

Dynamic switching between brain networks predicts creative ability

Corresponding Author: Dr Yoed Kenett

Version 0:

Reviewer comments:

Reviewer #1

(Remarks to the Author)

COMMSBIO-24-4080

I appreciate the opportunity to review this manuscript. The paper is generally well-written and discusses the results of an analysis across pulled resting-state brain imaging datasets from multiple centers around the world that focuses on what is discussed as switches between large scale brain networks, specifically the ECN & DMN, and their relation to creativity. It is argued that these switches represent the balance between segregation and integration in the brain that is hypothesized to predict individual differences in creative performance. The analyses reveal an inverted U-shaped relationship between network switching and creative performance, a relationship that is not replicated for measures of intelligence. Although I enjoyed reading the paper, and found the results interesting, I have some comments/concerns that are discussed below:

Novelty: Although not explicitly discussed in the manuscript, given the byline and nature of the datasets, it seems that this is a partial re-analysis of the datasets used for Beaty et al. (2018, PNAS) which is citation 21 in the paper. This paper is only mentioned peripherally in a parenthetical citation in the introduction, and not explicitly discussed. Except for the Japanese sample, it would seem that the rest of the datasets are the same? If so, this needs to be very clearly noted in the paper, especially given that the 2018 paper also involves connectivity analyses and discusses the power of the combined engagement of DMN and ECN as predictor of creativity. An argument is further made in this study about the sample size being the largest to date in a creativity study, and noted here as a key feature of the present investigation. It would be critical to state explicitly whether any of the included 10 datasets have already been used in published work, and especially if the prior publications have involved connectivity analyses as predictors of creativity—as that would potentially compromise the stated novelty of the present work.

Meta-analysis approach: The terminology used in the paper suggests this is a meta-analysis, though it is not clear from the methodology that a meta-analytic approach was used, including examination of assumptions, discussions of past literature, criteria for the selection of the datasets based on past papers (as opposed to samples of convenience) etc. This needs to be clarified. It seems that the paper pools datasets from different centers with the aim of conducting a new kind of analysis regarding ECN-DMN network switching, thus does not really function as a meta-analysis. This should be highlighted in the paper, so as to promote its novelty—as well as situated within prior work with these datasets, including the 2018 paper noted above from (mostly) the same authors. It might be important to remove any note of this work as a 'meta-analysis' as it does not meet the criteria for a meta-analysis, in my opinion.

Cross-cultural differences: There is plenty of literature discussing hypotheses regarding cross-cultural differences in creativity behaviorally. However, these don't translate necessarily into neural predictions. What are the hypothesized neural differences in large-scale network connectivity that would differ among cultures? Why? What would be the mechanism? The cross-cultural differences angle is sprinkled throughout the paper, but there is very limited rationale and literature presented across the paper, through which one can evaluate the claims.

Quantification of switches: The process via which the 'switches' from DMN-ECN and their 'balance' was determined is insufficiently presented in the main portion of the paper. There is no discussion of the quantification of these key variables that are only briefly discussed in the methods. This needs to be included very early on in the paper—especially if the authors argue it's a novel aspect of the methodological approach (i.e., their argument that the integration-segregation has not been examined thoroughly before). On this point, I am not sure that what is being calculated here as a switch truly represents a dynamic switch between the two network states. This is discussed in a very muddled way and somewhat hidden in the methods, thus it is not clear whether (a) the method followed represents anything new relative to past analyses, or (b) that

the method actually captures network 'switching' or integration—the premise on which the paper is designed around. Given the resting-state data used here, the notable variability across datasets from an imaging perspective, and the variability in the behavioral assessments of creativity across the samples, this aspect of the analysis needs to be crystal clear and incorporated early in the paper.

Duration of resting-state scans: I may have missed this, but what was the duration of the resting state scans for each dataset? Although the literature is a little inconsistent on recommendations for optimal resting state scan length, longer scans are associated with much more reliable datasets. This needs to be included in the paper and addressed.

Introduction: The introduction is really broad and fails to focus clearly on the novelty and key aspects of the work that may make this paper different from others (again, not sure the number of participants is, indeed, that impressive, if all of these participants' resting-state connectivity profiles and their relation to creativity have already been reported in past published work). In general, the introduction jumps around in its terminology from large-scale network dynamics, to connectivity, to the (presumed new) idea of segregation and integration. However, it fails to highlight clearly how this terminology is fundamentally different—if at all—from much of the authors' prior work that has reported increases in connectivity between DMN-ECN in creativity relative to other tasks, what can clearly align with the use of the term integration is presented in this paper. Is it, then, that the paper discusses the exact same ideas, just presenting them now with these two terms (segregation-integration) that are long-standing in the connectivity literature, but not as prominent in the authors' prior work on this topic? This needs to be clarified, to denote whether there is anything new theoretically that is presented in this work.

Discussion: Similar to the introduction, the discussion is also not particularly well focused. In the same way, for instance, there are references as to what these network dynamics represent (mindwandering? Generation? Memory?) but the paper and its methodology addresses none of these questions. I would suggest significantly condensing and refocusing the discussion to highlight the specific and novel contribution of this study, if any. A section on limitations would probably also be a good idea to include.

Reviewer #2

(Remarks to the Author)

The current study reflects a successful effort to synthesize a large collection of data for definitive testing of the DMN-ECN switching theory. The analyses performed appear to be valid, thoughtful, and rigorous. This work has likely not been attempted before based on the sheer computational (and communication) challenges involved. The large analysis was supplemented with a helpful and complementary fMRI investigation. I was impressed with the current efforts.

The primary issue that stands out to me is that the effect sizes observed for the DMN-ECN switching relationship to creative performance are quite modest ($r=.17$ overall, or less than 3% of the variance). It would be helpful to see the authors speak to this: while network switching is shown to be clearly involved, it doesn't appear to be a prominent predictor. This is the case even though larger networks with widespread BOLD signal as input, and correspondingly strong signal stability are used, so the weak relationship cannot be blamed on MRI signal. A large sample like this is a unique opportunity to estimate true effect size, so not discussing this seems like a missed opportunity. Of course, it runs the risk that we are making much ado about nothing - it seems possible the network switching is related to some creative process but ultimately is not itself important.

Of course, the results are what they are, and the authors of such an impressive analysis should not be penalized for not finding a more striking result. But I think theoretical exploration of this point would be valuable. Is the current paper a "Pyrrhic victory" for DMN-ECN switching theory?

A more minor point concerns the quadratic model fit analysis. First, isn't model fit going to be biased towards being superior when adding another model term (due to overfitting, if nothing else)? Second, the goal is to test a theory that balanced DMN-ECN integration/segregation is advantageous, i.e., an inverted U function. But the statistical test is simply whether a quadratic model is a better fit. without bearing on whether the quadratic model in question is an inverted or upright "u". Therefore, an upright U such as in GBB_S1, while inconsistent with the theory, would end up supporting it by virtue of having a quadratic fit.

Also, one of the strengths of the paper is that it draws upon public data for high reproducibility. However, while an additional, new dataset is reported alongside these data, it is not shared, which is not in keeping with the ethic that made the paper possible.

Overall this is an important and impressive effort that I feel should be published albeit with some reflection on the topics above.

Reviewer #3

(Remarks to the Author)

Summary: The manuscript provides evidence that the brain of individuals with high creative potential (i.e., high scores on a divergent thinking task) display a balanced back and forth between two meta-states (i.e., segregation and integration) of two large scale brain networks (i.e., the default mode network and the executive function network) during resting states and while performing a divergent thinking task. They first performed a meta- and mega-analysis of 10 studies originating from sites

covering 3 different continents and that included close to 2,500 participants. These analysis revealed that the resting states of individuals scoring high on divergent thinking tasks was associated 1) with more transitions back and forth between independent activity (i.e., segregation) and coordinated activity (i.e., integration) of the default mode and executive function networks and 2) with an equal amount of time spent in either meta-state. In an external validation study involving 31 participants, they found evidence that the patterns observed in the meta- and mega-analysis during resting state also applies to performance of a divergent thinking task. Compared to a task in which participants named common features of selected objects, having to produce original alternate uses of objects involved more transitions between the segregation and integration meta-states and individuals with higher originality scores were more likely to spend about the same amount of time in both meta-states.

Overall impression: This is an ambitious and important body of work that nicely complements prior work on the creative mind. Among its strength are the very large datasets comprising multiple cultures across 3 continents providing consistent patterns of results in a group of 10 independent studies separately and together, across 2 different brain atlas (Schaefer and Shen). It provides new insights into the study of the creative mind by new metrics derived from a meta-states approach, and critically, it replicates the resting state results with fMRI data collected while completing a divergent thinking task. This novel, large scale, high quality and thorough work is a great contribution to the field of creative cognition.

Here are my suggestions for improving the quality of the manuscript:

1. My biggest issue with the manuscript as it stands is about the reasoning behind focusing on resting state. There is only a brief mention line 113-116 and some indirect connections in the following paragraph. While the introduction and discussion focus heavily on creative cognition / creative processes, the bulk of the analyses (meta- and mega-analyses) rely on drawing a connection between dynamics of resting-state connectivity and divergent thinking scores obtained outside the scanner. What is special about this particular state that could explain why it is predictive of creative abilities?

The default network has been linked to pretty much all forms of internally generated cognition, but it seems unlikely the pattern of results described in this manuscript would be seen in an experimental task in which participants are asked to recall a past episode or engage in theory of mind. Yet, in the resting state context in which those results emerged, participants are highly likely to experience a succession of episodic and theory of mind thoughts. Why?

The resting state is a particularly interesting context of thoughts. In the dynamic framework of thoughts (Christoff et al., 2016), thought arising in this context are likely to be relatively free of constraints, allowing exploration of low probability associations. Such situations may be propitious for explanation through recombination of existence knowledge (see the NEXTUP model from chapter 8 of *When Brains Dream: Understanding the Science and Mystery of Our Dreaming Minds* (Zadra & Stickgold, 2021 and Sripada, C. S. (2018). An exploration/exploitation trade-off between mind wandering and goal-directed thinking. The Oxford handbook of spontaneous thought: Mind-wandering, creativity, and dreaming, 23-34). Consistently, there are many anecdotes of creative people finding creative solutions in dreams or using hypnagogic sleep for creative purposes. Our own work find resting state markers associated with creative potential with a Think Aloud task (Raffaelli, Q., Malusa, R., de Stefano, N. A., Andrews, E., Grilli, M. D., Mills, C., ... & Andrews-Hanna, J. R. (2024). Creative minds at rest: Creative individuals are more associative and engaged with their idle thoughts. *Creativity Research Journal*, 36(3), 396-412.).

Line 498-504: In the discussion, it could be interesting to further discuss the tasks and/or contexts in which the authors expect creative individuals to show a different patterns of resting-state connectivity dynamics as pointers for future research. Of note, mind wandering as it is most often defined is not necessarily spontaneous considering it can be classified as intentional, and internally directed cognition includes all forms of non-perceptual experiences, from directed one's thoughts towards writing a manuscript, which can hardly be characterized as a spontaneous process, to dream, which is extremely spontaneous (unless the person is lucid dreaming).

Overall, I believe the paper would be stronger if the introduction and conclusion provided an explanation as to why the resting state appears to be predictive of creative potential.

2. With regards to the external validation study, why ask participants to provide common characteristics of object and rate the originality of such characteristics as a comparison to the originality of the new use of the object? It seems like a better comparison would be to ask them to generate unusual features of the object. Considering the analysis are based on originality scores on both tasks, it creates an unnecessary asymmetry between the 2 tasks. Relatedly, unlike the rs-fMRI results, more switches between segregation and interaction were not associated with higher originality scores. More switches were observed in the AUT compared to the OCT task. Could this suggest that this marker may be the product of complex decision making as opposed to creative cognition per se. What is your interpretation of this discrepancy in results?

