

Macroscale brain states support the control of semantic cognition



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Reviewers' comments:

Reviewer #1 (Remarks to the Author):

The aim of this study was to investigate how the brain can support different flavours of controlled semantic cognition (global association vs feature matching). To this end, the authors built on previous research that has demonstrated differences in the patterns of activations elicited by different types of semantic tasks, semantic vs non-semantic tasks, and easy vs hard conditions. The novelty of this paper is concurrently investigating how the activation patterns evoked by these three types of cognitive manipulations relate to each other, as well as to whole-brain "states" as defined by the three main dimensions that explain variance in resting-state functional connectivity (also known as gradients).

The authors capitalized on three datasets, including task-based and resting-state fMRI data. The use of individualized parcellations to account for individual variability in functional neuroanatomy across individuals is a notable methodological strength. The analyses revealed differences in how the regions sensitive to increased control demands in the two semantic tasks relate to the three functional connectivity gradients. On this basis, the authors argue that controlled semantic processing relies on at least two brain "states", depending on the specific type of information the task demands attention to.

This study also demonstrates how the principal gradients of functional connectivity can be used as a coordinate system of brain "states" to inform our understanding of the neural underpinnings of cognition and further facilitate comparison between task-evoked activations across diverse tasks, datasets, and perhaps even populations. This approach can therefore be useful for researchers interested in investigating the neural basis of cognition in health and disease.

I really like the use of examples in the introductory paragraph, which aids comprehension of the phenomena under study. I also appreciate that the authors plotted thresholded as well as unthresholded activation maps.

Although generally clear and well-written, I believe the introduction would benefit from additional clarification of terminology and rationale, as outlined below.

Major Comments:

1. While integral to the manuscript, the default mode network (DMN) lacks a clear definition regarding its comprising brain regions.
2. The term "state" is employed in various contexts such as "brain state space", "task state", and "state of cognition", but lacks a precise definition within the scope of this manuscript.
3. Further refinement of the rationale is needed, particularly concerning:
 - 3.1. The role of the DMN in long-term memory representation.
 - 3.2. The theoretical background explaining why global association versus feature matching tasks might be supported by different brain "states", and the hypothesis that feature matching might be more closely related to non-semantic control.
 - 3.3. The importance of investigating whether global semantic associations lead to more anterior activations than feature selection.

Minor Comments:

- It would be helpful to include a picture showing the major brain networks mentioned in the manuscript (ideally using the same parcellation scheme used for the main results).
- With regard to the brain plots, showing colours on the same scale would aid direct visual comparison of effect sizes.
- On line 292, the authors claim: "We found that responses to difficulty in global association were more anterior compared to feature matching in the left lateral prefrontal, medial prefrontal, and left posterior temporal cortex, (Figure 3c)". However, Figure 3c does not show such an anterior-posterior distinction in mPFC in terms of activation.
- The p-value mentioned on line 206 doesn't match the one shown in Figure 2a.
- It is not clear what it means for the task demands to be "superficially matched". Could you expand?
- This statement on line 106 needs references: "Conversely, controlled non-semantic states are often associated with anti-correlation between control and DMN networks".
- On line 325, the authors state: 32% of brain regions in the semantic association task overlapped with non-semantic control regions that showed hard versus easy activation in either spatial working memory or math tasks (purple in Figure 4c), while 71% of parcels in the semantic feature

matching task showed this pattern of overlap (blue in Figure 4d). The colors mentioned don't match the ones in the figures. Same issue on line 353.

- Since "2AFC" is only used twice, there is no need to use the abbreviation.

Reviewer #2 (Remarks to the Author):

Wang and colleagues acquired and analyzed fMRI data from semantic association and semantic feature matching tasks that were parametrically modulated for difficulty. This allowed identification of brain regions responding to higher cognitive demands in different semantic contexts. They found an anterior-posterior distinction of semantic association from semantic feature matching tasks with greater difficulty. Using fMRI data from math and spatial working memory tasks with hard and easy levels, they identify regions in the MDN associated with non-semantic cognitive control. Overlaps of these maps were quantified to contrast difficulty effects across contexts, and feature matching difficulty showed more regions in common with non-semantic difficulty than association difficulty, which may relate to the association task's reliance on stored semantic knowledge as opposed to physical attributes. Regions identified as MDN through overlap of non-semantic tasks with greater activation for hard versus easy trials were used to extract and compare the difficulty effects in association versus feature matching, which showed feature matching to have a stronger relationship with MDN.

Cortical distance was measured from the sensory-motor cortex to the cognitive control parcels, categorized into four classes of overlaps from the set of maps (association only, association with non-semantic, feature matching with non-semantic, and feature matching only). Results showed feature matching to have the closest proximity and association to have the greatest (and more anterior) proximity from sensory-motor regions. These results were presented and discussed, with relevant references to the literature, to support that there is a topological distinction between association and feature matching semantic control.

Unthresholded maps were correlated to whole brain state space in three functional dimensions, allowing a relation of semantic control regions in different contexts to heteromodal-unimodal, primary sensory, and control-DMN intrinsic connectivity features. Semantic association difficulty was positively correlated with the first dimension while feature matching difficulty was negatively correlated with the first dimension and positively correlated with the third dimension. These results were interpreted to indicate that association engages more domain-general regions, drawing upon both control and default mode networks. Meanwhile, demanding feature matching more resembles non-semantic difficulty demands, which all rely more on cognitive control networks than DMN.

