Brain Functional Network Mechanisms of Rumination

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Abstract

Rumination refers to individuals' involuntary and repetitive contemplation of the causes, process, and outcomes of negative life events following their occurrence, characterized by negative self-referential processing, negative emotionality, and persistence. Employing brain functional network analysis methods, researchers have found that these three characteristics of rumination are respectively associated with abnormal activity patterns within the default mode network, alterations in functional connectivity of the salience network, and abnormal coupling patterns between attention-related networks. Future research should further clarify the causal relationships between rumination and relevant brain network activities, investigate the structural basis of brain functional networks in rumination, also attend to the aging characteristics of rumination and its brain networks, and dedicate efforts to the exploration of neuromodulation techniques for effective intervention.

Full Text

Functional Brain Networks Underlying Rumination

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Abstract

Rumination refers to the involuntary, repetitive thinking about the causes, course, and consequences of negative life events, characterized by negative self-referential processing, negative emotionality, and persistence. Using brain functional network analysis, researchers have found that these three features of rumination are associated with abnormal activity patterns within the default mode

network, altered functional connectivity of the salience network, and abnormal coupling patterns between attention-related networks, respectively. Future research should further clarify the causal relationship between rumination and related brain network activity, explore the structural basis of rumination' s brain functional networks, examine aging-related characteristics of rumination and its brain networks, and develop effective neuromodulation techniques for rumination intervention.

Keywords: rumination, brain network, default mode network, functional connectivity

Rumination is the tendency for individuals to repeatedly and uncontrollably think about the causes, course, and consequences of negative life events (such as academic failure, relationship setbacks, or work difficulties) after experiencing them (Nolen-Hoeksema, 1991; Nolen-Hoeksema et al., 2008). Individuals in a ruminative state typically exhibit the following cognitive and emotional characteristics (Morrow & Nolen-Hoeksema, 1990). First, rumination predisposes individuals to associate negative information with self-concept, engaging in negative self-referential processing (Santa et al., 2012; Yang & Liu, 2016). Second, this negative self-referential processing leads individuals to over-attend to negative information, resulting in negative emotions and information processing biases that impair problem-solving (Constantin et al., 2017; Nolen-Hoeksema, 2000; Kertz et al., 2019). Third, rumination is persistent; once individuals enter a ruminative state, they tend to dwell on the same event for extended periods (Joorman & D'Avanzato, 2010). In short, the negative self-referential processing, negative emotionality, and persistence of rumination impair individuals'problem-solving and emotion regulation capacities, representing a maladaptive cognitive style (Ando et al., 2020; Nolen-Hoeksema, 2000). Research has demonstrated that rumination is closely associated with various mental disorders, including depression, anxiety, bipolar disorder, and post-traumatic stress disorder (Constantin et al., 2017; Dodd et al., 2019; Kraus et al., 2020; Kertz et al., 2019; Mihailova & Jobson, 2020; Smith et al., 2018; Topper et al., 2017). Given rumination's significant impact on mental health, this article aims to review previous research on the neural mechanisms of maladaptive rumination to understand its brain functional network basis and provide theoretical support for rumination intervention.

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In recent years, numerous studies have used functional magnetic resonance imaging (fMRI) to investigate the large-scale brain network mechanisms of rumination. Brain network analysis can reveal important brain regions involved in

cognitive processes and the correlations between these regions (Xu, 2021), and has been widely applied in cognitive neuroscience research (Delaveau et al., 2017; Kuhn et al., 2012; Menon, 2011; Sanchez et al., 2016; Sporns, 2014; Sin et al., 2018). Major large-scale brain networks identified in previous research include the default mode network, salience network, frontoparietal network, and attention network (Menon, 2011; Petersen & Sporns, 2015; Yeo et al., 2011). Studies have shown that the negative self-referential processing in rumination is associated with the default mode network, which is primarily involved in internally-directed mental activity (Berman et al., 2011; Chen et al., 2020; Rosenbaum et al., 2017; Zhou et al., 2020); the negative emotionality of rumination is related to alterations in the salience network; and its persistence is associated with abnormal connectivity between attention networks (Hamilton et al., 2011; Kaiser, Andrews-Hanna, Wager, et al., 2015; Li et al., 2018; Lydon-Staley et al., 2019; Price et al., 2017). The following sections will elaborate on the brain network mechanisms underlying the negative self-referential processing, negative emotionality, and persistence of rumination, and propose future research directions.