3. Have you considered whether there may be an interaction between the number of switches and the balance of segregation/integration? The same balance score may be obtained by a participant who only switched once between segregation and integration and a participant who switched hundreds of time within the same timeframe. Is the balance predictive of creative potential only given a specific number of transitions between states have happened or is it the case regardless of how many switches occurred? Relatedly, any intuitions as to why more transitions between segregating and integrating states are better? Shouldn't there be a point at which the switching can become excessive and thus counterproductive as is the case with dwelling, suggesting this relationship should also have a u-shape form?

4. A potential limitation is that the analysis using the Shen atlas resulted in only 3 out of 10 studies showing significant

patterns of results compared to 7 out of 10 using the Shaeffer atlas. While the results are convergent, the success rate appears to favor a lack of effect (30% of studies are significant, or the effect is only true for about 25% of the entire sample). Are there any known differences between the atlases that may explain this difference in results?

5. Have you considered whether the results could have been impacted by the creativity assessment method (originality alone vs. sum of originality and fluency) ?

Here are some other less important suggestions for improvement in order of appearance in the text:

1. Line 68: I would not refer to externally-oriented processes when you describe the function of the ECN as it confuses the point you are trying to make. The important ECN function you want to highlight is that when coupled with the DMN, it is helpful in evaluating and selecting appropriate answers (refer to Ellamil et al., 2012)

2. Line 87: the US is actually not a continent, America or North America, which contains both the US and Canada, is a continent.

3. Line 89-90: this sentence suggest the ECN is solely responsible for evaluative processes, while the subsequent sentence correctly clarifies it is the coupling between DMN and ECN that supports this function.

4. Line 104-110: a bit nitpicky, but considering you mention generation and evaluation in that order, and that segregation maps to generation while integration maps to evaluation, I would order these elements in the same way throughout the manuscript: first segregation then integration.

5. Line 124-133: this paragraph has interesting but difficult to grasp ideas. It would be helpful to flesh it out a bit. For instance, hyperconnectivity would be expected to be related with rigid cognition while very low levels of connectivity would be associated with a lack of coherence.

6. Line 149: Specify the AUT were performed outside the scan for the meta-analytic studies.

7. Line 261: 'intelligence, regarded as control task'. This bit is confusing. Do you mean a control / comparison condition? It appears from the supplementals that intelligence was assessed with a variety of different tasks. Please clarify. On a related note, it could be useful to have a supplemental figure/table in which you present these results and in which one of the column would describe the task being used (e.g., site: UNCG, intelligence assessments: 'three measures of fluid intelligence (2): the number series task, the letter sets task, and the series completion task from the Culture Fair Intelligence Test', results). I understand the results are not significant so I'll leave this at your discretion.

8. Line 416: Here as well as many other places in the manuscript, be sure to specify your meta-analyses on resting-state analyses. Specify as well when prior work is based on resting-state data or a creativity task. Considering the framing of the paper, a reader may be easily lead to believe this was done based on fMRI data from creativity tasks.

9. Line 446-449: this statement seems extremely aligned with the results of Ellamil et al., 2012 who is not cited there.

10. Figure 2: I assume the scores are all z-scores? If so, specify in the legend. I would also consider adding the sample size next to the data site (e.g., UNCG (n = 169)).

11. Figure 5: I would consider adding statistics for the overall effect (black lines). Additionally, I would indicate which side is extreme integration and which side is extreme segregation and that the center (0) is the sweet spot.

12. Figure 6: A. Think Aloud refers to an actual task that is becoming popular to assess thoughts in real-time. My understanding is that participants just voiced aloud their answers, not every thought that popped into their mind during the process of generating the answers. If that is the case, I would use a different terminology so as not to create confusion. B. States' number on the y-axis is confusing. I think this refers to the average number of times a brain state was initiated. I would consider a less confusing label, maybe something like Number of occurrences? E-H: indicate statistics and significance, or at least significance.

13. Supplementary Table S2: please indicate the variables involved in the correlations. I assume the left side is age x creative achievement and the right side is age x intelligence. As it stands, there is no way to know from the table.

14. Specify in each figure whether the fMRI data is resting-state or task-based.

Version 1:

Reviewer comments:

Reviewer #2

(Remarks to the Author)

The authors have made effective changes and I am happy to endorse publication of the manuscript in its current form.

Reviewer #3

(Remarks to the Author)

I appreciate the efforts of the authors in taking to heart our suggestions. I am pleased to see the manuscript has significantly improved as a result. However, I am afraid I am still confused when reading the introduction and conclusion as to the reasoning of using resting-state analyses. While I believe these are important results worthy of publication, it would still be important to explain to the reader why.

As it stands, the introduction is greatly framed to justify the direct validation part of the research, in which participants performed the creativity data inside the scanner. The first paragraph puts the emphasis on creative thought and highlights its implementation relies on the DN and ECN. The second describes these networks before the third links the dual-step process of creativity or other related theories of creative thinking such as that of the dynamic framework of spontaneous thought to the authors' hypothesis that creativity requires a sweet spot between DN acting alone for generation and acting with the ECN for goal-directed evaluation. By this time, which is about half the introduction, the only thing I know about the resting-state is that it can be predictive of creative potential based on activity that mimics that observed during creative thinking. That is not a strong considering the manuscript is balanced towards resting-state analysis (2433 participants for the resting-state vs. 31 participants for the in-scanner creativity task).

The first hint comes in paragraph 4, lines 119-123: 'From the perspective of individual differences, people who have higher creative thinking abilities—potentially conducive to a more efficient cycle of generation and evaluation—may also exhibit altered dynamics of large-scale brain networks (namely, the DMN and ECN) at rest'. This and the following sentence suggests that based on prior work, a relationship may be observed, but does not hint as to why. The following paragraph I think tries to suggest it may have to do with more efficient memory retrieval process but the connection with resting-state and creative thinking is not clear. By the end of the introduction, my expectations as a reader is that the paper is going to focus on creative thinking and maybe look at resting-state as a secondary analysis. However, the analyses are 95% resting-state.

What is still missing is some argument(s) or line(s) of evidence that links more clearly the resting-state to creative thinking in a way that justifies looking at both and expecting similar results in terms of brain dynamics? Something that could be located somewhere after line 122 or in the 4th paragraph. Otherwise, it feels as if you equate resting-state and creative thoughts.

Potential arguments are:

- that the resting-state represents the intrinsic state of the brain and is therefore predictive of performance in various cognitive tasks
- high creative potential individuals use their resting time to explore their mind, a process that is similar to the creative process
- resting-state and creative thinking are similar in terms of the cognitive processes involved and thus the pattern of brain dynamics is similar across both thinking contexts
- the semantic network of high creative potential individuals has been showed to differ. Resting-state may be a time during which such semantic networks are being built while creative thinking is a time during which they are being practiced
- other potential avenues are hinted about by the authors in their rebuttal: differences. 'For example, higher creative individuals may exhibit a higher degree of internally directed cognition at rest (Sepulcre, 2014; Sepulcre, Sabuncu, Yeo, Liu, & Johnson, 2012)' AND 'Under a resting-state fMRI context, participants are not externally guided by any specific task, allowing for more spontaneous, undirected thought processes'

Whether it is one or a combination of these, or some other arguments I have not considered, bridging this gap in reasoning would greatly benefit the paper, especially considering the journal is aimed at a broader audience. It does not have to be long (a couple sentences would do), but it has to be there, especially because considering the scope of the study, it has the potential of becoming a reference article.

Similarly in the conclusion, commenting/speculating as to what happens during the resting-state, at the neural level and/or experiential/behavioral levels, that explains why it is 1) predictive of creative potential and 2) matching the neural patterns observed during creative thinking would nicely tie everything together.

Version 2:

Reviewer comments:

Reviewer #3

(Remarks to the Author)

The authors have made effective changes and I am happy to endorse publication of the manuscript in its current form.

Open Access This Peer Review File is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made.

In cases where reviewers are anonymous, credit should be given to 'Anonymous Referee' and the source.

The images or other third party material in this Peer Review File are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder.

To view a copy of this license, visit <https://creativecommons.org/licenses/by/4.0/>

Reviewer #1

I appreciate the opportunity to review this manuscript. The paper is generally well-written and discusses the results of an analysis across pulled resting-state brain imaging datasets from multiple centers around the world that focuses on what is discussed as switches between large scale brain networks, specifically the ECN & DMN, and their relation to creativity. It is argued that these switches represent the balance between segregation and integration in the brain that is hypothesized to predict individual differences in creative performance. The analyses reveal an inverted U-shaped relationship between network switching and creative performance, a relationship that is not replicated for measures of intelligence. Although I enjoyed reading the paper, and found the results interesting, I have some comments/concerns that are discussed below:

We thank the Reviewer for the time taken to review this manuscript; we appreciate their evaluation and hope that we have addressed their thoughts appropriately.

Novelty: Although not explicitly discussed in the manuscript, given the byline and nature of the datasets, it seems that this is a partial re-analysis of the datasets used for Beaty et al. (2018, PNAS) which is citation 21 in the paper. This paper is only mentioned peripherally in a parenthetical citation in the introduction, and not explicitly discussed. Except for the Japanese sample, it would seem that the rest of the datasets are the same? If so, this needs to be very clearly noted in the paper, especially given that the 2018 paper also involves connectivity analyses and discusses the power of the combined engagement of DMN and ECN as predictor of creativity. An argument is further made in this study about the sample size being the largest to date in a creativity study, and noted here as a key feature of the present investigation. It would be critical to state explicitly whether any of the included 10 datasets have already been used in published work, and especially if the prior publications have involved connectivity analyses as predictors of creativity—as that would potentially compromise the stated novelty of the present work.

We thank the Reviewer for pointing out the incomplete information for datasets and the need to clarify how the present work differs from prior studies which used the same datasets. In the present study, most of the datasets have been analyzed in previously published studies, but the analyses and findings in this study have not been previously conducted or published. For example, the present study utilized the creativity task data collected outside the fMRI scanner from the main study of Beaty et al. 2018 (N = 168), but the task-based fMRI data used by them was not employed in the present study. Instead, in the present work, we used the resting-state fMRI data collected concurrently in that study, which has been used in the research by Orwig et al. (2021) and Kenett et al. (2020), with different analyses than in the present study. Additionally, the resting-state data from Fink et al. (2018) has not been published, though the task-based and structural MRI data from these datasets has already been published.

Critically, although prior studies have used the data analyzed in the present work to assess brain connectivity related to creativity, no prior work has conducted the dynamic functional connectivity analyses assessed in the present study. Thus, the present manuscript offers novel

findings regarding the segregation and integration of large-scale brain networks related to individual creativity. In the revised manuscript, we have added the original references for each dataset in the methods section and provided the proper description to the included datasets (p. 15):

“The datasets analyzed in the current study for meta-analytic were from five centers in Austria⁹⁷⁻¹⁰⁰, Canada¹⁰¹, China^{68,102,103}, Japan^{29,104}, and the United States^{28,105}; constituting multi-center datasets including structural MRI, resting-state fMRI, and creative ability data (assessed by divergent thinking tests). There were 10 samples from four centers and one open-access source, including 3,533 healthy participants who completed MRI scans and 2,772 participants who also completed creativity assessment. The final valid sample consisted of 2,433 participants (male = 1,113), with an average age of 21.12 years (SD = 4 years), after passing a set of exclusion criteria including failed fMRIprep running (due to poor spatial normalization and/or signal quality, and incomplete raw data), excessive head motion, and incomplete or invalid behavioral data. For these 10 datasets, the resting-state fMRI data (including UNCG, GBB_S1, GBB_S2, SLIM_S1, UG_S3, and TKU) have been published elsewhere^{68,100,103-106}; the task-fMRI data collected has also been published, but the resting-fMRI data collected during the same period was not analyzed in prior work and is included in this study (e.g., Queen, UG_S1, UG_S2, UG_S3). Importantly, for all the datasets assessed in the present research, no prior study has utilized the analyses conducted in the present work or examined the patterns of DMN-ECN dynamic interaction using resting-state data in relation to individual creative performance. For more details on each sample, see Supplementary Table 1. All local institutional review boards permitted the use of the de-identified and anonymized data. All study participants provided written informed consent at their local institution prior to participation.”