The manuscript appears valid in methods and statistics, integrating state-of-the-art analysis methods, and using FDR correction for multiple comparison and spin permutation for null models. Results were presented in a clear and attractive fashion, and methods were described clearly. The discussion further references appropriate literature that aligns with the findings and fairly supports the main conclusions. The authors display and interpret the results of a complex set of analyses in a manner that is easy to comprehend and integrate into the current understanding of semantic and other control networks.

Delineating different aspects of semantic cognition (association vs. feature similarity) in a range of difficulty while including contrasting non-semantic (math and spatial working memory) tasks that also range in difficulty allows for a clear interpretation of the relationship of semantic cognition to the global topography of brain states in relation to difficulty across domains. The results and conclusions presented in this manuscript are of interest for those in the field of cognitive neuroscience, especially those exploring the roles of domain-general networks in relation to semantic cognition. The abstract, introduction, and conclusion of the manuscript are appropriate for the study and results presented. Overall, I found the manuscript easy to follow while simultaneously presenting complex concepts with unique conclusions that will contribute to the understanding of control network dynamics and topography in the brain.

We would like to thank the reviewers for their extremely helpful and thoughtful comments, which have allowed us to improve the quality of this manuscript. Here we explain the changes we have made to the paper – with these changes also highlighted in the manuscript file. Our responses to the reviewers' comments are highlighted in bold, and **corrections in the main text are marked with a yellow highlight**. We really hope that we have been able to address all the reviewers' concerns adequately and that the paper is now suitable for publication in the *Communications Biology*.

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The aim of this study was to investigate how the brain can support different flavours of controlled semantic cognition (global association vs feature matching). To this end, the authors built on previous research that has demonstrated differences in the patterns of activations elicited by different types of semantic tasks, semantic vs non-semantic tasks, and easy vs hard conditions. The novelty of this paper is concurrently investigating how the activation patterns evoked by these three types of cognitive manipulations relate to each other, as well as to whole-brain “states” as defined by the three main dimensions that explain variance in resting-state functional connectivity (also known as gradients).

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Many thanks for your very positive comments.

Although generally clear and well-written, I believe the introduction would benefit from additional clarification of terminology and rationale, as outlined below.

Major Comments:

1. While integral to the manuscript, the default mode network (DMN) lacks a clear definition regarding its comprising brain regions.

Many thanks for raising this great question. The Default Mode Network (DMN) is crucial to our study, and we have defined it and discussed its role in long-term memory on Page 5 Line 102 – 107.

The DMN comprises a set of widely distributed brain regions in the parietal, temporal and frontal cortex. These regions play a pivotal role when cognition relies on information from memory (Raichle, 2015; Smallwood et al., 2021; Vatansever et al., 2017; Wang et al., 2024): DMN is active during periods of future thinking (Schacter et al., 2012), the application of acquired task rules (Vatansever et al., 2017), semantic decisions that depend on strong conceptual associations (Davey

et al., 2016), and during spatial or numerical decisions made based on memory rather than perceptual input (Konishi et al., 2015; Smallwood et al., 2013).

2. The term "state" is employed in various contexts such as "brain state space", "task state", and "state of cognition", but lacks a precise definition within the scope of this manuscript.

Thank you for pointing out this important clarification. We have detailed these concepts. To clarify, a "brain state" refers to a specific pattern of neuronal activity across the brain that reflects different types of cognitive processes. "State of cognition" and "task state" describe the varying functional states of the brain as it engages in different cognitive activities and specific tasks, respectively. Please see Page 4 Line 55 – 59, Page 4 Line 71 – 75, and Page 5 Line 95 – 98.

However, current descriptions of brain networks underpinning conceptual representation and control fall short in explaining how we generate diverse brain states (i.e., patterns of brain activity or functional coupling that reflect different types of cognitive processes), which can support these different retrieval patterns.

Given that the MDN is recruited across various domains and the SCN is implicated in diverse semantic tasks, a pivotal question arises: How do we generate whole-brain states—i.e., patterns of correlation and anti-correlation across brain regions that relate to the configuration of large-scale networks—which allow us to focus on different aspects of knowledge appropriate for a specific task context (Greene et al., 2023)?

Different states of controlled cognition (i.e., the varying functional states of the brain as it engages in different cognitive activities) may reflect specific configurations of large-scale brain networks, which can be characterized in terms of multiple dimensions of intrinsic connectivity (Bolt et al., 2022; Margulies et al., 2016).

3. Further refinement of the rationale is needed, particularly concerning:

Many thanks for your constructive suggestions. We have add the corresponding rationale for each part.

3.1. The role of the DMN in long-term memory representation.

We added the role of the DMN in long-term memory representation. Please see Page 5 Line 102 – 107.

The DMN comprises a set of widely distributed brain regions in the parietal, temporal and frontal cortex. These regions play a pivotal role when cognition relies on information from memory (Raichle, 2015; Smallwood et al., 2021; Vatansever et al., 2017; Wang et al., 2024): DMN is active during periods of future thinking (Schacter et al., 2012), the application of acquired task rules (Vatansever et al., 2017), semantic decisions that depend on strong conceptual associations (Davey et al., 2016), and during spatial or numerical decisions made based on memory rather than perceptual input (Konishi et al., 2015; Smallwood et al., 2013).

