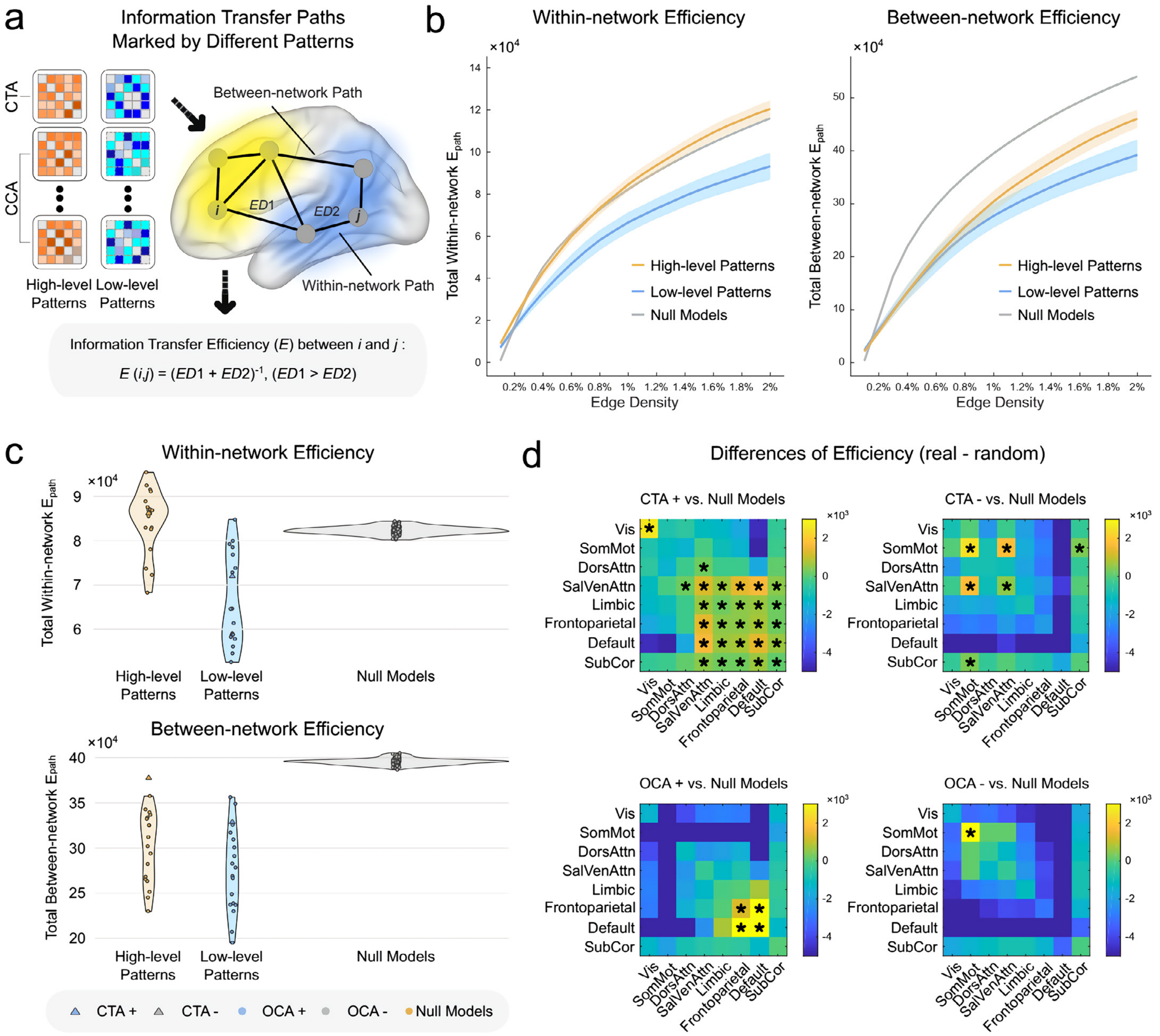

Fig. 5. Comparison of network level information transfer efficiency for different brain patterns. **(a)** The diagram for the identification of network level information transfer efficiency for different brain patterns. High-level/low-level patterns include high or low-level patterns for both creative thinking ability (CTA) and ordinary cognitive abilities (OCA). (**b)** The brain patterns' network level total information transfer efficiency (across 0.1–2% edge densities). The solid lines along with shaded areas indicate mean values of efficiency for all patterns and 95% confidence intervals, respectively. **(c)** Comparison of brain patterns' network level total information transfer efficiency at 1% edge density. The shaded areas reflect the density of the data points at different values. CTA + and CTA - separately indicate high and low-level brain patterns of creative thinking ability; OCA + and OCA - separately indicate high and low-level brain patterns of various ordinary cognitive abilities. The corresponding label for each dot of the ordinary cognitive ability can be seen in Fig S5. **(d)** Comparison of network level total information transfer efficiency between real and random patterns (real – null models) at 1% edge density for different brain patterns. Only the significant differences are marked by * (corrected by FDR, $p < 0.05$ (right-tail)). Vis: visual network; SomMot: somatomotor network; DorsAttn: dorsal attention network; SalVenAttn: salience/ ventral attention network; Limbic: limbic network; frontoparietal: frontoparietal control network; Default: default mode network; SubCor: subcortical network.

toparietal control networks) exhibit higher information transfer efficiency in the high-level brain patterns; whereas, the efficiency of unimodal areas (especially the somatomotor network) is greater in the low-level brain patterns. This antagonism could be a common phenomenon for both creative thinking and different ordinary cognitive abilities. Notably, the high-creative pattern surpassed other brain patterns in their capacity for functional integration between different transmodal brain networks. Further interrogation of this capacity within the identified modules could reveal that the high-creative brain pattern shows significantly higher internal information transfer efficiency within all subordinate modules, as well as between modules of Module 2 and Module 3 in comparison to the null models (one sample *t*-test (right-tail), corrected by FDR, $p < 0.05$; Fig. 6a). Such results indicate the enhanced between-network communication in high-creative brain pattern that can potentially facilitate further integration of functional networks into superordinate modules (Fig. 6b).