It's worth noting that we are not simply integrating existing data to form a large dataset for re-analysis or reproducibility validation (though this is also important). In this study, we investigate a novel question of whether individual creative ability can be reliably predicted by the dynamic interaction between the DMN and ECN, based on the processing characteristics of creative thinking and the dynamic reconfiguration of brain networks. Our study firstly demonstrates how the DMN and ECN dynamically interact (i.e., through segregated and integrated patterns between the two networks) to predict individual creative performance. Our findings, to some extent, suggest that intrinsic or trait-level brain dynamics related to creativity show that more creative individuals exhibit more efficient and flexible interactions between the DMN and the ECN. This perspective underscores creativity as an internally-focused set of component processes that encompasses both spontaneous associative processes and controlled executive functions. In addition, as the Reviewer mentioned, this study included large-scale, multi-center datasets with structural MRI, resting-state fMRI, and creative ability data (assessed by divergent thinking tests) from five centers in Austria, Canada, China, Japan, and the United States (N = 2,433)—constituting (to our knowledge) the largest and most ethnically diverse brain-based analysis of creativity to date. In sum, despite the present work utilizing existing datasets, we offer novel evidence regarding how dynamic interactions between brain networks relate to creative ability.

Meta-analysis approach: The terminology used in the paper suggests this is a meta-analysis, though it is not clear from the methodology that a meta-analytic approach was used, including examination of assumptions, discussions of past literature, criteria for the selection of the datasets based on past papers (as opposed to samples of convenience) etc. This needs to be clarified. It seems that the paper pools datasets from different centers with the aim of conducting a new kind of analysis regarding ECN-DMN network switching, thus does not really function as a meta-analysis. This should be highlighted in the paper, so as to promote its novelty—as well as situated within prior work with these datasets, including the 2018 paper noted above from (mostly) the same authors. It might be important to remove any note of this work as a ‘meta-analysis’ as it does not meet the criteria for a meta-analysis, in my opinion.

We thank the Reviewer for the helpful suggestions regarding the terminology. Indeed, the meta-analysis we employed differs from traditional meta-analysis methods, such as extracting data from published papers and conducting statistical analysis on that data. In this study, we obtained the original data from these published studies and preprocessed them according to a unified standard (e.g., using fmriprep). Due to the heterogeneity in fMRI acquisition protocols across and within centers, as well as the diversity of divergent thinking measurement tools used, we were unable to pool all the data for a single analysis (although we did supplement with the results of this analysis). Instead, we analyzed each dataset separately and then integrated the results using meta-analytic approach. Therefore, we have consistently used the term "meta-analytical network neuroscience" and "meta-analytical approach" throughout the paper to avoid any confusion regarding the research methods we employed. We have emphasized this method in the introduction of the revised manuscript (p. 4-5):

“In the present study, we investigate whether individual differences in creative ability can be reliably predicted by the dynamic interaction between the DMN and ECN. To this end, we analyze large-scale, multi-center datasets including structural MRI, resting-state fMRI, and creative ability data (assessed by divergent thinking tests administered outside the scanner) from five centers in Austria, Canada, China, Japan, and the United States (N = 2,433)—constituting (to our knowledge) the largest and most ethnically diverse brain-based analysis of creativity to date. We applied a meta-analytic network neuroscience approach to integrate the findings by conducting a new analysis using the raw data from each dataset. ”

Cross-cultural differences: There is plenty of literature discussing hypotheses regarding cross-cultural differences in creativity behaviorally. However, these don’t translate necessarily into neural predictions. What are the hypothesized neural differences in large-scale network connectivity that would differ among cultures? Why? What would be the mechanism? The cross-cultural differences angle is sprinkled throughout the paper, but there is very limited rationale and literature presented across the paper, through which one can evaluate the claims.

We thank the Reviewer for raising this important point and acknowledge that we unintentionally overgeneralized the methods and conclusions discussed in our manuscript. As the Reviewer mentioned, the concept of "culture-invariant" is complex, involving experimental

design and methods, among other factors, which were simplified in this study. In this manuscript, we aim to emphasize that our findings are cross-cultural and reproducible; however, socioculturally relevant demographics that reflect cultural diversity, such as ethnicity, religion, and nationality, were not collected or assessed. Our study involves the assessment of data collected from several countries; specifically, resting-state fMRI data along with data from various assessments of creativity. However, this may not constitute a cross-culturally informed study. Based on this, we have decided to remove statements related to cross-cultural aspects from the revised manuscript to avoid misleading readers and to better focus on our core topic—the dynamic switching between brain networks predicts creative ability.

Quantification of switches: The process via which the 'switches' from DMN-ECN and their 'balance' was determined is insufficiently presented in the main portion of the paper. There is no discussion of the quantification of these key variables that are only briefly discussed in the methods. This needs to be included very early on in the paper—especially if the authors argue it's a novel aspect of the methodological approach (i.e., their argument that the integration-segregation has not been examined thoroughly before). On this point, I am not sure that what is being calculated here as a switch truly represents a dynamic switch between the two network states. This is discussed in a very muddled way and somewhat hidden in the methods, thus it is not clear whether (a) the method followed represents anything new relative to past analyses, or (b) that the method actually captures network 'switching' or integration—the premise on which the paper is designed around. Given the resting-state data used here, the notable variability across datasets from an imaging perspective, and the variability in the behavioral assessments of creativity across the samples, this aspect of the analysis needs to be crystal clear and incorporated early in the paper.

We thank the Reviewer for raising this point. The neuroscientific literature on creative cognition and individual differences in creative ability aims to identify domain-general and domain-specific cognitive functions associated with particular brain regions and functional networks. The brain's functional states during the creative process can be uncovered by assessing connectivity within either static or dynamic brain networks. However, activity in static networks does not provide sufficient information about the functional changes in the brain that occur over short periods, as multiple cognitive states are recruited during an fMRI scan. Therefore, there is a need to apply dynamic reconfiguration-based functional analysis to identify the modular architectures of evolving networks during creative tasks. Similarly, for individual differences in creative ability, the reconfiguration-based method can more precisely characterize differences in brain functional connections, thereby better predicting an individual's creativity. For example, functional segregation and integration in brain FC networks have been proven to be reliable biomarkers for diverse cognitive functions (Cohen et al., 2016), and abnormalities in these connected networks have also been linked to many brain disorders (Shine et al., 2019). In summary, dynamic reconfigurations can be analyzed through both resting-state and task-based fMRI data, segmented into time windows, to better understand interactions between brain regions. This approach is more sensitive than static reconfigurations in detecting changes in cognitive states.

We acknowledge the Reviewer's point regarding the need to provide more details about

the specific method we used to investigate switching. Essentially, clarifying that we are measuring the switch between segregation and integration of brain networks (i.e., not switching from “pure” DMN activity to “pure” ECN activity). Basically, we are measuring switches in how the DMN and ECN are interacting across time (whether they are more integrated or segregated in their activity) and how this dynamic intrinsic connectivity pattern relates to creative ability. For these points, we have added more relevant content in the introduction (p. 3-4):

“Numerous neuroimaging studies have consistently found that creative thinking recruits regions within the DMN and ECN^{9,22-27}. **In addition, individual creative thinking ability can be predicted by functional interactions within and between the DMN and ECN both at rest and during creative task performance using static networks methods²⁸⁻³⁵. For example, functional connectivity features associated with the default mode, executive control, and salience networks can predict individual creative performance during divergent thinking tasks, and these features can be generalized across several independent resting-state fMRI samples²⁸. Given the roles of the DMN and ECN in spontaneous and controlled cognition, respectively, DMN-ECN connectivity is thought to reflect a coordination between spontaneous/generative and controlled/evaluative processes^{6,36,37}. However, static network approaches fail to capture the dynamic coordination of cognitive states related to reconfiguration and interactions between networks^{26,33,38,39}. Therefore, dynamic reconfiguration-based functional analyses are needed to identify specific interaction patterns between the DMN and ECN related to creative ability.**

How does the creative brain achieve dynamic coordination between spontaneity and control? According to the dynamic framework of spontaneous thought^{37,40}, creativity is a mental state that requires an optimal balance between spontaneous thought generation and goal-directed processing—corresponding to a balanced state of DMN and ECN communication. **Dual-process theories of creativity also emphasize that creative cognition involves two different phases—idea generation and evaluation—dominated by cooperation between large-scale functional brain networks including the DMN and ECN^{1,2,4,26,36,39}. Therefore, one possibility is that highly creative people can flexibly switch between segregation and integration of DMN and ECN—oscillating between states where the brain networks operate independently and cooperatively, respectively—which may reflect an optimal balance or “sweet spot” between the networks that leverages their independent and collective capacities. Despite the intuitive appeal of this theory, there is very little empirical evidence to support this claim. Several studies based on stages of creative processing have pointed out that the DMN predominantly acts on the generative phase in the early stages of creative production, whereas increased coupling between the DMN and ECN underlies the evaluative phase in the later stage^{22,39,41}, implying that the ECN may monitor and guide spontaneous associative/generative processes^{26,42-44}. Additionally, the temporal connectivity of large-scale brain networks based on resting-state fMRI data supports the dynamic functional configuration associated with creative cognition^{33,45}. However, the precise interaction patterns and the mechanistic role of this DMN-ECN coupling in creative thinking remain unclear. ”**

For the second point, we now provide additional details on the calculations of the switching and balance of DMN-ECN integration and segregation metrics in the methods section (p. 16-17):

“To determine the specific state for one cartographic profile, we compared the mean scores of regional W_T and B_T scores across the two states using an independent samples t-test. Here, one state with a higher B_T score and lower W_T score suggests cooperation and integration between DMN and ECN (i.e., integrated state, T_{In}), and the other state means segregation between the two networks (i.e., segregated state, T_{se} ; supplementary Fig. 3B). Referring to previous studies^{47,51}, we can determine which state (i.e., integrated state or segregated state) dominates the functional connections between the two networks in each time window. Across the time windows, the switching frequency that measures the transition number segregated and integrated states were calculated, which was defined as: Switching frequency = $N(T_{In} \rightarrow T_{se}) + N(T_{se} \rightarrow T_{In})$; and the balance of the two states was computed by the difference of dwell time in the two states divided by the whole time, which was defined as: Balance = $(T_{In} - T_{se}) / T_{all}$, where T_{all} is the total dwell time of T_{In} and T_{se} . **Previous studies have shown that frequent switching between dynamically segregated and integrated states over long time periods leads to balance. Consequently, switching frequency and balance exhibit an inverted U-shaped relationship (supplementary Fig. 3C)⁴⁷ ”**

Duration of resting-state scans: I may have missed this, but what was the duration of the resting state scans for each dataset? Although the literature is a little inconsistent on recommendations for optimal resting state scan length, longer scans are associated with much more reliable datasets. This needs to be included in the paper and addressed.