3.2. The theoretical background explaining why global association versus feature matching tasks might be supported by different brain "states", and the hypothesis that feature matching might be more closely related to non-semantic control.

Thank you for your constructive suggestion. We have elaborated on why global association tasks and feature matching tasks are supported by different brain states and provided detailed explanations on how feature matching tasks are particularly linked to non-semantic control processes. This information is thoroughly discussed on Page 6 Line 108 – 121.

When controlled semantic retrieval is required to establish relevant thoughts and behaviors without an externally-imposed goal (e.g., focusing on globally weak associations relevant to the context), heteromodal regions that support long-term semantic knowledge are thought to integrate with control processes tailored to the circumstances (Davey et al., 2016; Luppi et al., 2024, 2022; Wang et al., 2020).

Conversely, states of top-down control and selection, which are prevalent in feature matching, often involve anti-correlation between control networks and DMN (Wang et al., 2020; 2024). Semantic feature matching judgments are thought to rely on a domain-general selection process that operates post-retrieval to resolve competition among active representations (Badre et al., 2005; Badre and Wagner, 2007; Gold et al., 2006). This process might demand the engagement of domain-general control mechanisms together with sensory-motor systems, necessitating the separation of DMN from executive networks within heteromodal cortex. These distinctions motivated us to predict that different cognitive tasks would employ varied neural mechanisms and control strategies (i.e., brain states), with the feature matching task aligning more closely with non-semantic control functions than the retrieval of weak associations.

3.3. The importance of investigating whether global semantic associations lead to more anterior activations than feature selection.

Thank you for prompting further explanation on this important aspect of our research. We have expanded upon why it is crucial to explore whether global semantic associations lead to more anterior activations compared to feature selection. Please see Page 5 Line 89 – 94.

Consequently, we hypothesize that the difficulty effects in semantic association and semantic feature matching will not only show topographical differences in the left lateral prefrontal cortex but that these differences will extend to anterior and posterior areas of the posterior temporal and medial prefrontal areas, where the SCN and MDN are adjacent (Jackson, 2021; Noonan et al., 2013). Should this hypothesis be validated, it would elucidate how the functional architecture of the brain varies according to the cognitive demands of semantic tasks. It would indicate that adjacent, yet functionally distinct large-scale neural networks are systematically organized on the brain's surface, supporting different facets of semantic control. This would support the contemporary understanding

that cortical geometry, or the spatial layout of brain regions, critically influences their functions (Margulies et al., 2016; Pang et al., 2023; Wang et al., 2024).

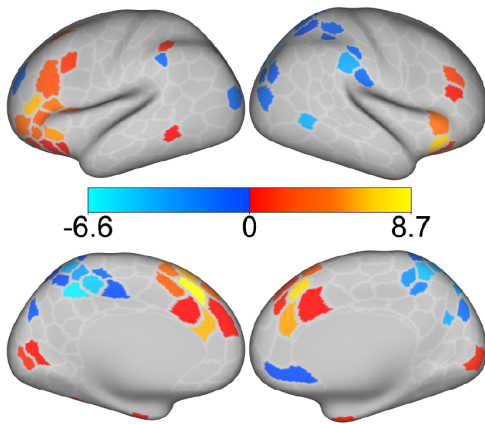
Minor Comments:

4. It would be helpful to include a picture showing the major brain networks mentioned in the manuscript (ideally using the same parcellation scheme used for the main results).

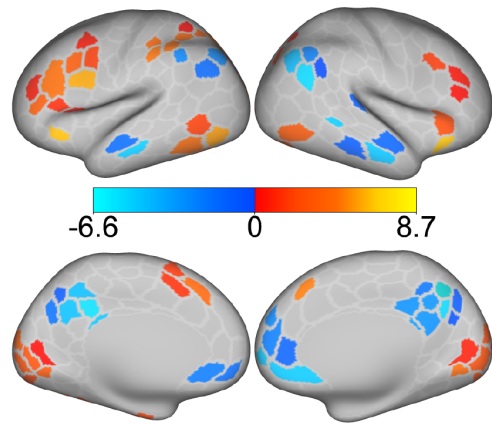
Thank you for your valuable suggestion. We have added a figure that depicts the parcellation and a figure shows the major brain networks discussed in our manuscript, specifically the domain-general control network and the DMN, using the same parcellation scheme employed for our main results (Kong et al., 2021). Please refer to Figure 3e and 3f for this detailed illustration (Page 15, Page 16 Line 341 – 345).