2. Negative Self-Referential Processing in Rumination

Individuals in a ruminative state tend to connect negative information with the self and engage in excessive interpretation of it (Santa et al., 2012; Martin & Tesser, 1989). Specifically, when negative events occur, high ruminators are more likely to engage in self-reflective thinking such as "Why did I perform so poorly?" or "Why did this happen to me?" rather than objectively analyzing "Why did this event occur?" (Watkins et al., 2008). Research indicates that the self-referential processing in rumination is associated with altered activity patterns in the default mode network.

The default mode network (DMN) shows decreased activity during tasks requiring attention to external information, but increased activity during rest or internally-directed mental activities such as self-related abstract thinking, episodic memory, and future imagination (Li & Shu, 2014; Buckner et al., 2008; Smallwood et al., 2021). Alterations in the DMN play a crucial role in the development of rumination (Andrews-Hanna et al., 2014; Hamilton et al., 2015; Kaiser, Andrews-Hanna, Wager et al., 2015; Zhou et al., 2020). Research has identified three functionally distinct subsystems within the DMN: (1) the core subsystem, comprising the anterior medial prefrontal cortex and posterior cingulate cortex, which participates in self-referential processing and facilitates interactions between the other two subsystems; (2) the dorsomedial prefrontal subsystem, including the dorsomedial prefrontal cortex, temporoparietal junction, lateral temporal cortex, and temporal pole, which plays an important role in theory of mind and metacognitive processing (Andrews-Hanna, 2012; Andrews-Hanna et al., 2014); and (3) the medial temporal lobe subsystem, composed of the ventromedial prefrontal cortex, posterior inferior parietal lobule, retrosplenial cortex, parahippocampal cortex, and hippocampus, which is involved

in autobiographical memory processing and the formation of future situational expectations based on this memory (Andrews-Hanna et al., 2010; Spreng et al., 2009). During rumination, both the activity and functional connectivity of these three subsystems undergo corresponding changes (Andrews-Hanna et al., 2010; Tozzi et al., 2021).

First, the three subsystems show different levels of activation during rumination. Multiple studies have induced rumination by asking participants to judge trait adjectives, recall negative personal events, or think about others' evaluations of themselves, followed by fMRI scanning. Results show that compared to distraction states, rumination states exhibit increased activity in the core subsystem (responsible for self-referential processing) and the dorsomedial prefrontal subsystem (responsible for theory of mind processing). However, most regions of the medial temporal lobe subsystem (which facilitates goal-directed behavior) remain inactive during rumination (Apazoglou et al., 2019; Burkhouse et al., 2017; Cooney et al., 2010; Steinfurth et al., 2017; Vecchio et al., 2017; Zhou et al., 2020). The hyperactivity of the DMN core subsystem during rumination suggests that when external stimuli trigger rumination, individuals excessively process self-related information. The dorsomedial prefrontal subsystem reflects mental states triggered by external stimuli: when facing negative life events, rumination leads individuals to engage in excessive self-reflection and self-criticism, projecting these thoughts onto how others might view them (e.g., after a competition loss, individuals in a ruminative state may believe they performed poorly and that others share this view). The medial temporal lobe subsystem forms future expectations based on autobiographical memory, so its reduced activity during rumination can be understood as difficulty retrieving positive past experiences and a belief that one will likely fail in future goals (e.g., believing one will never perform well in future competitions after a single loss).

Second, functional connectivity between the three DMN subsystems changes during rumination. Chen et al. (2020) used a continuous mental state paradigm to examine the DMN during rumination and obtained highly consistent results across three different MRI scanners. Compared to a distraction state (imagining self-unrelated matters), rumination states (repeatedly thinking about negative events and their potential consequences) showed abnormal functional connectivity between the three DMN subsystems (Chen et al., 2020). Specifically, during rumination, functional connectivity decreased between the core subsystem and dorsomedial prefrontal subsystem, while it increased between the core subsystem and medial temporal lobe subsystem (Bartova et al., 2015; Christoff et al., 2016; Chen et al., 2020; Provenzano et al., 2021; Zhu et al., 2017). The core subsystem is responsible for integrating other subsystems, while the dorsomedial prefrontal subsystem handles metacognitive processing. Decreased connectivity between them suggests reduced constraint of the core subsystem over the dorsomedial prefrontal cortex (Christoff et al., 2016), leading individuals to expend more cognitive resources on negative self-examination. Enhanced connectivity between the core and medial temporal lobe subsystems suggests over-constraint of the latter by the former, making it difficult for individuals to retrieve positive

autobiographical memories and form adaptive mental activities. Furthermore, graph-theoretical analysis of brain networks shows that higher rumination scores are associated with higher entropy levels within the DMN in both healthy participants and depressed patients (Jacob et al., 2020). Entropy reflects a system' s orderliness, and increased entropy indicates greater system disorder (Jacob et al., 2016). These findings suggest that rumination levels can be characterized by the degree of internal order within the DMN.