We agree with the Reviewer that the duration of the resting state scans may affect the reliability of the metrics derived from resting-state brain networks. Previous methodological papers have explored the stability of network metrics in relation to the duration of resting state scans. For example, according to Birn et al. (2013), it is standard to use 5–7 min of resting-state data, the test-retest reliability and across-session similarity of functional connectivity estimates can be greatly improved by increasing the imaging duration. In this study, all datasets had a scanning duration exceeding 5 minutes (ranging from 300.2 seconds to 484 seconds). As pointed out by the Reviewer, there is no definitive optimal length for resting state scans, although longer durations are generally preferred. Based on this, we have added the scan durations in Table 1 of the supplementary materials. Additionally, we included scan duration as an extra variable in the random-effects model, and the results showed that it did not affect our previously reported outcomes. Furthermore, scan duration did not act as a moderating variable to influence the overall effect. We have added these results in the results section (p. 7):

“In addition, sample size, $QB(1) = 2.66, p = .103$, age, $QB(1) = 3.66, p = .06$, scanning time, $QB(1) = 0.85, p = .36$, and gender ratio of sample, $QB(1) = 1.36, p = .244$, did not significantly moderate the overall effect, indicating that data origin (including the locations and MRI and scoring protocol) but not participant-related variables influenced the overall effect. ”

Introduction: The introduction is really broad and fails to focus clearly on the novelty and key aspects of the work that may make this paper different from others (again, not sure the number of participants is, indeed, that impressive, if all of these participants' resting-state connectivity profiles and their relation to creativity have already been reported in past published work). In general, the introduction jumps around in its terminology from large-scale network dynamics, to connectivity, to the (presumed new) idea of segregation and integration. However, it fails to highlight clearly how this terminology is fundamentally different—if at all—from much of the authors' prior work that has reported increases in connectivity between DMN-ECN in creativity relative to other tasks, what can clearly align with the use of the term integration is presented in this paper. Is it, then, that the paper discusses the exact same ideas, just presenting them now with these two terms (segregation-integration) that are long-standing in the connectivity literature, but not as prominent in the authors' prior work on this topic? This needs to be clarified, to denote whether there is anything new theoretically that is presented in this work.

Based on the Reviewer's recommendations, we have now reorganized the introduction. It is important to note that we did not rewrite this section; instead, we added more content regarding research on individual differences in creativity based on brain functional connectivity and derived special interactive patterns of DMN-ECN (dynamic segregation and integration of DMN and ECN), which are associated with potentially conducive to a more efficient cycle of idea generation and evaluation. This is a topic that existing research has not yet explored, particularly with large sample data validation. Furthermore, we clarified that although our data are sourced from previous studies, these studies did not investigate the relationship between dynamic interaction patterns of the DMN-ECN (i.e., integration and segregation) and creativity.

Discussion: Similar to the introduction, the discussion is also not particularly well focused. In the same way, for instance, there are references as to what these network dynamics represent (mindwandering? Generation? Memory?) but the paper and its methodology addresses none of these questions. I would suggest significantly condensing and refocusing the discussion to highlight the specific and novel contribution of this study, if any. A section on limitations would probably also be a good idea to include.

We thank the Reviewer for the helpful suggestions. In the revised manuscript, we reorganized and refined the discussion section. We condensed the description of the research findings (for example, we removed the first paragraph of the original text to provide a more concise summary of our findings) and focused on the consistency and differences. In addition, we emphasized the novel contributions of our findings compared to existing research, particularly regarding resting-state network dynamics relating to individual creative ability. In the discussion, we specifically highlighted that our findings, to some extent, support the importance of the generation-evaluation cycle process for divergent thinking. Due to the significant amount of modifications, please see the discussion section for text in bold font. In addition, according with the Reviewer's suggestion, we independently listed a limitations section, outlining the shortcomings of our study and future research prospects. We added the following text to the discussion (p. 14).

References:

- Birn, R. M., Molloy, E. K., Patriat, R., Parker, T., Meier, T. B., Kirk, G. R., ... & Prabhakaran, V. (2013). The effect of scan length on the reliability of resting-state fMRI connectivity estimates. *Neuroimage*, 83, 550-558.
- Cohen, J. R., & D'Esposito, M. (2016). The segregation and integration of distinct brain networks and their relationship to cognition. *Journal of Neuroscience*, 36(48), 12083-12094.
- Orwig, W., Diez, I., Vannini, P., Beaty, R., & Sepulcre, J. (2021). Creative connections: Computational semantic distance captures individual creativity and resting-state functional connectivity. *Journal of Cognitive Neuroscience*, 33(3), 499-509.
- Beaty, R. E., Kenett, Y. N., Christensen, A. P., Rosenberg, M. D., Benedek, M., Chen, Q., . . . Kane, M. J. (2018). Robust prediction of individual creative ability from brain functional connectivity. *Proc. Natl Acad. Sci. USA*, 115(5), 1087-1092.

Reviewer #2

The current study reflects a successful effort to synthesize a large collection of data for definitive testing of the DMN-ECN switching theory. The analyses performed appear to be valid, thoughtful, and rigorous. This work has likely not been attempted before based on the sheer computational (and communication) challenges involved. The large analysis was supplemented with a helpful and complementary fMRI investigation. I was impressed with the current efforts.

We appreciate the Reviewer's evaluation of our work, and hope that we have addressed their comments appropriately.

The primary issue that stands out to me is that the effect sizes observed for the DMN-ECN switching relationship to creative performance are quite modest ($r = .17$ overall, or less than 3% of the variance). It would be helpful to see the authors speak to this: while network switching is shown to be clearly involved, it doesn't appear to be a prominent predictor. This is the case even though larger networks with widespread BOLD signal as input, and correspondingly strong signal stability are used, so the weak relationship cannot be blamed on MRI signal. A large sample like this is a unique opportunity to estimate true effect size, so not discussing this seems like a missed opportunity. Of course, it runs the risk that we are making much ado about nothing - it seems possible the network switching is related to some creative process but ultimately is not itself important.

We agree with the Reviewer that highlighting the true effect size estimated using a large sample is important. A considerable body of research has focused on reproducible associations between brain structure/function and behavioral phenotypes, raising questions like: How large does the sample need to be? What kind of effect size is not inflated? These have long been central topics in brain-behavior association studies. A recent study (Marek et al., 2022) provides valuable insights into these questions, suggesting that larger sample sizes are required to replicate smaller true effect sizes (e.g., $r = 0.1$). As the sample size increases, sampling

variability decreases, allowing effect sizes to stabilize and approach their true value. Moreover, with a sample size of $N = 2000$, brain-behavior associations stabilize, with the highest correlation around $r = 0.16$.

Returning to our study, as the Reviewer mentioned, 'A large sample like this is a unique opportunity to estimate the true effect size.' In this research, we conducted a large-scale, cross-center meta-analytic network neuroscience study to examine the association between DMN-ECN dynamic interactions and divergent thinking ability. The sample size we used is sufficiently large (ranging from $N = 52$ to 1076), and the effect size falls within a reasonable range. Even so, we found that the effect size varied with sample size across different datasets, aligning with existing findings. For example, in the TKU dataset, the effect size was 0.09 ($N = 1076$), whereas in the UG_S3 dataset, it was 0.44 ($N = 52$). Because of this, we employed a meta-analytic network neuroscience approach to integrate the effect sizes from each dataset and account for the impact of sample size. Therefore, the observed $r = 0.17$ likely represents the true relationship between DMN-ECN switching and divergent thinking ability.

We have removed sections of the discussion that we considered self-evident. Instead, we now highlight that despite the modest effect size in a large sample, the findings provide a valid result regarding the relationship between DMN-ECN switching and creative performance (p. 14):

“Our approach, employs standard and acceptable meta-analytic methods, and the sample sizes of the included studies are adequate for network neuroscience research⁹³. A recent study offers valuable insights into sample sizes and true effect sizes in brain-behavioral phenotype associations, suggesting that typical sample sizes often lead to inflated effect sizes and replication failures. However, as sample sizes increase into the thousands (e.g., $N = 2000$), replication rates improve, and effect size inflation decreases, even though the true associations may be smaller⁸⁸. Therefore, the observed effect size in our study likely reflects the true relationship between DMN-ECN dynamic interaction and divergent thinking ability. ”

Yet, we recognize that the "true" effect size is small, and thus the switching between DMN-ECN integration and segregation is only one factor contributing to creative ability. Therefore, we provided an interpretation of the results in the limitations section (p. 14):

“We acknowledge several limitations in our study. First, we recognize that the “true” effect size is small, meaning that the dynamic reconfiguration between the DMN and ECN is only one factor contributing to creative ability. Based on resting-state fMRI data, our meta-analytic findings suggest that more efficient DMN-ECN interactions support higher creative ability; alternatively, as individuals develop their creative skills, that may increase the efficiency of DMN-ECN interactions, even at rest (e.g., Ref ⁸⁴). Importantly, many other factors beyond the dynamic DMN-ECN patterns observed here are certainly involved in creative ability, such as personality, attention, perception, curiosity, and creative self-beliefs. Yet, similar DMN-ECN interaction patterns have been found for other^{85,86} forms of spontaneous thinking (e.g., mind wandering). Therefore, future research is needed to further explore large-scale brain networks and their dynamic

interactions across different creative task contexts, to distinguish between the recruitment of ordinary and creativity-specific neural patterns. ”

Of course, the results are what they are, and the authors of such an impressive analysis should not be penalized for not finding a more striking result. But I think theoretical exploration of this point would be valuable. Is the current paper a "Pyrrhic victory" for DMN-ECN switching theory?

While the effect size observed in our study is modest, we believe it still contributes meaningful evidence to the ongoing topic on DMN-ECN dynamic interactions and creative performance. The smaller effect size may, in fact, reflect the true nature of such relationships, as large-scale studies often reveal more realistic associations compared to smaller, potentially inflated findings. In the revised discussion, we clarify the implications of our findings, particularly the extension of the DMN-ECN switching theory, and highlight that our results align with the latest findings from refined experimental research, such as task-based fMRI and iEEG studies (p. 12-13):

“A body of studies have shown that creative thinking is generally dependent on the capacity of the DMN to synchronize with other brain networks^{26,39}, such as the ECN⁴¹, salience network⁶³, sensorimotor network⁶⁴⁻⁶⁷, and visual network^{68,69}. While coupling between the DMN and ECN has been consistently highlighted as a marker of creativity, such a coupling has been largely shown in “static” functional connectivity research and the role of a specific coupling dynamic as a driver of creativity has so far been largely speculative by analyzing the whole-brain functional connectivity^{1,70}. However, few studies have focused on examining the interactions within these networks and how they influence creative cognition^{26,39}. Although our research relies on methods involving brain–behavioral phenotype associations, by combining evidence from both resting-state networks with a large sample size and cognitive function networks (i.e., task-based fMRI), our findings further support the idea that functional coupling among regions in the DMN and ECN may reflect a domain-general mechanism of creative cognition. Importantly, a new dynamic interaction pattern between the DMN and ECN was observed in this study, namely that higher creative individuals exhibit optimal neural cooperation between the DMN and ECN. Specifically, the degree of balance between the segregated and integrated states demonstrated an inverted U-shaped relationship with creative performance, where too much (or too little) DMN-ECN coupling may impair creative performance. This finding aligns with previous creativity theories, proposing that creative ideation emerges from the delicate balance between flexibility and stability of cognitive states⁷¹⁻⁷³. This equilibrium is crucial for maintaining the optimal combination of novelty and utility throughout the process of creative cognition⁷¹.

Previous research suggested that the DMN may be centrally involved in active recollection of memories, associative processes that yield diverse ideas; whereas the ECN may act to guide associative processes through monitoring, inhibition, and related top-down control processes^{27,42,61}. These studies explain the roles of the DMN, ECN, and other networks in creative cognition two stages: generation and evaluation^{4,22,26,39}. Previous

creativity theories have suggested that creativity is a continuum⁷⁴ and creative outputs occur along a set of cognitive continuums, such as the divergent–convergent thinking continuum, the defocused–focused continuum, the spontaneous–deliberate continuum, the mind-wandering–mindfulness continuum, etc.⁷⁵. In the present neurocognitive framework, such cognitive continuums can map onto the DMN–ECN coupling, in which the DMN and ECN together realize the cycle of generation and evaluation. For example, DMN-ECN coupling might reflect forms of goal-directed memory retrieval and episodic simulation in the stage of idea generation that requires cognitive control^{6,76}; whereas similar coupling patterns act to constrain and direct evaluation processes to output ideas that are both novel and appropriate in the stage of idea evaluation⁴¹. Some evidence suggests that different proportions of DMN and ECN activity within coupling patterns might correspond to generative and evaluative stages of creative thinking^{6,22,26,39}. Thus, it is likely that dynamically shifting between generation and evaluation could provide an optimal way to produce a constant stream of creative outputs. Yet, such dynamic switching between generation and evaluation must be carefully balanced, as too much of one without the other is unlikely to produce both novel and appropriate ideas^{44,48,49,77}.