Difficulty effects of semantic tasks

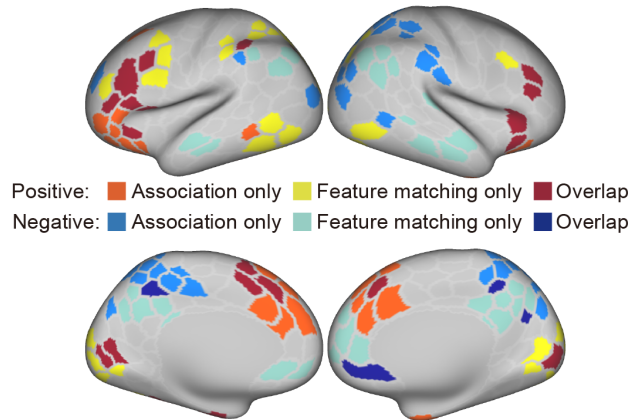
a. Difficulty effect of association strength



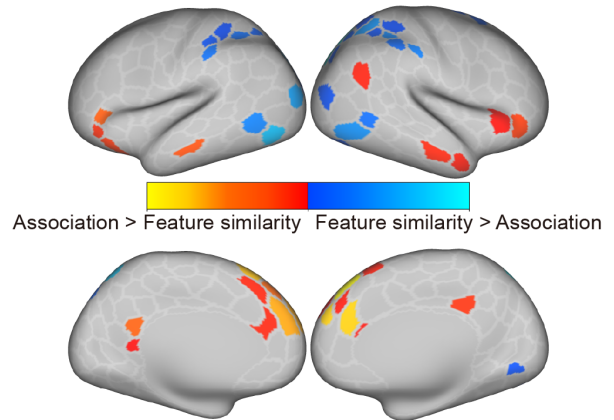
b. Difficulty effect of feature similarity



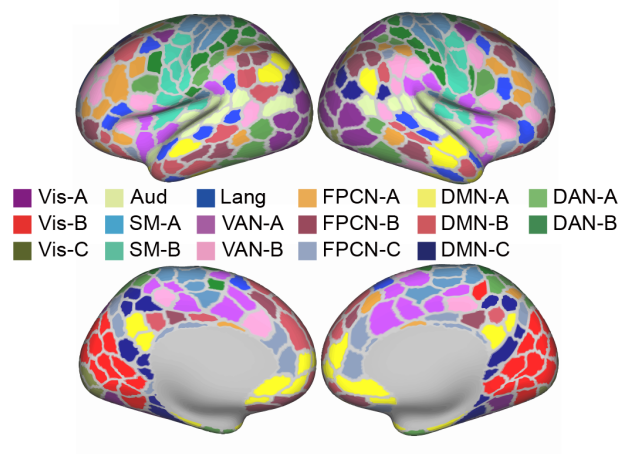
c. Overlap of difficulty effect



d. Differences in difficulty effect



e. Parcellation (N=400)



f. Regions of FPCN-A and DMN

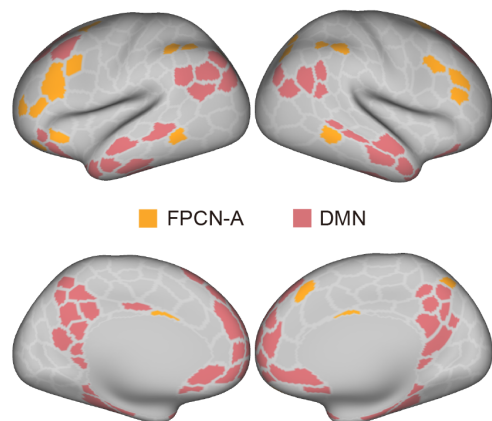


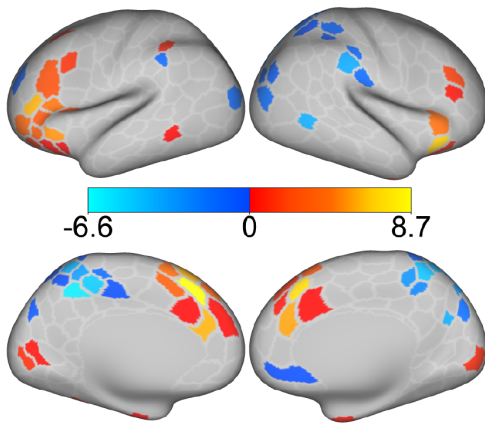
Figure 3. e – Individual-specific parcellation divided the whole brain into 400 parcels across 17 networks (Kong et al., 2021). f – The regions of the domain-general control network – FPCN (Wang et al., 2024) and DMN which includes its three subnetworks. Vis = Visual, Aud = Auditory, SM = Sensory-motor, DAN = Dorsal attention network, VAN = Ventral attention network, FPCN = Fronto-parietal control network, Lang = Language, DMN = Default mode network.

5. With regard to the brain plots, showing colours on the same scale would aid direct visual comparison of effect sizes.

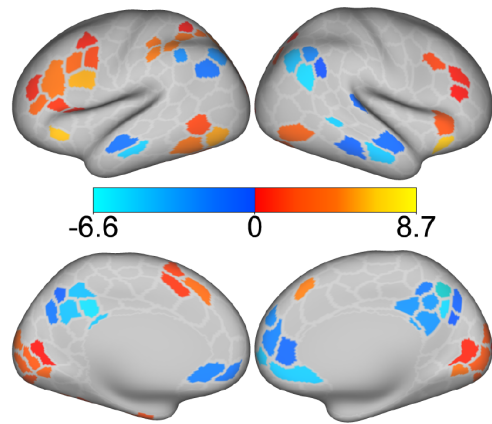
Thank you for your constructive suggestion. We have standardized the color scale for the brain plots in Figures 3a, 3b, 4a, 4b, 6a, and 6b to enhance clarity and comparability.