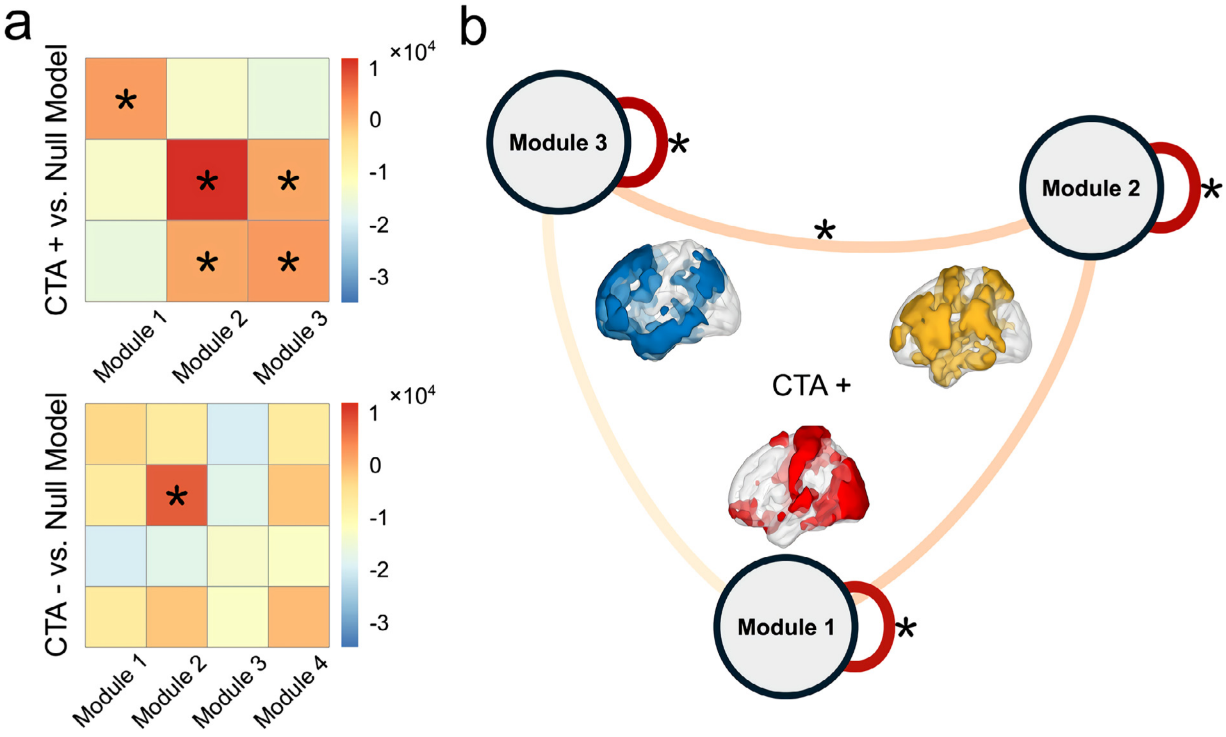

Fig. 6. Enhanced information transfer efficiencies of different modules in creativity-related brain patterns. **(a)** The difference of module level total information transfer efficiency between creativity-related brain patterns and null models. CTA + and CTA - separately indicate high and low-level brain patterns of creative thinking ability. Only the significant differences are marked by * (corrected by FDR, $p < 0.05$ (right-tail)). **(b)** The schematic diagram corresponding to the top left heat map, that illustrates how high-creative brain pattern (CTA +) facilitates further integration of functional networks into super-ordinate modules and enhances their information transfer efficiencies. * indicates the information transfer efficiency of a given path is significantly higher than null models (corrected by FDR, $p < 0.05$ (right-tail)).

3.5. Validation results

Given the importance of the modular structure of creative brain patterns in the present study, a supplementary analysis was carried out to test whether the module-based features could independently predict individual's creative thinking ability. Following the methods described in the Methods and materials (see also the Fig. S6a), the analyses supported our hypothesis that, the more individuals' functional network organization approaches to the high-creative pattern, the higher their creative thinking ability would be. Although the low-creative pattern could not predict creative thinking ability independently, it could still offer valuable information, given that the aggregate indicator considering both high and low-creative patterns get slightly higher correlation tendency than applying the single indicator of high-creative pattern. In detail, PTC significantly positively related to creative thinking ability ($r = 0.194$, $p < 0.05 \times 10–7$ (two-tails), 95% CI = 0.131–0.255); VI_{pos} significantly negatively related to creative thinking ability ($r = -0.118$, $p < 0.05 \times 10–2$ (two-tails), 95% CI = −0.181–−0.054); there was no significant result in VI_{neg}, though a weak positive correlation trend could be observed ($r = 0.053$, $p = 0.11$ (two-tails), 95% CI = −0.111–0.117) (Fig. S6b). Further analysis at the regional level revealed that brain regions whose module affiliations were of great importance to creative thinking ability were mainly located in the default mode and visual networks (corrected for multiple comparisons using the false discovery rate (FDR) at the level of $p < 0.01$; Fig. S6c).

In addition, the validation analysis was also implemented via two strategies to the feature importance matrix (Fig. S7a). The results of the identification strategy revealed high reliability (defined as the identification effect) of different feature importance matrices (i.e., patterns underlying psychological variates), in that most of the feature importance matrices could fully identify (identification effect = 1) their counterpart trained using data from a different time of scan (Fig. S7b). The results of the prediction strategy also confirmed the reliability (defined as correlation coefficients between predicted values and true values) of different feature importance matrices, that all the correlations are significant and the average correlation coefficients ranged from 0.20 to 0.41 (Fig. S7c). As such, the results indicate that the threshold used in this study ($p < 0.005$) could lead to an optimal reliability of feature importance matrix, in that the general reliability values calculated by different strategies were always at a high level compared to the values under other thresholds (Fig. S8).