Our work further—albeit indirectly—establishes a connection between DMN-ECN switching dynamics and the theoretical generation-evaluation creativity model. Direct evidence supporting this hypothesis is needed, and future research should aim to elucidate the neural basis and underlying mechanisms driving this balance. ”

A more minor point concerns the quadratic model fit analysis. First, isn't model fit going to be biased towards being superior when adding another model term (due to overfitting, if nothing else)? Second, the goal is to test a theory that balanced DMN-ECN integration/segregation is advantageous, i.e., an inverted U function. But the statistical test is simply whether a quadratic model is a better fit. without bearing on whether the quadratic model in question is an inverted or upright "u". Therefore, an upright U such as in GBB_S1, while inconsistent with the theory, would end up supporting it by virtue of having a quadratic fit.

Regarding the balance of DMN-ECN integration/segregation, we hypothesized that higher creative performance may benefit from a functional balance between segregation and integration in these brain networks. That is, in the case of the dynamic interaction between DMN and ECN, neither excessive segregation nor integration would enhance creative thinking. Therefore, an inverted U-shaped function for this relationship is what we hoped to observe. In the statistical analysis, the quadratic model compared to the linear model introduces additional predictor terms. However, to test whether the quadratic model fits better than the linear model, we performed a differential test. In this study, ANOVA and the Akaike Information Criterion (AIC) were used to determine which model better fit the data if both the linear and quadratic models were significant based on the F statistic. A smaller AIC value indicated a better fit, and a difference of > 2 in AIC was considered to reflect a significant difference between the models.

We agree with the Reviewer that the quadratic model test should align with our hypothesis, and their observation regarding an upright U, such as in GBB_S1. We examined the model fitting for this dataset, and both the linear model and the quadratic model were non-significant. Furthermore, the differences between these two models were also not significant. As mentioned

by the Reviewer, we did not constrain the quadratic coefficient (e.g., to be negative) during model estimation. In the 10 datasets, we found that the quadratic term was negative in 7 datasets, while the remaining 3 datasets had positive tendency. However, these models with positive values (i.e., upright U model) were not significant.

Also, one of the strengths of the paper is that it draws upon public data for high reproducibility. However, while an additional, new dataset is reported alongside these data, it is not shared, which is not in keeping with the ethic that made the paper possible.

In our study, we used 10 datasets from five centers. Due to varying data-sharing permissions across centers, we have made all accessible data available, including pre-processed time series data from six datasets, behavioral data, and code. The processed data generated in this study are available on the Open Science Framework [<https://osf.io/83arw/>]. Please note that legal and ethical rules prevent the sharing of some of the data, but we have shared (or can share upon request) everything that we are allowed to. In addition, some of the raw data used in the present study have been publicly available and analyzed in previous studies.

Overall this is an important and impressive effort that I feel should be published albeit with some reflection on the topics above.

We thank the Reviewer for their positive and encouraging words and thoughtful comments.

References:

Marek, S., Tervo-Clemmens, B., Calabro, F. J., Montez, D. F., Kay, B. P., Hatoum, A. S., . . . Hendrickson, T. J. (2022). Reproducible brain-wide association studies require thousands of individuals. *Nature*, 603(7902), 654-660.

Reviewer #3

Summary: The manuscript provides evidence that the brain of individuals with high creative potential (i.e., high scores on a divergent thinking task) display a balanced back and forth between two meta-states (i.e., segregation and integration) of two large scale brain networks (i.e., the default mode network and the executive function network) during resting states and while performing a divergent thinking task. They first performed a meta- and mega-analysis of 10 studies originating from sites covering 3 different continents and that included close to 2,500 participants. These analysis revealed that the resting states of individuals scoring high on divergent thinking tasks was associated 1) with more transitions back and forth between independent activity (i.e., segregation) and coordinated activity (i.e., integration) of the default mode and executive function networks and 2) with an equal amount of time spent in either meta-state. In an external validation study involving 31 participants, they found evidence that the patterns observed in the meta- and mega-analysis during resting state also applies to performance of a divergent thinking task. Compared to a task in which participants named common features of selected objects, having to produce original alternate uses of objects involved more transitions between the segregation and integration meta-states and individuals

with higher originality scores were more likely to spend about the same amount of time in both meta-states.

Overall impression: This is an ambitious and important body of work that nicely complements prior work on the creative mind. Among its strength are the very large datasets comprising multiple cultures across 3 continents providing consistent patterns of results in a group of 10 independent studies separately and together, across 2 different brain atlas (Schaefer and Shen). It provides new insights into the study of the creative mind by new metrics derived from a meta-states approach, and critically, it replicates the resting state results with fMRI data collected while completing a divergent thinking task. This novel, large scale, high quality and thorough work is a great contribution to the field of creative cognition.

We thank the Reviewer for the time taken to review this manuscript, we appreciate their positive evaluation and hope that we have addressed their thoughts appropriately.

Here are my suggestions for improving the quality of the manuscript:

1. My biggest issue with the manuscript as it stands is about the reasoning behind focusing on resting state. There is only a brief mention line 113-116 and some indirect connections in the following paragraph. While the introduction and discussion focus heavily on creative cognition / creative processes, the bulk of the analyses (meta- and mega-analyses) rely on drawing a connection between dynamics of resting-state connectivity and divergent thinking scores obtained outside the scanner. What is special about this particular state that could explain why it is predictive of creative abilities?

We thank the Reviewer for pointing out the weakly-described motivation for resting-state fMRI in the introduction. Over the past two decades, advances in fMRI techniques have enabled researchers to study functional activation, functional networks, and their dynamic interactions involved in creative cognition. Among these methods, resting-state functional connectivity studies have suggested that activity in the DMN contributes to the generation of candidate ideas, while executive control networks exert top-down monitoring to meet specific task goals or constraints (Beaty et al., 2016; Beaty, Silvia, Nusbaum, Jauk, & Benedek, 2014). Using brain fingerprinting methods, researchers have found stable patterns of resting-state functional connectivity that can predict individual creative abilities. Additionally, resting-state studies have shown that temporal variability of DMN connectivity correlates with divergent thinking, and the frequency of transitions between functional connectivity states is associated with creative ability (Feng et al., 2019; Sun et al., 2019; Liu et al., 2018; Gao et al., 2017; Li et al., 2017; Takeuchi et al., 2012). Although task-based fMRI can observe brain activation and connectivity patterns during creative tasks, thereby enhancing our understanding of the cognitive neuroscience of creative thinking, resting-state fMRI can also provide insights into creativity, particularly regarding individual differences. For example, higher creative individuals may exhibit a higher degree of internally directed cognition at rest, reflected in lower connectivity within primary visual systems and increased connectivity to areas of multimodal integration (Sepulcre, 2014; Sepulcre, Sabuncu, Yeo, Liu, & Johnson, 2012). In summary, resting-state fMRI combined with creativity task scores obtained outside the scanner can enhance our understanding of individual differences in creativity and inspire insights into

the mechanisms of creative thinking. In particular, analyzing dynamic functional connectivity can provide a deeper understanding of how key brain networks interact under resting-state conditions to influence individual differences in creativity. We have now added the following text to the introduction (p. 3-4):

“In addition, individual creative thinking ability can be predicted by functional interactions within and between the DMN and ECN both at rest and during creative task performance using static networks methods²⁸⁻³⁵. For example, functional connectivity features associated with the default mode, executive control, and salience networks can predict individual creative performance during divergent thinking tasks, and these features can be generalized across several independent resting-state fMRI samples²⁸. Given the roles of the DMN and ECN in spontaneous and controlled cognition, respectively, DMN-ECN connectivity is thought to reflect a coordination between spontaneous/generative and controlled/evaluative processes^{6,36,37}. However, static network approaches fail to capture the dynamic coordination of cognitive states related to reconfiguration and interactions between networks^{26,33,38,39}. Therefore, dynamic reconfiguration-based functional analyses are needed to identify specific interaction patterns between the DMN and ECN related to creative ability.

How does the creative brain achieve dynamic coordination between spontaneity and control? According to the dynamic framework of spontaneous thought^{37,40}, creativity is a mental state that requires an optimal balance between spontaneous thought generation and goal-directed processing—corresponding to a balanced state of DMN and ECN communication. **Dual-process theories of creativity also emphasize that creative cognition involves two different phases—idea generation and evaluation—dominated by cooperation between large-scale functional brain networks including the DMN and ECN^{1,2,4,26,36,39}. Therefore, one possibility is that highly creative people can flexibly switch between segregation and integration of DMN and ECN—oscillating between states where the brain networks operate independently and cooperatively, respectively—which may reflect an optimal balance or “sweet spot” between the networks that leverages their independent and collective capacities. Despite the intuitive appeal of this theory, there is very little empirical evidence to support this claim. Several studies based on stages of creative processing have pointed out that the DMN predominantly acts on the generative phase in the early stages of creative production, whereas increased coupling between the DMN and ECN underlies the evaluative phase in the later stage^{22,39,41}, implying that the ECN may monitor and guide spontaneous associative/generative processes^{26,42-44}. Additionally, the temporal connectivity of large-scale brain networks based on resting-state fMRI data supports the dynamic functional configuration associated with creative cognition^{33,45}. However, the precise interaction patterns and the mechanistic role of this DMN-ECN coupling in creative thinking remain unclear. ”**

The default network has been linked to pretty much all forms of internally generated cognition, but it seems unlikely the pattern of results described in this manuscript would be seen in an experimental task in which participants are asked to recall a past episode or engage in theory of mind. Yet, in the resting state context in which those results emerged, participants are highly

likely to experience a succession of episodic and theory of mind thoughts. Why?

We agree with the Reviewer that the DMN has been linked to nearly all forms of internally generated cognition. A large number of studies have shown that the DMN interacts with other brain networks to facilitate various internal cognitive activities, including some non-creative cognitive tasks. For example, following a manipulation that facilitates detailed episodic retrieval, Madore et al. (2019) observed stronger connectivity between a core brain network linked to episodic processing and a frontoparietal brain network linked to cognitive control during divergent thinking relative to an object association control task that requires little divergent thinking. In addition, the DMN-ECN connectivity patterns have been reported in relation to working memory (Spreng et al., 2010), mind wandering (Fox et al., 2015), and cognitive reasoning (Hearne et al., 2015).

Under a resting-state fMRI context, participants are not externally guided by any specific task, allowing for more spontaneous, undirected thought processes, such as mind-wandering, which could include a natural succession of episodic memory retrieval and ToM-related thoughts. For example, prior research has indicated that stimulus-independent, task-unrelated thought, which includes various types of spontaneous thinking (measured through questionnaires outside of the scanner), can reliably be observed through functional connectivity in the DMN and other networks, and can predict individual differences in task-unrelated thought (Kucyi et al., 2016, 2021). In the realm of creativity, research suggests that the DMN and ECN are involved in generating creative ideas, with their internal and inter-network functional connections serving as neural markers predicting individual creativity. In other words, the roles of the DMN and ECN in creative thinking are substantial. However, there is limited research focusing on delineating individual differences in creativity from a dynamic brain perspective, particularly regarding these two networks. This study demonstrates how the DMN and ECN dynamically interact—through segregated and integrated patterns—to predict individual creative performance during creative tasks.

In sum, our findings suggest that dynamic interactions between DMN and ECN at rest are related to creative ability, reflecting that more creative people more flexibly switch between these networks at rest (i.e., during internally-focused cognition, which could include episodic memory or ToM). However, future research would be necessary to determine how DMN-ECN switching relates to performance on episodic memory or ToM tasks.