Difficulty effects of semantic tasks

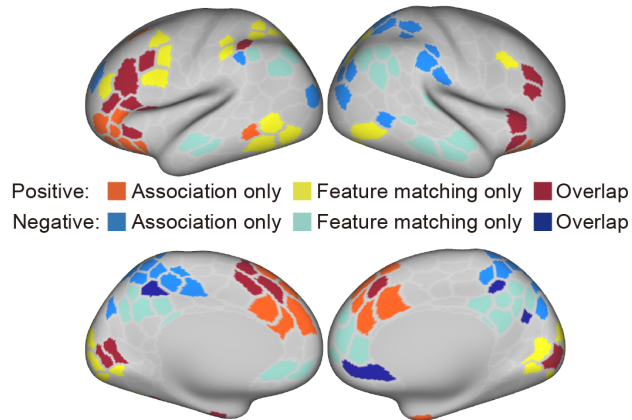
a. Difficulty effect of association strength



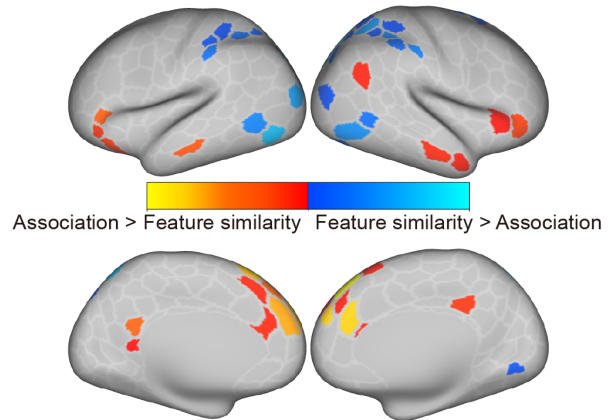
b. Difficulty effect of feature similarity



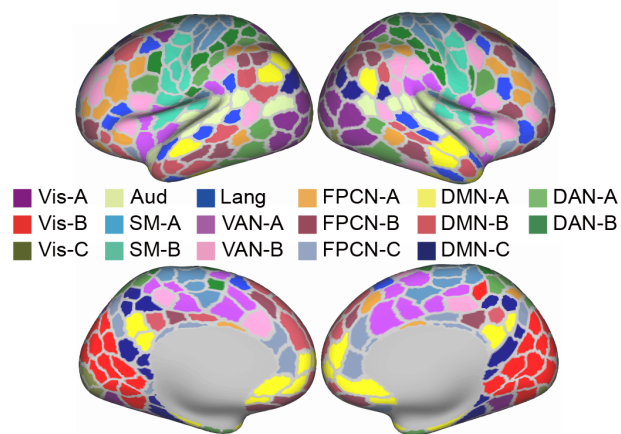
c. Overlap of difficulty effect



d. Differences in difficulty effect



e. Parcellation (N=400)



f. Regions of FPCN-A and DMN

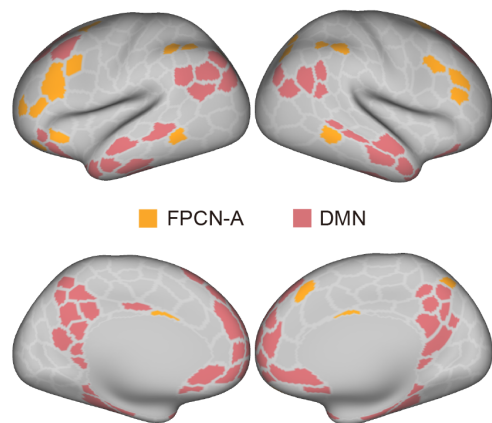
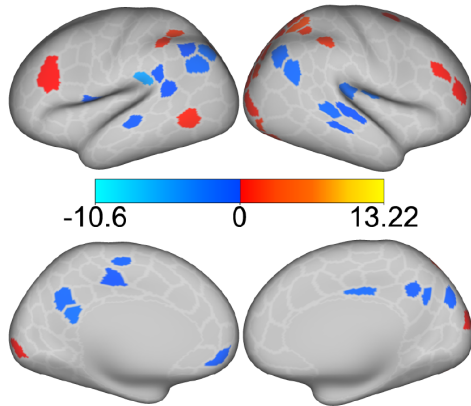


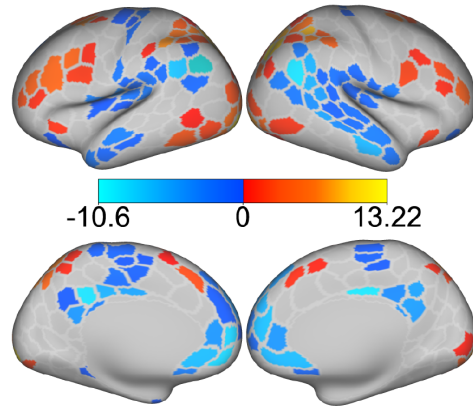
Figure 3. (Page 15)

Difficulty effects of non-semantic tasks

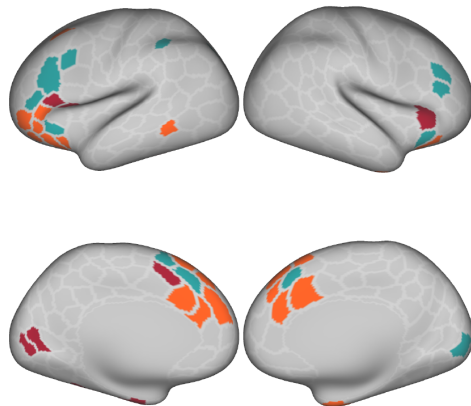
a. Difficulty effect of spatial working memory