The DMN plays an important adaptive role in supporting internally-directed mental activity, and rumination is associated with abnormal DMN activity. This helps explain why rumination manifests as excessive self-referential processing. However, the causal relationship between rumination and abnormal DMN activity remains unclear, and future research should employ directed functional connectivity or neuromodulation methods to clarify their interaction patterns.

3. Negative Emotionality of Rumination

Nolen-Hoeksema (1987) proposed that rumination represents a response style to depressive mood. After experiencing negative life events, individuals high in rumination pay more attention to their own negative emotions, excessively processing event details and their emotional states. The cognitive biases triggered by negative emotions hinder objective problem-solving (Nolen-Hoeksema et al., 2008). Research indicates that alterations in the salience network can explain the generation of negative emotions during rumination.

The salience network (SN) has two key functions: monitoring the external environment and acquiring corresponding cognitive resources based on this monitoring. The SN primarily includes the amygdala, fronto-insular cortex, and anterior cingulate cortex (Lydon et al., 2019; Peters et al., 2016). Studies using the Stroop task have found that, compared to healthy controls, depressed patients show more negative self-referential processing, suggesting a strong association between depression and rumination (Wagner et al., 2013). During the task, the anterior cortical midline structure, composed of the anterior cingulate cortex (a key SN node) and the medial prefrontal cortex (part of the DMN), showed hyperactivation and enhanced functional connectivity. Nejad et al. (2013) systematically reviewed brain network studies of rumination in depression and found that hyperactivation of the anterior cortical midline structure reduced functional connectivity between the dorsolateral prefrontal cortex and amygdala. Since the dorsolateral prefrontal cortex is responsible for cognitive control (Nejati et al., 2021) and the amygdala is involved in emotional processing (Bordi & LeDoux, 1992), reduced connectivity between them during rumination suggests that individuals have difficulty encoding and representing information accurately and forming constructive emotion regulation strategies, resulting in negative emotional responses. This is supported by graph-theoretical analysis results. Node centrality, a common graph-theoretical metric, characterizes a node' s role and position in a network, with higher values indicating greater information transmission function (Liang et al., 2010; Sun et al., 2010; Gao et al.,

2018). Research has shown that after inducing rumination through emotional instructions, depressed patients with high rumination traits exhibit reduced amygdala node centrality compared to healthy controls (Zhang et al., 2020). This indicates that when depressed patients enter a ruminative state, the amygdala cannot fully perform its emotion regulation function, and emotional states cannot be properly adjusted.

The fronto-insular cortex in the SN participates in sensory and emotional processing (Li et al., 2018). Studies have shown that enhanced resting-state functional connectivity of the right fronto-insular cortex is associated with negative, persistent introspective tendencies (Kaiser et al., 2016), reflecting rumination levels in depressed patients. Additionally, individuals with high rumination traits (high scores on rumination scales) show attentional bias toward negative self-descriptive information, and this bias is modulated by dynamic functional connectivity of the fronto-insular cortex. Specifically, greater changes in fronto-insular dynamic functional connectivity correlate with stronger tendencies to attend to negative self-information among high ruminators (Kaiser et al., 2018; Kaiser et al., 2019). Fronto-insular activity reflects differences in somatic states when subjective expectations conflict with reality (Craig, 2009; Sridharan et al., 2008). Therefore, hyperactivity of the fronto-insular cortex indicates that high ruminators are more likely to experience intense negative emotions when reality fails to meet their subjective expectations. Since goal pursuit is highly subjective, larger discrepancies between failed and expected goals increase the likelihood of negative rumination.

In summary, the salience network, which monitors internal and external environments, undergoes alterations during rumination, causing individuals to focus attention on negative emotional experiences—neither beneficial for mental health nor problem-solving. Negative emotionality also explains why rumination is associated with mental disorders such as depression and anxiety. These findings suggest that rumination interventions could focus on cultivating emotional insensitivity to self-related negative emotions in high ruminators to reduce excessive mental exhaustion.