The resting state is a particularly interesting context of thoughts. In the dynamic framework of thoughts (Christoff et al., 2016), thought arising in this context are likely to be relatively free of constraints, allowing exploration of low probability associations. Such situations may be propitious for explation through recombination of existence knowledge (see the NEXTUP model from chapter 8 of When Brains Dream: Understanding the Science and Mystery of Our Dreaming Minds (Zadra & Stickgold, 2021 and Sripada, C. S. (2018). An exploration/exploitation trade-off between mind wandering and goal-directed thinking. The Oxford handbook of spontaneous thought: Mind-wandering, creativity, and dreaming, 23-34). Consistently, there are many anecdotes of creative people finding creative solutions in dreams or using hypnogogic sleep for creative purposes. Our own work find resting state markers associated with creative potential with a Think Aloud task (Raffaelli, Q., Malusa, R., de Stefano,

N. A., Andrews, E., Grilli, M. D., Mills, C., ... & Andrews-Hanna, J. R. (2024). *Creative minds at rest: Creative individuals are more associative and engaged with their idle thoughts. Creativity Research Journal*, 36(3), 396-412.).

Thanks for referring us of these very relevant articles. We have added these references into the introduction section (p. 3):

“The DMN consists of cortical midline (including the medial prefrontal cortex and posterior cingulate cortex), posterior inferior parietal regions, and the medial temporal lobe; this brain network is known to involve internally-directed or self-generated thought, such as the spontaneous activation of memories, mind wandering, semantic integration, associative idle thoughts, and mental simulation—cognitive processes thought to support creative idea generation⁸⁻¹⁵...According to the dynamic framework of spontaneous thought^{37,40}, creativity is a mental state that requires an optimal balance between spontaneous thought generation and goal-directed processing—corresponding to a balanced state of DMN and ECN communication.”

Line 498-504: In the discussion, it could be interesting to further discuss the tasks and/or contexts in which the authors expect creative individuals to show a different patterns of resting-state connectivity dynamics as pointers for future research. Of note, mind wandering as it is most often defined is not necessarily spontaneous considering it can be classified as intentional, and internally directed cognition includes all forms of non-perceptual experiences, from directed one's thoughts towards writing a manuscript, which can hardly be characterized as a spontaneous process, to dream, which is extremely spontaneous (unless the person is lucid dreaming). Overall, I believe the paper would be stronger if the introduction and conclusion provided an explanation as to why the resting state appears to be predictive of creative potential.

We thank the Reviewer for raising this point. The neuroscientific literature on creative cognition and individual differences in creative ability aims to identify domain-general and domain-specific cognitive functions associated with specific brain regions and functional networks. The brain's functional states during the creative process can be uncovered by assessing connectivity within either static or dynamic brain networks. However, activity in static networks does not provide sufficient information about the functional changes in the brain that occur over short periods, as multiple cognitive states are recruited during an fMRI scan. Therefore, there is a need to apply dynamic reconfiguration-based functional analysis to identify the modular architectures of evolving networks during creative tasks. Similarly, for individual differences in creative ability, the reconfiguration-based method can more precisely characterize differences in brain functional connections, thereby better predicting an individual's creativity.

On the other hand, the Reviewers' comment helps us frame the findings as intrinsic or trait-level brain dynamics related to creativity. Thus, during rest or various tasks, higher creative individuals exhibit more efficient and flexible switching between the DMN and ECN. In the relevant sections of introduction and conclusion, we emphasize the importance of the methods used in this study for characterizing individual differences in creativity.

2. *With regards to the external validation study, why ask participants to provide common characteristics of object and rate the originality of such characteristics as a comparison to the originality of the new use of the object? It seems like a better comparison would be to ask them to generate unusual features of the object. Considering the analysis are based on originality scores on both tasks, it creates an unnecessary asymmetry between the 2 tasks. Relatedly, unlike the rs-fMRI results, more switches between segregation and interaction were not associated with higher originality scores. More switches were observed in the AUT compared to the OCT task. Could this suggest that this marker may be the product of complex decision making as opposed to creative cognition per se. What is your interpretation of this discrepancy in results?*

We thank the Reviewer for pointing out this issue. In a large number of previous studies, researchers typically used the OCT as a control task to explore brain activity patterns and cognitive mechanisms involved in generating novel uses in the AUT. This task involves recalling characteristics of objects (e.g., “metallic” or “wooden”). The AUT and OCT are highly similar in format, differing only in the nature of the response (most creative idea in the AUT and most prototypical characteristic in the OCT). Even so, the OCT generally hard to capture the novel ideas generated from the OCT, because participants were usually required to come up with a single idea within a set time (e.g., 8 seconds or 12 seconds). In this experiment, we asked participants to generate four ideas over a relatively longer period of time. We found that even when prompted to come up with conventional features, relatively novel and unique ideas were produced, which may be related to the serial order effect, though this was not explored further in our study. Nevertheless, we agree that the two tasks may not be well-matched for comparing originality. As suggested by the Reviewer, adopting the 'generate unusual features of the object' as a control task would help address this issue, and we look forward to employing this design in future research. The generation of creative ideas is the result of the interplay of multiple complex cognitive processes. Although many studies have found consistent brain activity patterns associated with creative idea generation, it is still unclear whether these brain regions and networks are specific to creative processing. Therefore, our results only partially suggest that generating new ideas in the AUT rely on the dynamic segregation and integration of the DMN and ECN, and that the balance of this interaction is particularly important.

3. *Have you considered whether there may be an interaction between the number of switches and the balance of segregation/integration? The same balance score may be obtained by a participant who only switched once between segregation and integration and a participant who switched hundreds of time within the same timeframe. Is the balance predictive of creative potential only given a specific number of transitions between states have happened or is it the case regardless of how many switches occurred? Relatedly, any intuitions as to why more transitions between segregating and integrating states are better? Shouldn't there be a point at which the switching can become excessive and thus counterproductive as is the case with dwelling, suggesting this relationship should also have a u-shape form?*

In Fig S3C, we show the relationship between switching frequency and the balance of segregated and integrated states, and this consistent pattern has been confirmed in previous

studies (Shine et al., 2016; Wang et al., 2021). This pattern indicates that a higher number of switches leads to a balance between the two states, while fewer switches suggest that only one state (segregation or integration) dominates the interaction between the DMN and ECN. Therefore, we believe that balance depends on the number of switches, but how many instances of segregation/integration are needed to achieve balance depends on factors such as the number of time windows and the participant's current task. This is indeed a very interesting and worthy issue to investigate, especially in the context of creative tasks. Our data only hint at this interaction, and future research may need to manipulate time windows (i.e., the duration of each task trial) to explore this issue further.

Based on the dynamic thinking framework and the hypothesized generation-evaluation cycle in creative thinking, we propose that the cooperation between the DMN and ECN may involve iterative cycles, leading to frequent switching and balance. If the DMN or ECN alone dominates—i.e., only segregation—or if they are fully integrated all the time, it would likely not facilitate the generation of creative ideas. Therefore, an inverted U-shape relationship seems like a reasonable hypothesis.

4. A potential limitation is that the analysis using the Shen atlas resulted in only 3 out of 10 studies showing significant patterns of results compared to 7 out of 10 using the Shaeffer atlas. While the results are convergent, the success rate appears to favor a lack of effect (30% of studies are significant, or the effect is only true for about 25% of the entire sample). Are there any known differences between the atlases that may explain this difference in results?

The difference in predicting creative ability between the Shen (Shen et al., 2017) and Schaefer atlases (Schaefer et al., 2018) could indeed be attributed to several known methodological differences. First, the Shen atlas is purely functional, based on rs-fMRI connectivity patterns, while the Schaefer atlas integrates both structural and functional data. Generally, the Shen atlas could make it more sensitive to predicting abilities that are closely tied to moment-to-moment cognitive processes using task-based fMRI, while the Schaeffer atlas could potentially be more robust for predicting general, stable traits such as intelligence, personality traits, or cognitive performance across a variety of tasks. Second, the Schaefer atlas tends to focus on large-scale brain networks (e.g., default mode network, executive control network), it may be more powerful in predicting abilities that rely on stable network interactions. Lastly, in this study, the Shaeffer atlas, with finer functional parcellation, included 300 ROIs, of which 108 ROIs were affiliated with the DMN and ECN, while the Shen atlas consists of 268 ROIs, of which 54 ROIs were affiliated with the DMN and ECN, potentially reducing predictive power. This may lead to less functional information being captured for predicting individual creative ability. We added the following text to the limitation section (p. 14):

“Another potential limitation of the present study is that the spatial resolutions of the chosen atlases, particularly the number of regions included within the DMN and ECN, may affect the overall effect of this study. Some studies have indicated that the choice of brain atlas significantly influences the strength of the association between functional connectivity and cognitive abilities⁹⁴⁻⁹⁶. Therefore, future research is needed to replicate and extend our findings using additional brain atlases with different spatial resolutions.”

5. Have you considered whether the results could have been impacted by the creativity assessment method (originality alone vs. sum of originality and fluency) ?

In 7 out of 10 datasets, the scoring method used originality alone, while in the other 3 datasets, the sum of originality and fluency was applied. Moderator analyses revealed scoring methods significantly and jointly moderated the overall effect, $QB(2) = 14.02, p < .001$. It is worth noting, however, that this is a rather coarse analysis. Ideally, we would expect all datasets to use the same scoring method to eliminate measurement heterogeneity, but achieving this in multi-center dataset research projects is challenging. We have added relevant results in the results section (p. 7):

“Datasets with scoring using originality alone ($k = 7$) have a significant and medium positive effect, $g = 0.18$, 95% CI [0.09, 0.28], $Z = 3.74, p < .001$, and datasets with scoring using the sum of originality and fluency ($k = 3$) have a weak but significant effect, $g = 0.14$, 95% CI [0.01, 0.27], $Z = 2.04, p = .042$. ”

Here are some other less important suggestions for improvement in order of appearance in the text:

1. Line 68: *I would not refer to externally-oriented processes when you describe the function of the ECN as it confuses the point you are trying to make. The important ECN function you want to highlight is that when coupled with the DMN, it is helpful in evaluating and selecting appropriate answers (refer to Ellamil et al., 2012)*

We thank the Reviewer for pointing out this issue and sharing a more appropriate citation with us. We have now modified the ECN function and also included the citation in the manuscript (p. 3):

“The ECN consists of lateral prefrontal and anterior inferior parietal regions, and when coupled with the DMN, supports controlled semantic retrieval and cognitive flexibility, which benefits the selection and evaluation of creative ideas¹⁶⁻²¹.”

2. Line 87: *the US is actually not a continent, America or North America, which contains both the US and Canada, is a continent.*

We have corrected the statement.

3. Line 89-90: *this sentence suggest the ECN is solely responsible for evaluative processes, while the subsequent sentence correctly clarifies it is the coupling between DMN and ECN that supports this function.*

We agree with the Reviewer that this sentence may have caused confusion for readers. In the revised manuscript, we have rewritten this sentence for clarity (p. 3):

“Dual-process theories of creativity also emphasize that creative cognition involves two different phases—idea generation and evaluation—dominated by cooperation between large-scale functional brain networks including the DMN and ECN^{1,2,4,26,36,39}. ”

4. Line 104-110: a bit nitpicky, but considering you mention generation and evaluation in that order, and that segregation maps to generation while integration maps to evaluation, I would order these elements in the same way throughout the manuscript: first segregation then integration.

We have revised the manuscript according to the suggestion of the reviewer.

5. Line 124-133: this paragraph has interesting but difficult to grasp ideas. It would be helpful to flesh it out a bit. For instance, hyperconnectivity would be expected to be related with rigid cognition while very low levels of connectivity would be associated with a lack of coherence.

We have now revised and adjusted this paragraph (p. 4):

“By contrast, hyper-connectivity (i.e., increased positive connectivity) between the DMN and the ECN, or other networks, is associated with rigid behaviors and thoughts linked to certain psychiatric conditions (e.g., autism spectrum disorder), while hypo-connectivity (i.e., decreased positive connectivity) is associated with impairments in executive function and social cognition⁵²⁻⁵⁴. Returning to the present study, no research to date has investigated dynamic interactions between the DMN and ECN in creative thinking regarding which patterns of switching between segregated and integrated states can benefit individual creativity.”