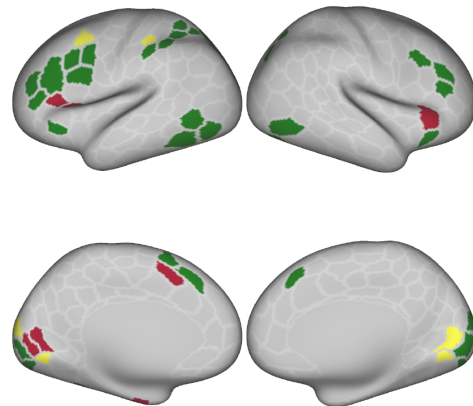
b. Difficulty effect of math



c. Overlap between non-semantic and association difficulty

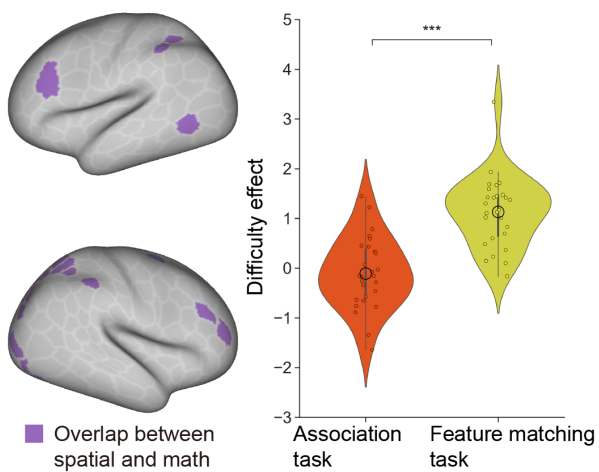


d. Overlap between non-semantic and feature matching difficulty



■ Association only ■ Association overlap with either spatial or math ■ Both semantic tasks
■ Feature matching only ■ Feature matching overlap with either spatial or math

e. Comparison of difficulty effects across tasks



f. Global minimum distance to sensory-motor cortex

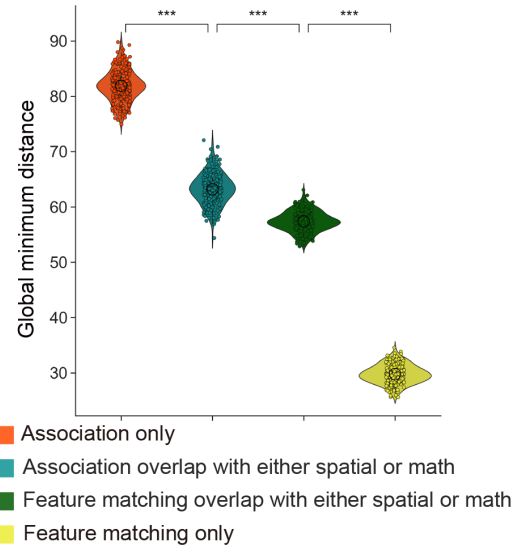


Figure 4. (Page 19)

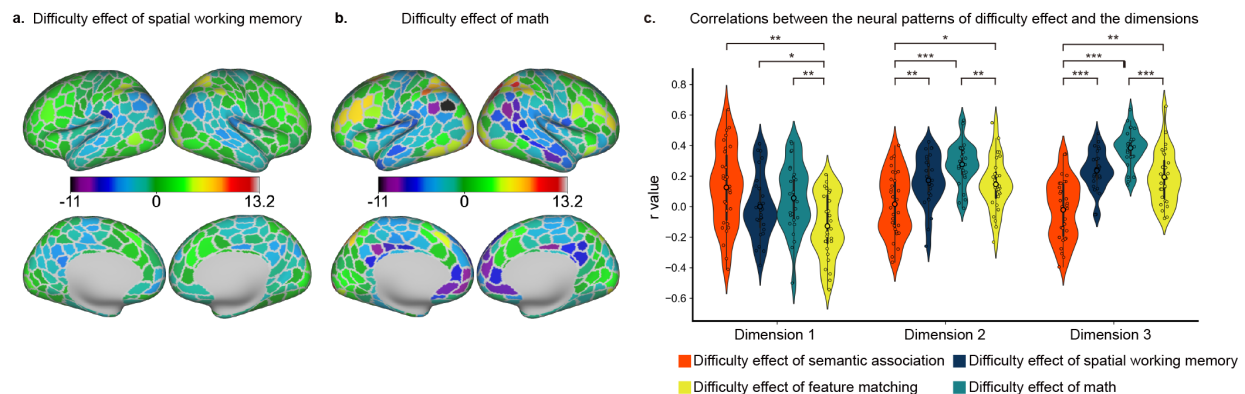


Figure 6. (Page 25)

6. On line 292, the authors claim: “We found that responses to difficulty in global association were more anterior compared to feature matching in the left lateral prefrontal, medial prefrontal, and left posterior temporal cortex, (Figure 3c)“. However, Figure 3c does not show such an anterior-posterior distinction in mPFC in terms of activation.