4. Discussion

Creative thinking constitutes a vital component of our normal psychological functioning, the neural correlates of which require further investigation. To this end, using comprehensive datasets from large population samples, our study characterized neural patterns of functional interactions amongst large-scale brain networks that were associated with high versus low creative thinking ability across individuals, referred to as the high versus low-creative brain patterns (Fig. 1). From a graph theoretical perspective, the high-creative brain pattern illustrated distinct modules, yet with considerable functional integration amongst large-scale brain networks in comparison to the low-creative brain pattern (Fig. 2). Employing a traveling pattern prediction analysis, we then revealed that the identified brain patterns, specifically the module involving functional interactions among default mode and frontoparietal control networks in the high-creative brain pattern, encoded vital rs-FC features that could also predict cognitive abilities such as episodic memory, working memory and relational processing (Fig. 3). In addition, using a meta-analytic approach we found that the modules in high-creative brain pattern were systematically dominated by hubs associated with different fundamental cognitive processes including sensorimotor processing, executive control function and memory-based processing. On the contrary, the low-creative brain pattern was mainly driven by brain areas that serve motor and visual processing roles (Fig. 4). Moreover, our results indicated that the high-creative brain pattern particularly optimizes between-network information transfer efficiency (Fig. 5) that potentially enables an enhanced integrative capacity within the specific modular organization (Fig. 6). Collectively, these results indicate that creative thinking may constitute an emergent property of ordinary cognitive processes, in which the specific wiring rules of the highly creative brain may facilitate integration across functional networks into modules that contribute to a more efficient interplay of relevant cognitive operations in service of creative thinking.

Mounting evidence from cognitive neurosciences now suggests that creative thinking is supported by functional interactions across large-scale brain networks that play distinct roles within higher cognitive processes such as memory, attention, cognitive control and action simulations (Benedek, 2018; Chrysikou, 2019; Matheson and Kenett, 2020; RE et al., 2020). This dynamic interplay across cognitive processes and their neural instantiations is hypothesized to provide a mechanistic backbone for the emergence of creative thinking (Beaty et al., 2019; Benedek and Fink, 2019). Although experimental evidence for this model remains scarce, emerging reports investigating brain functional network organization allude to the central importance of such cognitive and neural integration in the evolution of creativity (Beaty et al., 2018; Liu et al., 2018). For example, Kenett and colleagues have recently demonstrated that a creativity-related network integration is reflected in the mesoscale brain network organization, which was marked by the consolidation of areas within the temporal lobes into cohesive clusters (Kenett et al., 2020). Using a complementary data-driven approach, we further extend upon this finding by explicitly portraying the network integration tendency of high-creative brain pattern, dominated by modules that include functional interactions amongst transmodal areas as well as those that support visual and sensorimotor functions. Moreover, we also found that this structure was perturbed in the low-creative brain pattern which highlight the vital importance of a balance between integration and segregation amongst large-scale brain networks in creative thinking. In other words, the sets of basic functions embedded within different modules may potentially facilitate more rapid task related adaptation (Kashtan and Alon, 2005), and different forms of non-linear dynamical behavior (Meunier et al., 2010), that may meet the need to carry out more unstructured, open-ended, and non-linear processing in creative thinking (Abraham, 2014).

Furthermore, through traveling pattern prediction analysis, we uncovered functional connectivity features within these modules that could support the link between creative thinking and various ordinary cognitive abilities. In line with this observation, recent studies report considerable overlap in functional connectivity features between creative thinking ability and cognitive performance across controlled semantic retrieval, higher-order reasoning, vocabulary knowledge and mental manipulation (Frith et al., 2019). Based on two large-scale and independent datasets with robust characterization of both neural and neuropsychological assessments, our study provides further reliable evidence (avoiding the common method biases (Podsakoff et al., 2003)) for shared neural resources among creative thinking and multiple cognitive abilities. In detail, the creativity-related rs-FC features can specifically predict a wide range of cognitive abilities (over 60% of included HCP cognitive factors), which can be roughly divided into memory and language related processing (including episodic memory, reading decoding, sentence judgment and relational processing), attention (including sustained attention), executive control (including inhibition, spatial orientation and working memory), as well as reasoning and intelligence (including Raven's Matrices). The profound and complicated connections of multiple cognitive processes with creativity have been highlighted in the neurocognitive theories of creative cognition (Jung and Vartanian, 2018). Notably, it has been claimed that creative thinking can be commonly characterized by at least three core cognitive processes: the constructive memory processes that serve to generate novel representations; different attentional processes that enable people to consider more task-relevant information synchronously; and the cognitive control functions that implement goal-directed memory and attention processes (Benedek and Fink, 2019). Therefore, creative thinking can be assessed by examining multiple ordinary cognitive processes under explicitly generative conditions (Abraham, 2013, 2018). Here, our findings well resonated with these hypotheses, suggesting that creative thinking is not an independent mental operation, but deeply grounded in the core cognitive processes such as memory, attention and executive control functions.