6. Line 149: Specify the AUT were performed outside the scan for the meta-analytic studies.

We have clarified this in the relevant part of the manuscript.

7. Line 261: ‘intelligence, regarded as control task’. This bit is confusing. Do you mean a control/comparison condition? It appears from the supplementals that intelligence was assessed with a variety of different tasks. Please clarify. On a related note, it could be useful to have a supplemental figure/table in which you present these results and in which one of the column would describe the task being used (e.g., site: UNCG, intelligence assessments: ‘three measures of fluid intelligence (2): the number series task, the letter sets task, and the series completion task from the Culture Fair Intelligence Test’, results). I understand the results are not significant so I’ll leave this at your discretion.

Thanks for raising this point. Given the conditional relationship between creativity and intelligence, we conducted a meta-analysis to determine whether intelligence, regarded as a control task, showed the same pattern of effects as the creativity condition. Our intention was to provide evidence that the switching effect was also specific to creative thinking and could not be explained by general intelligence. We have included more information, including correlation between creative performance and switching frequency, sample size, and intelligence measurement tools in the supplementary Table S7.

8. Line 416: *Here as well as many other places in the manuscript, be sure to specify your meta-analyses on resting-state analyses. Specify as well when prior work is based on resting-state data or a creativity task. Considering the framing of the paper, a reader may be easily lead to believe this was done based on fMRI data from creativity tasks.*

Throughout the manuscript, we have specified in each figure which type of fMRI data (resting-state fMRI or task-based fMRI) was used for the findings of this study. In particular, in the discussion section, we have clarified the research findings based on the methods employed (resting-state fMRI or task-based fMRI).

9. Line 446-449: *this statement seems extremely aligned with the results of Ellamil et al., 2012 who is not cited there.*

We have added “Some evidence suggests that different proportions of DMN and ECN activity within coupling patterns might correspond to generative and evaluative stages of creative thinking (Ellamil et al., 2012; Lloyd-Cox et al., 2022).” to our list of evidence in this sentence.

10. Figure 2: *I assume the scores are all z-scores? If so, specify in the legend. I would also consider adding the sample size next to the data site (e.g., UNCG (n = 169)).*

We computed the correlation between creative performance (i.e., divergent thinking ability) and switching frequency (the integration and segregation of the DMN and ECN) while controlling for gender, age, mean framewise displacement (FD), and global mean signal. Therefore, both the x and y axes are represented as z-scores. We have added the sample size for each dataset and clarified the x and y axis titles in the legend of this figure.

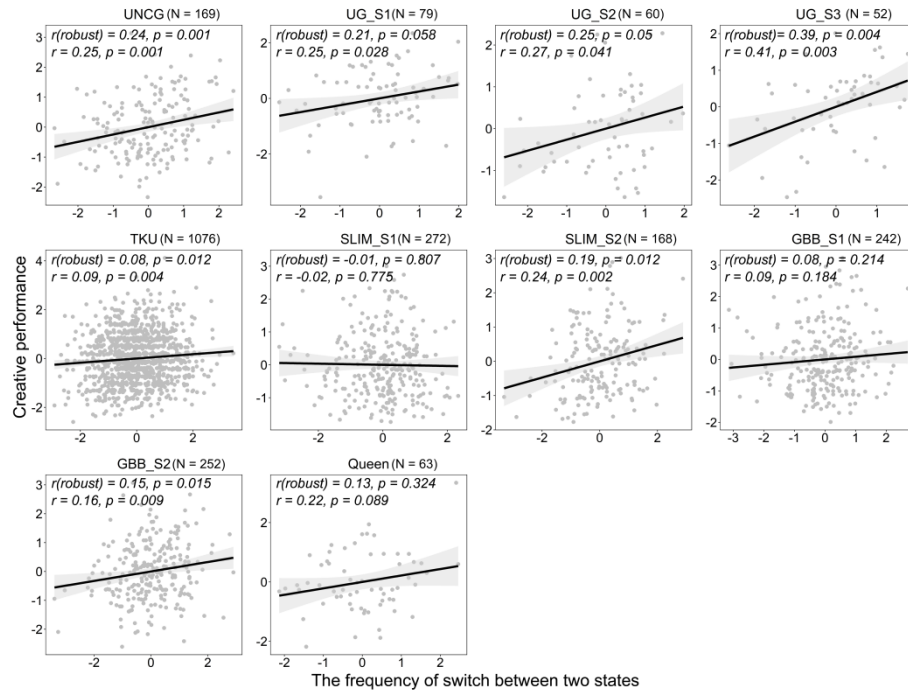


Fig. 2. The scatterplots show the Pearson correlations between creative performance (y axis) and the switching frequency of DMN-ECN segregation and integration (x axis) using resting-state fMRI data from each dataset. The $r(\text{robust})$ indicated the value of robust correlation in each dataset. Both the x and y axes are standardized value after adjusting for gender, age, mean framewise displacement (FD), and global mean signal.

11. Figure 5: I would consider adding statistics for the overall effect (black lines). Additionally, I would indicate which side is extreme integration and which side is extreme segregation and that the center (0) is the sweet spot.

We have now added black lines to represent the overall effect and included the legend. In Fig. 5B, we have marked the areas of extreme integration, extreme segregation, and the optimal balance (sweet spot).

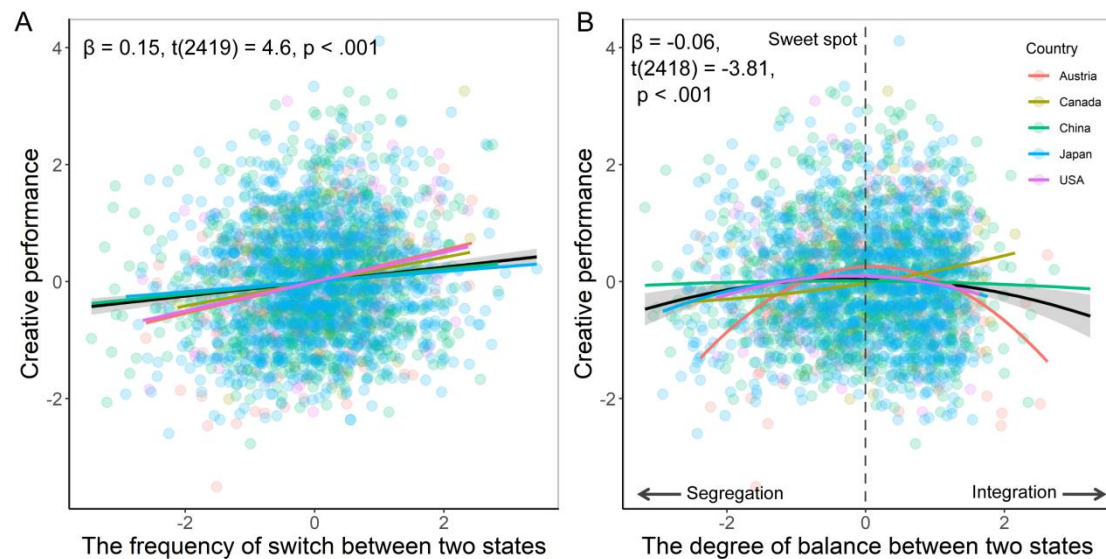


Fig. 5. Mixed effect models. (A) The linear relationship between creative performance and switching frequency between segregated and integrated DMN-ECN states (calculated using resting-state fMRI data); The black line marks the overall trend ($\beta = 0.15$, $t(2419) = 4.6$, $p < .001$). **(B)** The quadratic relationship between creativity score and functional balance between segregated and integrated DMN-ECN states (calculated using resting-state fMRI data); The black line marks the overall trend ($\beta = -0.06$, $t(2418) = -3.81$, $p < .001$), while the colored lines depict trends for each center. The left side of the x-axis indicates extreme segregation, the right side indicates extreme integration, and the dotted line in the center represents the optimal balance or "sweet spot."

12. Figure 6: A. Think Aloud refers to an actual task that is becoming popular to assess thoughts in real-time. My understanding is that participants just voiced aloud their answers, not every thought that popped into their mind during the process of generating the answers. If that is the case, I would use a different terminology so as not to create confusion. B. States' number on the y-axis is confusing. I think this refers to the average number of times a brain state was initiated. I would consider a less confusing label, maybe something like Number of occurrences? E-H: indicate statistics and significance, or at least significance.

In the revised Figure 6:

(A) We have changed "think aloud novel ideas" to "speak novel ideas out loud"

(B) We agree with the reviewer and have updated the y-axis title to "Number of occurrences."

(E - H) We have included the statistics and significance in the figure.

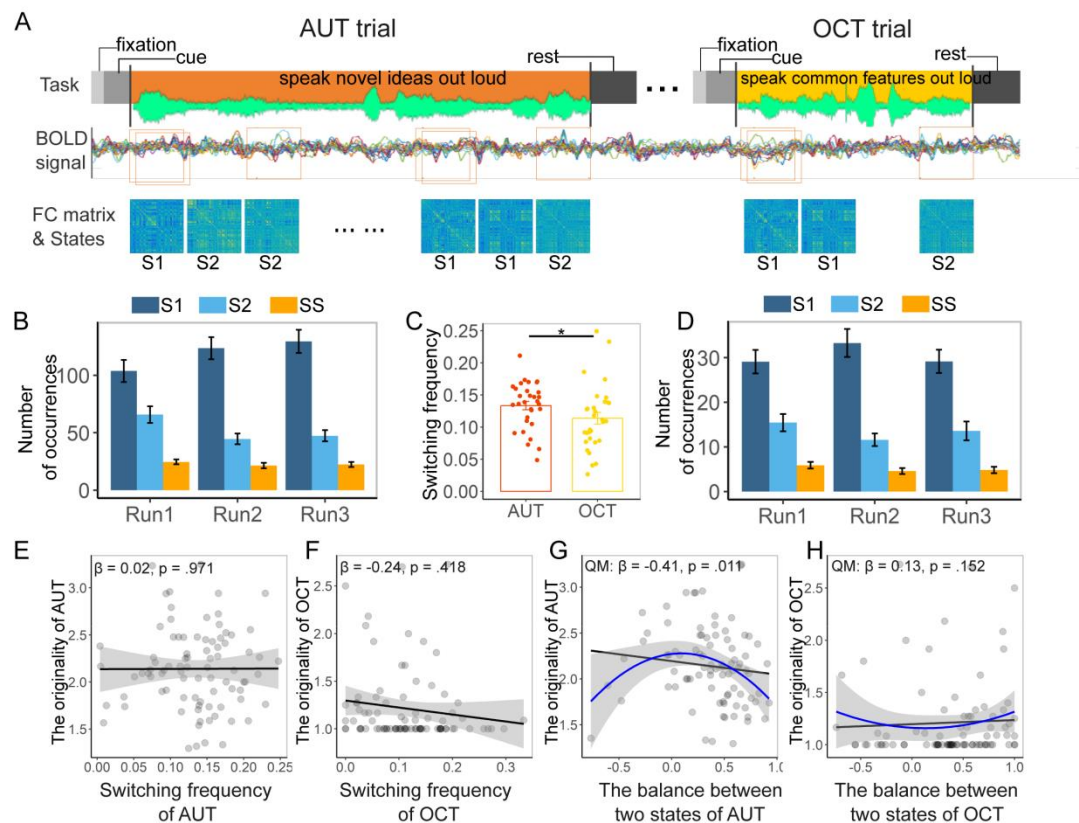


Fig. 6. fMRI task design, main analysis, and results. (A) Experimental paradigm of the

divergent thinking task, in which participants had to complete an Alternate Uses Task (AUT) and an Object Characteristics Task (OCT) during fMRI scanning. The task paradigm consisted of a fixation cross (1 s), a cue indicating the upcoming condition (“novel uses” or “common characteristics”; 4 s), a thinking period presenting an object cue in text (60 s for AUT; 30 s for OCT). **Participants responded by pressing a key and speaking their responses out loud into an MRI-compatible microphone until they either generated four ideas or ran out of thinking time. This was followed by a rest period of at least 6 seconds, or the remaining time from the thinking phase if applicable..** Task fMRI data were preprocessed using fmriprep, and then time courses were extracted from 106 ROIs affiliated with the default and executive control networks derived from Schaefer Atlas; subsequently, a sliding-window approach was used to compute the functional connectivity (FC) matrix and each matrix was partitioned into segregated (state 1, S1) and integrated (state 2, S2) states using k-means clustering. (B) The left panel shows the mean number of segregated, integrated, and switching states (SS) during the AUT task across three runs. (C) The average switching frequency for the AUT and OCT task, and paired-sample t-tests comparing AUT v.s. OCT (the error bar represents the standard errors) * $p < .05$. (D) The right panel shows the mean number of segregated, integrated states, and switching during the OCT task across three runs. (E&F) The scatterplots show the Pearson correlations between the originality score (i.e., creative performance in the task, y-axis) and the switching frequency of DMN-ECN segregation and integration (x-axis) in AUT and OCT, respectively. (G&H) Linear (black fitted line) and quadratic relationship (i.e., quadratic model, QM; blue fitted line) of originality score (y-axis) and DMN-ECN segregation and integration balance (x-axis), and with the comparison between linear fitted model and quadratic fitted model for AUT and OCT, respectively.