Thank you for your attention to detail regarding the anterior-posterior distinctions in our findings. Upon reevaluating Figure 3c, we acknowledge that the distinction in the medial prefrontal cortex (mPFC) is less pronounced than in other regions. The figure illustrates that some parcels in the mPFC, marked in orange, are specific to difficulty in global association, while others, colored in dark red, respond to difficulty in both global association and feature matching. The parcels specific to global association are somewhat anterior to those involved in both tasks, though this distinction is subtle, and there are no parcels that respond specifically to feature matching.

We have moderated the language in our manuscript to reflect this nuance more accurately. Please refer to the revised description on Page 13 Line 310 – 315, where we now state that the anterior-posterior distinction in the mPFC is relatively weak.

We found that responses to difficulty in global association judgements were more anterior compared to feature matching in the left lateral prefrontal, medial prefrontal, and left posterior temporal cortex (although the anterior-posterior distinction in the medial prefrontal cortex was relatively weak given the absence of difficulty effects specific to feature matching within this region; Figure 3c).

7. The p-value mentioned on line 206 doesn't match the one shown in Figure 2a.

Thank you for pointing out this discrepancy. The p-value mentioned on line 206 is derived from a linear mixed-effects model, which provides a comprehensive statistical analysis but is complex to visualize. To maintain clarity in our visual presentation, Figure 2 instead displays Pearson correlations that illustrate the relationships between association strength and response time, feature similarity and response time, and feature similarity and accuracy. Although these visualizations stem from a different statistical approach, they support the conclusions of the linear mixed-effects models.

We have explained this methodological distinction and the reason behind our choice of visualization in the manuscript to prevent any confusion. Please see the updated text on Page 10 Line 227 – 232 for a detailed explanation.

To maintain clarity in our visual presentation, Figure 2 instead displays Pearson correlations that illustrate the relationships between association strength and response time, feature similarity and response time, and feature similarity and accuracy. Although these visualizations stem from a different statistical approach, they support the conclusions of the linear mixed-effects models.

8. It is not clear what it means for the task demands to be “superficially matched”. Could you expand?

Thank you for pointing out the need for clarification. We have explained "superficially matched" in our manuscript. Please see the updated description on Page 7 Line 153 – 156.

In this way, we found a variety of brain states underpinned controlled cognition even when tasks were superficially matched – i.e., utilizing identical stimuli and with the same presentation and response format, such that the primary distinction between these tasks concerned the nature of the controlled retrieval process.

9. This statement on line 106 needs references: "Conversely, controlled non-semantic states are often associated with anti-correlation between control and DMN networks".

Thank you for highlighting this point. We have added the necessary references to support this statement and thoroughly document the established research in this area. Please refer to the updated text on Page 6 Lines 112 – 114.

Conversely, states of top-down control and selection, which are prevalent in feature matching, often involve anti-correlation between control networks and DMN (Wang et al., 2020; 2024).

10. On line 325, the authors state: 32% of brain regions in the semantic association task overlapped with non-semantic control regions that showed hard versus easy activation in either spatial working memory or math tasks (purple in Figure 4c), while 71% of parcels in the semantic feature matching task showed this pattern of overlap (blue in Figure 4d). The colors mentioned don't match the ones in the figures. Same issue on line 353.

Thank you for pointing out this discrepancy. We apologize for the oversight and have corrected the color descriptions in Figure 4c and 4d to ensure they match the figures accurately. Please see Page 16 Line 352 – 356 and Page 17 Line 378 – 381.

Specifically, 32% of brain regions in the semantic association task overlapped with non-semantic control regions that showed hard versus easy activation in either spatial working memory or math tasks (turquoise in Figure 4c), while 71% of parcels in the semantic feature matching task showed this pattern of overlap (green in Figure 4d).

We categorized parcels into four distinct groups based on their response to difficulty: (i) parcels responsive to difficulty solely during the semantic association task (orange in Figure 4c), (ii) parcels showing difficulty effects in both semantic association and non-semantic tasks (turquoise in Figure 4c), (iii) parcels showing difficulty effects in both feature matching and non-semantic tasks (green in Figure 4d), and (iv) parcels responsive only to difficulty during the semantic feature matching task (yellow in Figure 4d).

11. Since "2AFC" is only used twice, there is no need to use the abbreviation.

Thank you for your suggestion. We have deleted 2AFC. Please see Page 31 Line 708 – 709 and Page 32 Line 716 – 718.

This was followed by a decision phase, which showed two grids side by side (i.e., two-alternative forced choice paradigm).

Participants were presented with an addition expression on the screen for 1.45s and, subsequently made a two-alternative forced choice decision indicating their solution within 1s.

Reviewer #2 (Remarks to the Author):

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association from semantic feature matching tasks with greater difficulty. Using fMRI data from math and spatial working memory tasks with hard and easy levels, they identify regions in the MDN associated with non-semantic cognitive control. Overlaps of these maps were quantified to contrast difficulty effects across contexts, and feature matching difficulty showed more regions in common with non-semantic difficulty than association difficulty, which may relate to the association task's reliance on stored semantic knowledge as opposed to physical attributes. Regions identified as MDN through overlap of non-semantic tasks with greater activation for hard versus easy trials were used to extract and compare the difficulty effects in association versus feature matching, which showed feature matching to have a stronger relationship with MDN. Cortical distance was measured from the sensory-motor cortex to the cognitive control parcels, categorized into four classes of overlaps from the set of maps (association only, association with non-semantic, feature matching with non-semantic, and feature matching only). Results showed feature matching to have the closest proximity and association to have the greatest (and more anterior) proximity from sensory-motor regions. These results were presented and discussed, with relevant references to the literature, to support that there is a topological distinction between association and feature matching semantic control.