4. Persistence of Rumination

Rumination is a maladaptive cognitive style characterized by repetitive, sustained thinking about negative events (Grafton et al., 2016; Nolen-Hoeksema et al., 2008). Why is rumination difficult to stop once initiated? The impaired attention disengagement theory proposes that rumination arises from difficulty disengaging attention from negative stimuli, leading to repetitive, sustained processing of self-related negative information (Grafton et al., 2016; Hur et al., 2019; Koster, 2011; Nejad et al., 2019; Valenas et al., 2017). Research indicates that the persistence of rumination is associated with abnormal functional connectivity between attention-related networks.

The frontoparietal network (FPN), comprising the dorsolateral prefrontal cor-

tex and posterior parietal cortex, is primarily involved in attentional control, response selection, and response inhibition (Chang, Liu, et al., 2013; Lydon et al., 2019). The dorsal attention network (DAN), composed of the frontal eye fields and intraparietal sulcus, helps focus and maintain attention on external stimuli, and its activation is negatively correlated with rumination (Buckner & Krienen, 2013; Rosenbaum, Thomas, et al., 2018; Rosenbaum, Maier, et al., 2018). Studies have shown that compared to healthy controls, depressed patients with high rumination levels exhibit weakened functional connectivity between the FPN and DAN, and enhanced connectivity between the FPN and DMN (Kaiser, Andrews-Hanna, Wager, et al., 2015; Kaiser, 2017). Specifically, the FPN participates in both top-down attentional and emotional regulation and manages cognitive resource allocation to the DAN and DMN. When connectivity between the FPN and externally-directed DAN weakens while connectivity between the FPN and internally-directed DMN strengthens, cognitive resources intended for attending to and acquiring information from the external world are consumed by internally-directed mental activities. Excessive cognitive resources are allocated to self-referential and autobiographical memory processing systems, causing individuals to over-focus on the self.

Dynamic brain network studies also provide evidence for the impaired attention disengagement hypothesis of rumination. Dynamic brain network analysis can describe the stability of functional connectivity over time and reflect brain network flexibility (i.e., more stable functional connectivity indicates lower network flexibility) (Gonzalez-Castillo & Bandettini, 2018; Li, Lu et al., 2020). Research has found that compared to a distraction control group (imagining non-emotional scenes), rumination groups show increased stability of FPN functional connectivity and decreased stability of DMN connectivity during self-reflection (Chen & Yan, 2021). This suggests that during rumination, individuals exhibit rigid thinking patterns and abnormally prominent self-referential processing (Christoff et al., 2016; Kaiser et al., 2016). Chen and Yan (2021) propose that decreased DMN stability relates to overly dense interactions among its internal regions, though this requires future verification. Overall, abnormal dynamic activity patterns in the FPN and DMN may reflect individuals' difficulty disengaging attention from self-related information during rumination.

However, some scholars propose alternative explanations for rumination persistence. Yang et al. (2017) found through meta-analysis that high ruminators show decreased cognitive control ability, making it difficult to inhibit negative information. However, few brain network analyses have examined the relationship between inhibitory ability and rumination persistence, leaving its neural mechanisms unclear. Whether rumination persistence stems from difficulty shifting attention away from negative self-information or from difficulty inhibiting negative stimuli remains an open question for future research.

5. Summary and Outlook

In summary, rumination is a maladaptive response following negative life events, characterized by negative self-referential processing, negative emotionality, and persistence. The negative self-referential processing of rumination can be explained by abnormal activity patterns in the DMN' s core subsystem, dorsomedial prefrontal subsystem, and medial temporal lobe subsystem. The negative emotions generated by rumination relate to abnormal functional connectivity of the anterior cingulate cortex and amygdala in the salience network. Frequent dynamic functional connectivity changes in the fronto-insular cortex reflect how conflicts between real situations and expected goals easily produce intense negative emotional experiences in high ruminators. Finally, individuals' inability to actively stop persistent rumination relates to abnormal coupling patterns among the frontoparietal network, dorsal attention network, and default mode network. Although research on the brain network mechanisms of rumination has made progress, future studies should deepen our understanding in several ways.

First, the vast majority of previous studies have demonstrated correlations between rumination and brain network activity, but correlation does not establish causality. Future research should employ neuromodulation techniques to examine causal relationships between rumination and altered brain functional connectivity, thereby deepening our understanding of rumination' s brain network mechanisms.