Despite the shared neural representations between creative thinking and multiple cognitive abilities, however, we also revealed that the identified modules played unequal roles in their ability to predict individual variation in behavior. That is, the module which largely involved the default mode and frontoparietal control networks in the high-creative pattern, explained the greatest individual variability in creative thinking, which is highly consistent with findings from a prior report (Beaty et al., 2018). Furthermore, this module showed the highest contribution to the correlations between creative thinking and different cognitive abilities, which implies that the cooperation of these two networks is one of the most important neural bases bridging ordinary cognitive processes and creative thinking. The default mode network along with the frontoparietal control network are both situated at the peak of a hierarchy across macro-scale brain network organization (Margulies et al., 2016). The brain regions that give rise to these two transmodal areas display late myelination during development, suggesting that they might be responsible for especially advanced forms of human cognition (Sowell et al., 2003). Modern theories postulate that the default mode network may play a central role in the integration of multimodal information (Kernbach et al., 2018; Vatansever et al., 2015) to generate memory-based representations (Buckner and DiNicola, 2019; Vatansever et al., 2017). Conversely, the frontoparietal control network is hypothesized to be responsible for retaining and manipulating task-relevant information from the outputs of the default mode network (Spreng et al., 2010). As a "flexible hub", this control network is suggested to rapidly update the pattern of global functional network configuration for adaptive implementation of task demands (Cole et al., 2013). As such, the emergence of the "default mode-frontoparietal" interaction as a strong predictor of creative thinking ability in our study may underline the central importance of this cooperation in enabling greater integrative capacity in service of creative thinking.

Moreover, our study interrogated the network level information transfer efficiency in connectivity paths marked by the identified brain patterns. We demonstrated that the specific wiring rule of high-creative brain pattern displayed particularly enhanced between-network information transfer efficiency and thus greater capacity to facilitate integration across functional networks into super-ordinate modules. In addition, we found the hub-like structures linked to different fundamental cognitive processes (from sensorimotor processing to higher order memory-based processing) were embedded in these modules. It further demonstrated the functional interactions in the highly creative brain could be parallelly driven by multiple cognitive processes, which again supports the notion that creative thinking is an emergent property of ordinary cognitive operations.

From the above, the highly creative brain can be characterized by distinct modules, that are largely dominated by hubs in charge of different cognitive functions (Module 1: sensory processing; Module 2: general executive functions; PM3: memory-based processing). Particularly, the wiring rule of high-creative brain pattern can not only ensure the information transfer within these modules, but also highlight the interaction between Module 2 and 3. Thus, this kind of layout may provide an optimized information processing framework for creative thinking. More precisely, it is acknowledged that creative thinking involves at least two iterative phase: a generation phase and an evaluation phase.

The generation phase (regarded as the core process) mainly takes charge of combination of remote associations in a unique way, that relies on search processes through semantic (Kenett et al., 2018a) and autobiographical memory (Madore et al., 2017). The outputs of first phase would then suffer from a complementary evaluation processes mainly dependent on the executive control processes. However, it is argued that the evaluation not only happens in the second phase, but also included in the first phase, divided into lenient and stringent cognitive control (Kleinmintz et al., 2019). Based on this view, Module 3 with the dominant function of memory-based processing may be responsible to the generation phase, where default mode network takes charge of generating novel ideas from memory system, and frontoparietal control network in this phase provides a mechanism for goal-directed lenient control in order to shield the ongoing train of thought from irrelevant information. The Module 2, the context-dependent attention system under the leadership of frontoparietal control network (regions in charge of executive control functions), may be recruited in the evaluation phase, providing a function of stringent executive control to ensure that the generated ideas are compatible to task environment. Notably, the high-efficiency pathway between Module 2 and 3 can well guarantee the cyclic motion between generation and evaluation phase.