Unthresholded maps were correlated to whole brain state space in three functional dimensions, allowing a relation of semantic control regions in different contexts to heteromodal-unimodal, primary sensory, and control-DMN intrinsic connectivity features. Semantic association difficulty was positively correlated with the first dimension while feature matching difficulty was negatively correlated with the first dimension and positively correlated with the third dimension. These results were interpreted to indicate that association engages more domain-general regions, drawing upon both control and default mode networks. Meanwhile, demanding feature matching more resembles non-semantic difficulty demands, which all rely more on cognitive control networks than DMN.

The manuscript appears valid in methods and statistics, integrating state-of-the-art analysis methods, and using FDR correction for multiple comparison and spin

permutation for null models. Results were presented in a clear and attractive fashion, and methods were described clearly. The discussion further references appropriate literature that aligns with the findings and fairly supports the main conclusions. The authors display and interpret the results of a complex set of analyses in a manner that is easy to comprehend and integrate into the current understanding of semantic and other control networks.

Delineating different aspects of semantic cognition (association vs. feature similarity) in a range of difficulty while including contrasting non-semantic (math and spatial working memory) tasks that also range in difficulty allows for a clear interpretation of the relationship of semantic cognition to the global topography of brain states in relation to difficulty across domains. The results and conclusions presented in this manuscript are of interest for those in the field of cognitive neuroscience, especially those exploring the roles of domain-general networks in relation to semantic cognition. The abstract, introduction, and conclusion of the manuscript are appropriate for the study and results presented. Overall, I found the manuscript easy to follow while simultaneously presenting complex concepts with unique conclusions that will contribute to the understanding of control network dynamics and topography in the brain.

Many thanks for your very positive comments.

REVIEWERS' COMMENTS:

Reviewer #1 (Remarks to the Author):

I am very happy with the authors' response to my comments. This work offers interesting insights into controlled semantic cognition, and I am looking forward to seeing it published!

Reviewer #2 (Remarks to the Author):

In reviewing the manuscript once more, as I initially had no specific comments to the authors, I will address the rebuttal to Reviewer #1. Overall, I found that the modifications made in response to specific reviewer comments appropriately addressed the issues highlighted. Moreover, the changes enhanced the clarity of the study rationale. The figure additions and modifications also enhanced the ease of visual interpretation of the results.

Only minor suggestions regarding the response to Reviewer #1's comments:

1) The description of comprising brain regions of the DMN could still be more specifically defined in the cortex.

2) While your reply in the rebuttal letter clearly associates "state of cognition" and "task state" in the second contextual definition of "state," you have omitted it in the manuscript. You could also include this association there. (Page 5 Line 95 – 98)

We would like to thank the reviewers for their extremely helpful and thoughtful comments, which have allowed us to improve the quality of this manuscript. Here we explain the changes we have made to the paper – with these changes also highlighted in the manuscript file. Our responses to the reviewers' comments are highlighted in bold, and **corrections in the main text are marked with a yellow highlight**. We really hope that we have been able to address all the reviewers' concerns adequately and that the paper is now suitable for publication in the *Communications Biology*.

Reviewers' comments:

Reviewer #1 (Remarks to the Author):

I am very happy with the authors' response to my comments. This work offers interesting insights into controlled semantic cognition, and I am looking forward to seeing it published!

Many thanks for your very positive comments.

Reviewer #2 (Remarks to the Author):

In reviewing the manuscript once more, as I initially had no specific comments to the authors, I will address the rebuttal to Reviewer #1. Overall, I found that the modifications made in response to specific reviewer comments appropriately addressed the issues highlighted. Moreover, the changes enhanced the clarity of the study rationale. The figure additions and modifications also enhanced the ease of visual interpretation of the results.

Many thanks for your very positive comments.

Only minor suggestions regarding the response to Reviewer #1's comments:

The description of comprising brain regions of the DMN could still be more specifically defined in the cortex.

Many thanks for your constructive suggestions. We have added a more specific definition of the comprising brain regions of the DMN. Please see Page 5, Line 102 – Line 106.

The DMN comprises a set of widely distributed brain regions in the parietal, temporal, and frontal cortex, including the ventral medial prefrontal cortex, the dorsal medial prefrontal cortex, the posterior cingulate cortex and adjacent precuneus, the lateral parietal cortex, and the entorhinal cortex.

2) While your reply in the rebuttal letter clearly associates “state of cognition” and “task state” in the second contextual definition of “state,” you have omitted it in the manuscript. You could also include this association there. (Page 5 Line 95 – 98)

Many thanks for your constructive suggestions. We have included the association between “state of cognition” and “task state”. Please see Page 5 Line 95 – 98.

Different states of controlled cognition (i.e., the varying functional states of the brain as it engages in different cognitive activities and specific tasks) may reflect specific configurations of large-scale brain networks, which can be characterized in terms of multiple dimensions of intrinsic connectivity (Bolt et al., 2022; Margulies et al., 2016).