Second, does the altered brain functional network in rumination have a structural basis? Existing research has confirmed significant functional network alterations in rumination, but functional connectivity changes alone are insufficient to infer structural connectivity changes (Koch et al., 2002). Currently, few studies have specifically explored the relationship between functional and structural networks in rumination, representing an important direction for future research.

Third, aging-related characteristics of rumination. Previous rumination research has primarily focused on young and middle-aged adults. However, the brain changes continuously with age (Gu et al., 2015), making it inappropriate to generalize these findings directly to older adults. Studies show that compared to younger individuals, older adults are more likely to use distraction strategies and less likely to engage in rumination when facing negative emotions (Ricarte Trives et al., 2016). This may be due to the positivity effect in older adults, who tend to focus more on positive than negative stimuli (Reed et al., 2014). Whether abnormal brain network connectivity in rumination improves with this emotional positivity effect requires verification in future research.

Finally, the clinical value of large-scale brain networks. The impact of rumination on mental disorders such as depression and anxiety is receiving increasing attention. Currently, few studies have applied existing brain network findings to clinical intervention and treatment of rumination. Future research should develop brain network-based neuromodulation techniques for effective rumination

intervention.

References

Liang, X., Wang, J., & He, Y. (2010). Human connectome research: Brain structural networks and brain functional networks. *Chinese Science Bulletin*, 55(16), 1565–1583.

Li, Y., & Shu, H. (2014). Neural mechanisms, functional hypotheses, and clinical applications of the default mode network. *Advances in Psychological Science*, 22(2), 234–249.

Sun, J., Hong, X., & Tong, S. (2010). Advances in complex brain network research: Structure, function, computation, and application. *Complex Systems and Complexity Science*, 7(4), 74–90.

Xu, L. (2021). *Research on self-organized critical behavior of large-scale brain networks based on fMRI brain imaging data* (Master' s thesis). Lanzhou University.

Yang, Y., & Liu, Y. (2016). Cognitive and neural mechanisms of depressive rumination. *Advances in Psychological Science*, 24(7), 1042–1049.

Andrews-Hanna, J. R. (2012). The brain' s default network and its adaptive role in internal mentation. *Neuroscientist*, 18(3), 251–270.

Andrews-Hanna, J. R., Reidler, J. S., Sepulcre, J., Poulin, R., & Buckner, R. L. (2010). Functional-anatomic fractionation of the brain' s default network. *Neuron*, 65(4), 550–562.

Andrews-Hanna, J. R., Smallwood, J., & Spreng, R. N. (2014). The default network and self-generated thought: Component processes, dynamic control, and clinical relevance. *Annals of the New York Academy of Sciences*, 1316(1), 29–52.

Ando, A., Giromini, L., Ales, F., & Zennaro, A. (2020). A multimethod assessment to study the relationship between rumination and gender differences. *Scandinavian Journal of Psychology*, 61(6), 740–745.

Apazoglou, K., Küng, A. L., Cordera, P., Aubry, J. M., Dayer, A., Vuilleumier, P., & Piguet, C. (2019). Rumination related activity in brain networks mediating attentional switching in euthymic bipolar patients. *International Journal of Bipolar Disorders*, 7(1), 3.

Bartova, L., Meyer, B. M., Diers, K., Rabl, U., Scharinger, C., Popovic, A., Pail, G., Kalcher, K., Boubela, R. N., Huemer, J., Mandorfer, D., Windischberger, C., Sitte, H. H., Kasper, S., Praschak-Rieder, N., Moser, E., Brocke, B., & Pezawas, L. (2015). Reduced default mode network suppression during a working memory task in remitted major depression. *Journal of Psychiatric Research*, 64, 9–18.

Bordi, F., & LeDoux, J. (1992). Sensory tuning beyond the sensory system: An initial analysis of auditory response properties of neurons in the lateral amygdaloid nucleus and overlying areas of the striatum. *The Journal of Neuroscience*, 12(7), 2493–2503.

Berman, M. G., Peltier, S., Nee, D. E., Kross, E., Deldin, P. J., & Jonides, J. (2011). Depression, rumination and the default network. *Social Cognitive and Affective Neuroscience*, 6(5), 548–555.

Buckner, R. L., & Krienen, F. M. (2013). The evolution of distributed association networks in the human brain. *Trends in Cognitive Sciences*, 17(12), 648–665.