Furthermore, the high-creative brain pattern also highlighted brain areas in charge of sensorimotor processing (Module 1), which have often been overlooked by previous studies. This finding is consistent with the latest perspective, which suggested the cognitive process of generating creative output, not just executing it, is deeply embedded in motor processes (Matheson and Kenett, 2020). The related brain regions, especially the supplementary motor area, may be attributable to mental imagination and motor simulation, that generally contribute to different kinds of creativity tasks (Chen et al., 2020). Hereby, our findings suggest that the highly creative brain can also provide effective information transfer paths to facilitate sensorimotor processing. This is in line with prior findings that report a relationship between creativity and higher functional integration in sensorimotor areas (Kenett et al., 2018b).

The main limitation of the current study is that the individuals' creative ability was assessed solely by their performance in tasks that probed divergent thinking. Though divergent thinking is assumed to lie at the heart of creative thinking (Jauk, 2019; Runco and Acar, 2012), convergent thinking (generally captured by problem-solving tasks), may also constitute an important aspect of creativity (Benedek et al., 2019). One recent behavioral study indicated that cognitive abilities such as working memory and verbal fluency contribute both to divergent and convergent thinking, but to differing degrees (Dygert and Jarosz, 2020). Thus, based on the identified brain patterns in this study, a promising direction for future research will be to focus on how different aspects of creative thinking can emerge from different combinations of ordinary cognitive abilities along with corresponding brain network configurations. In addition, given that creative thinking is fundamentally a property of ongoing cognitive processes, only capturing the trait-like brain patterns may not meet the need to understand how different cognitive processes dynamically give rise to creativity. Thus, future studies should also explore the fluctuations in brain dynamics through task-based designs across different cognitive demands of creative thinking.

In conclusion, our study provides strong evidence based on whole-brain functional connectivity patterns to support the notion that creativity is not an independent mental operation, but it is rather an emergent property of multiple ordinary cognitive processes. Particularly, we provide direct evidence for a shared mechanism in the neural instantiation of creative and ordinary cognitive processes within the complex brain network organization. Furthermore, we also show that the integrative capacity of human connectomes plays a central role in this regard, which may constitute a valid marker of creative thinking ability to be used in future studies investigating this aspect of human cognition in both healthy and disease states. These findings together provide new insights for understanding how creative thinking can emerge from more fundamental cognitive processes through specific network configurations.

Author contributions

Methodology and analysis, K.Z.; Interpretation, K.Z., D.V., J.Z.; Subjective scoring for creative thinking, W.Y., Y.L., Q.C.; Data organization, preprocessing and screening, W.Y., Y.L., K.Z.; Data collection, W.Y., Y.L., Q.C., D.W., J.S., K.Z., J.M., Y.M., X.W., L.H.; Manuscript, K.Z., D.V., W.Y., J.Z.; Funding acquisition, J.Q., D.V., J.Z.

Data and code availability statement

All analysis code used in this study is openly available on https://github.com/Zhuang2KX/MANA/tree/master/Project/CTA. Due to restrictions imposed by the administering institution, the SWU dataset is only available from the authors upon request. Sharing and reuse of this dataset require a formal data sharing agreement, as well as approval from the relevant Institutional Review Boards. The HCP Open Access Data is publicly available on the ConnectomeDB database (https://db.humanconnectome.org).

Ethics statement

This research project was approved by the Southwest University Brain Imaging Center Institutional Review Board. For the SWU dataset, informed consent was obtained from each participant in accordance with the relevant rules and regulations outlined in the Declaration of Helsinki for experiments involving humans. The reanalysis of the publicly released Human Connectome Project (HCP) Open Access Data and the reporting of results pertaining to this dataset has also been reviewed and approved by the Southwest University Brain Imaging Center Institutional Review Board. As per the data use agreement, we strictly adhered to the HCP Open Access Data Use Terms and Conditions.

Declaration of Competing Interest

The authors declare no competing interests.

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Supplementary materials

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