13. Supplementary Table S2: please indicate the variables involved in the correlations. I assume the left side is age x creative achievement and the right side is age x intelligence. As it stands, there is no way to know from the table.

[We have modified Table S2 to make this clearer.](#)

14. Specify in each figure whether the fMRI data is resting-state or task-based.

[We have specified the type of fMRI data in each figure.](#)

References:

- Beaty, R. E., Benedek, M., Barry Kaufman, S., & Silvia, P. J. (2015). Default and executive network coupling supports creative idea production. *Scientific reports*, 5(1), 10964.
- Beaty, R. E., Benedek, M., Silvia, P. J., & Schacter, D. L. (2016). Creative cognition and brain network dynamics. *Trends Cogn. Sci.*, 20(2), 87-95.
- Christoff, K., Irving, Z. C., Fox, K. C., Spreng, R. N., & Andrews-Hanna, J. R. (2016). Mind-wandering as spontaneous thought: a dynamic framework. *Nat. Rev. Neurosci.*, 17(11), 718-731.
- Ellamil, M., Dobson, C., Beeman, M., & Christoff, K. (2012). Evaluative and generative modes of thought during the creative process. *Neuroimage*, 59(2), 1783-1794.

doi:10.1016/j.neuroimage.2011.08.008

- Feng, Q., He, L., Yang, W., Zhang, Y., Wu, X., & Qiu, J. (2019). Verbal creativity is correlated with the dynamic reconfiguration of brain networks in the resting state. *Frontiers in psychology*, 10, 894.
- Fox, K. C., & Christoff, K. (2018). *The Oxford handbook of spontaneous thought: mind-wandering, creativity, and dreaming*: Oxford University Press.
- Li, J., Zhang, D., Liang, A., Liang, B., Wang, Z., Cai, Y., . . . Jiao, B. (2017). High transition frequencies of dynamic functional connectivity states in the creative brain. *Sci. Rep.*, 7.
- Raffaelli, Q., Malusa, R., de Stefano, N.-A., Andrews, E., Grilli, M. D., Mills, C., . . . Andrews-Hanna, J. R. (2024). Creative minds at rest: creative individuals are more associative and engaged with their idle thoughts. *Creativity Research Journal*, 36(3), 396-412.
- Schaefer, A., Kong, R., Gordon, E. M., Laumann, T. O., Zuo, X.-N., Holmes, A. J., . . . Yeo, B. T. (2018). Local-global parcellation of the human cerebral cortex from intrinsic functional connectivity MRI. *Cereb. Cortex.*, 28(9), 3095-3114.
- Shen, X., Finn, E. S., Scheinost, D., Rosenberg, M. D., Chun, M. M., Papademetris, X., & Constable, R. T. (2017). Using connectome-based predictive modeling to predict individual behavior from brain connectivity. *Nat. Protoc.*, 12(3), 506-518.
- Sepulcre, J. (2014). Integration of visual and motor functional streams in the human brain. *Neuroscience letters*, 567, 68-73.
- Sepulcre, J., Sabuncu, M. R., Yeo, T. B., Liu, H., & Johnson, K. A. (2012). Stepwise connectivity of the modal cortex reveals the multimodal organization of the human brain. *Journal of Neuroscience*, 32(31), 10649-10661.
- Shine, J. M., Bissett, P. G., Bell, P. T., Koyejo, O., Balsters, J. H., Gorgolewski, K. J., . . . Poldrack, R. A. (2016). The dynamics of functional brain networks: integrated network states during cognitive task performance. *Neuron*, 92(2), 544-554.

Reviewer #2:

The authors have made effective changes and I am happy to endorse publication of the manuscript in its current form.

We thank the Reviewer for their praise of our efforts in revising the manuscript, and for endorsing our manuscript for publication.

Reviewer #3:

I appreciate the efforts of the authors in taking to heart our suggestions. I am pleased to see the manuscript has significantly improved as a result. However, I am afraid I am still confused when reading the introduction and conclusion as to the reasoning of using resting-state analyses. While I believe these are important results worthy of publication, it would still be important to explain to the reader why.

We appreciate the Reviewer for acknowledging that our manuscript has substantially improved and for providing substantive and detailed suggestions to help us address the remaining points.

As it stands, the introduction is greatly framed to justify the direct validation part of the research, in which participants performed the creativity data inside the scanner. The first paragraph puts the emphasis on creative thought and highlights its implementation relies on the DN and ECN. The second describes these networks before the third links the dual-step process of creativity or other related theories of creative thinking such as that of the dynamic framework of spontaneous thought to the authors' hypothesis that creativity requires a sweet spot between DN acting alone for generation and acting with the ECN for goal-directed evaluation. By this time, which is about half the introduction, the only thing I know about the resting-state is that it can be predictive of creative potential based on activity that mimics that observed during creative thinking. That is not a strong considering the manuscript is balanced towards resting-state analysis (2433 participants for the resting-state vs. 31 participants for the in-scanner creativity task).

The first hint comes in paragraph 4, lines 119-123: 'From the perspective of individual differences, people who have higher creative thinking abilities—potentially conducive to a more efficient cycle of generation and evaluation—may also exhibit altered dynamics of large-scale brain networks (namely, the DMN and ECN) at rest'. This and the following sentence suggests that based on prior work, a relationship may be observed, but does not hint as to why. The following paragraph I think tries to suggest it may have to do with more efficient memory retrieval process but the connection with resting-state and creative thinking is not clear. By the end of the introduction, my expectations as a reader is that the paper is going to focus on creative thinking and maybe look at resting-state as a secondary analysis. However, the analyses are 95% resting-state.

What is still missing is some argument(s) or line(s) of evidence that links more clearly the resting-state to creative thinking in a way that justifies looking at both and expecting similar results in terms of brain dynamics? Something that could be located somewhere after line 122 or in the 4th paragraph. Otherwise, it feels as if you equate resting-state and creative thoughts.

Potential arguments are:

- that the resting-state represents the intrinsic state of the brain and is therefore predictive of performance in various cognitive tasks
- high creative potential individuals use their resting time to explore their mind, a process that is similar to the creative process
- resting-state and creative thinking are similar in terms of the cognitive processes involved and thus the pattern of brain dynamics is similar across both thinking contexts
- the semantic network of high creative potential individuals has been showed to differ. Resting-state may be a time during which such semantic networks are being built while creative thinking is a time during which they are being practiced
- other potential avenues are hinted about by the authors in their rebuttal: differences. 'For example, higher creative individuals may exhibit a higher degree of internally directed cognition at rest (Sepulcre, 2014; Sepulcre, Sabuncu, Yeo, Liu, & Johnson, 2012)' AND 'Under a resting-state fMRI context, participants are not externally guided by any specific task, allowing for more spontaneous, undirected thought processes'

Whether it is one or a combination of these, or some other arguments I have not considered, bridging this gap in reasoning would greatly benefit the paper, especially considering the journal is aimed at a broader audience. It does not have to be long (a couple sentences would do), but it has to be there, especially because considering the scope of the study, it has the potential of becoming a reference article.

*To address the concern raised by the Reviewer regarding better contextualizing the resting-state analysis, we have now strengthened our introduction to more clearly explain the relationship between resting-state network dynamics and creative ability. We have added text (**bold font**) in paragraph 4 (p. 4):*

“This dynamic reconfiguration of brain network connectivity can be divided into two distinct patterns or “states” that the brain routinely occupies: segregation and integration. The segregated pattern corresponds to independent processing within networks, whereas the integrated pattern corresponds to cooperation between networks⁴⁶. Previous research has reported the importance of brain network segregation and integration for performance on diverse cognitive tasks⁴⁷, although no prior work has examined such brain network dynamics in relation to creativity. Several studies have, however, observed variations in temporal cooperation between functional networks during creative cognition, suggesting the existence of a possible dynamic transition between functional segregation and integration^{33, 41}. **From the perspective of individual differences, highly creative individuals are more likely to engage in internally directed cognition during rest, which is characterized by intrinsic functional networks and their interactions^{1, 48, 49}. Given that resting-state functional networks shape cognitive task activations⁵⁰, individuals with higher creative thinking abilities—potentially conducive to a more efficient cycle of generation and evaluation—may also exhibit altered dynamics of large-scale brain networks (namely, the DMN**

and ECN) at rest^{51, 52}. **Studies have consistently shown that intrinsic network dynamics during rest reflect fundamental organizational properties that predict individual differences in cognitive abilities^{47, 53, 54, 55}. The pattern and frequency of network switching between segregated and integrated states appears particularly important, as it indicates the brain's capacity to flexibly coordinate different cognitive processes^{55, 56, 57, 58}. Examining these dynamics during rest allows us to characterize stable individual differences in network organization across large samples, complementing and extending insights from task-based studies of creative cognition. This approach is especially valuable given evidence that creative ability relates to intrinsic patterns of brain network interaction that persist across both rest and task states.** Consistent with this view, dynamic connectivity studies have reported that the temporal variability of resting-state functional connectivity among regions within DMN and ECN was positively related to creative thinking ability^{45, 59}. Further, a recent study provided a more nuanced understanding of the neurocognitive mechanisms of the creative brain, indicating that generative and evaluative stages may involve different combinations of associative and controlled processes, and thus recruit different proportions of DMN and ECN activity⁶. ”

Similarly in the conclusion, commenting/speculating as to what happens during the resting-state, at the neural level and/or experiential/behavioral levels, that explains why it is 1) predictive of creative potential and 2) matching the neural patterns observed during creative thinking would nicely tie everything together.

Based on this comment, we have now enhanced the discussion to more explicitly connect our resting-state findings to the task-based validation results, emphasizing how similar patterns of network dynamics emerge in both contexts and specifically predict creative performance (p. 13):

“Our meta-analytic analyses revealed that creative performance can be reliably predicted from the frequency of switches between the segregated and integrated states of the DMN and ECN at rest: people who switch between these states more often produce more original ideas. Furthermore, high creative thinking ability was associated with a balance between the segregated and integrated states because frequent transitions between these states provided a means to maintain this balance. **The convergence between these resting-state patterns across a large sample and their selective emergence during creative task performance (compared to control tasks) suggests these network dynamics represent a specific marker of creative ability. These findings advance our understanding of the neural mechanisms of creativity by identifying specific patterns of network interaction that characterize both the capacity for and active engagement in creative thought.**”