Buckner, R. L., Andrews-Hanna, J. R., & Schacter, D. L. (2008). The brain' s default network: Anatomy, function, and relevance to disease. *Annals of the New York Academy of Sciences*, 1124, 1–38.

Burkhouse, K. L., Jacobs, R. H., Peters, A. T., Ajilore, O., Watkins, E. R., & Langenecker, S. A. (2017). Neural correlates of rumination in adolescents with remitted major depressive disorder and healthy controls. *Cognitive, Affective & Behavioral Neuroscience*, 17(2), 394–405.

Chang, C., Liu, Z., Chen, M. C., Liu, X., & Duyn, J. H. (2013). EEG correlates of time-varying BOLD functional connectivity. *NeuroImage*, 72, 227–236.

Chen, X., Chen, N. X., Shen, Y. Q., Li, H. X., Li, L., Lu, B., ···Yan, C. G. (2020). The subsystem mechanism of default mode network underlying rumination: A reproducible neuroimaging study. *NeuroImage*, 221, 117–129.

Chen, X., & Yan, C. G. (2021). Hypostability in the default mode network and hyperstability in the frontoparietal control network of dynamic functional architecture during rumination. *NeuroImage*, 241, 118427.

Christoff, K., Irving, Z. C., Fox, K. C. R., Spreng, R. N., & Andrews-Hanna, J. R. (2016). Mind-wandering as spontaneous thought: A dynamic framework. *Nature Reviews Neuroscience*, 17(11), 718–731.

Constantin, K., English, M. M., & Mazmanian, D. (2017). Anxiety, depression, and procrastination among students: Rumination plays a larger mediating role than worry. *Journal of Rational-Emotive and Cognitive-Behavior Therapy*, 36(1), 15–27.

Cooney, R. E., Joormann, J., Eugene, F., Dennis, E. L., & Gotlib, I. H. (2010). Neural correlates of rumination in depression. *Cognitive, Affective & Behavioral Neuroscience*, 10(4), 470–478.

Craig, A. D. (2009). How do you feel—now? The anterior insula and human awareness. *Nature Reviews Neuroscience*, 10(1), 59–70.

Delaveau, P., Arruda Sanchez, T., Steffen, R., Deschet, K., Jabourian, M., Perlbarg, V., ···Fossati, P. (2017). Default mode and task-positive networks connec-

tivity during the N-Back task in remitted depressed patients with or without emotional residual symptoms. *Human Brain Mapping*, 38(7), 3491–3501.

Dodd, A., Lockwood, E., Mansell, W., & Palmier-Claus, J. (2019). Emotion regulation strategies in bipolar disorder: A systematic and critical review. *Journal of Affective Disorders*, 246, 262–284.

Gao, W., Wu, H., Siddiqui, M. K., & Baig, A. Q. (2018). Study of biological networks using graph theory. *Saudi Journal of Biological Sciences*, 25(6), 1212–1219.

Gonzalez-Castillo, J., & Bandettini, P. A. (2018). Task-based dynamic functional connectivity: Recent findings and open questions. *NeuroImage*, 180(Pt B), 526–533.

Grafton, B., Southworth, F., Watkins, E., & MacLeod, C. (2016). Stuck in a sad place: Biased attentional disengagement in rumination. *Emotion*, 16(1), 63–72.

Gu, S., Satterthwaite, T. D., Medaglia, J. D., Yang, M., Gur, R. E., Gur, R. C., & Bassett, D. S. (2015). Emergence of system roles in normative neurodevelopment. *Proceedings of the National Academy of Sciences of the United States of America*, 112(44), 13681–13686.

Hamilton, J. P., Farmer, M., Fogelman, P., & Gotlib, I. H. (2015). Depressive rumination, the default-mode network, and the dark matter of clinical neuroscience. *Biological Psychiatry*, 78(4), 224–230.

Hamilton, J. P., Furman, D. J., Chang, C., Thomason, M. E., Dennis, E., & Gotlib, I. H. (2011). Default-mode and task-positive network activity in major depressive disorder: Implications for adaptive and maladaptive rumination. *Biological Psychiatry*, 70(4), 327–333.

Hur, J., Gaul, K., & Berenbaum, H. (2019). Different patterns of attention bias in worry and rumination. *Cognitive Therapy and Research*, 43(4), 713–725.

Jacob, Y., Winetraub, Y., Raz, G., Ben-Simon, E., Okon-Singer, H., Rosenberg-Katz, K., Hendler, T., & Ben-Jacob, E. (2016). Dependency network analysis (DEPNA) reveals context related influence of brain network nodes. *Scientific Reports*, 6, 27444.

Jacob, Y., Morris, L. S., Huang, K. H., Schneider, M., Rutter, S., Verma, G., Murrough, J. W., & Balchandani, P. (2020). Neural correlates of rumination in major depressive disorder: A brain network analysis. *NeuroImage: Clinical*, 25, 102142.

Joorman, J., & D' Avanzato, C. (2010). Emotion regulation in depression: Examining the role of cognitive processes. *Cognition and Emotion*, 24, 913–939.

Kaiser, R. H. (2017). Neurocognitive markers of depression. *Biological Psychiatry*, 81(4), e29–e31.

Kaiser, R. H., Andrews-Hanna, J. R., Wager, T. D., & Pizzagalli, D. A. (2015). Large-scale network dysfunction in major depressive disorder: A meta-analysis of resting-state functional connectivity. *JAMA Psychiatry*, 72(6), 603–611.

Kaiser, R. H., Snyder, H. R., Goer, F., Clegg, R., Ironside, M., & Pizzagalli, D. A. (2018). Attention bias in rumination and depression: Cognitive mechanisms and brain networks. *Clinical Psychology: Science and Practice*, 6(6), 765–782.

Kaiser, R. H., Whitfield-Gabrieli, S., Dillon, D. G., Goer, F., Beltzer, M., Minkel, J., ···Pizzagalli, D. A. (2016). Dynamic resting-state functional connectivity in major depression. *Neuropsychopharmacology*, 41(7), 1822–1830.

Kaiser, R. H., Kang, M. S., Lew, Y., Van Der Feen, J., Aguirre, B., Clegg, R., ···Pizzagalli, D. A. (2019). Abnormal frontoinsular-default network dynamics in adolescent depression and rumination: A preliminary resting-state co-activation pattern analysis. *Neuropsychopharmacology*, 44(9), 1604–1612.

Kertz, S. J., Petersen, D. R., & Stevens, K. T. (2019). Cognitive and attentional vulnerability to depression in youth: A review. *Clinical Psychology Review*, 71, 63–77.

Koster, E. H., De Lissnyder, E., Derakshan, N., & De Raedt, R. (2011). Understanding depressive rumination from a cognitive science perspective: The impaired disengagement hypothesis. *Clinical Psychology Review*, 31(1), 138–145.

Kraus, C., Mkrtchian, A., Kadriu, B., Nugent, A. C., Zarate, C. A., Jr., & Evans, J. W. (2020). Evaluating global brain connectivity as an imaging marker for depression: Influence of preprocessing strategies and placebo-controlled ketamine treatment. *Neuropsychopharmacology*, 45(6), 982–989.

Koch, M. A., Norris, D. G., & Hund-Georgiadis, M. (2002). An investigation of functional and anatomical connectivity using magnetic resonance imaging. *NeuroImage*, 16(1), 241–250.

Kuhn, S., Vanderhasselt, M. A., De Raedt, R., & Gallinat, J. (2012). Why ruminators won't stop: The structural and resting state correlates of rumination and its relation to depression. *Journal of Affective Disorders*, 141(2-3), 352–360.

Li, R., Zhang, S., Yin, S., Ren, W., He, R., & Li, J. (2018). The fronto-insular cortex causally mediates the default-mode and central-executive networks to contribute to individual cognitive performance in healthy elderly. *Human Brain Mapping*, 39(11), 4302–4311.

Li, L., Lu, B., & Yan, C. G. (2020). Stability of dynamic functional architecture differs between brain networks and states. *NeuroImage*, 216, 116–230.

Lydon-Staley, D. M., Kuehner, C., Zamoscik, V., Huffziger, S., Kirsch, P., & Bassett, D. S. (2019). Repetitive negative thinking in daily life and functional connectivity among default mode, fronto-parietal, and salience networks. *Translational Psychiatry*, 9(1), 234.

Martin, L. L., & Tesser, A. (1989). *Toward a motivational and structural theory of ruminative thought*. Guilford Press.

Menon, V. (2011). Large-scale brain networks and psychopathology: A unifying triple network model. *Trends in Cognitive Sciences*, 15(10), 483–506.

Mihailova, S., & Jobson, L. (2020). The impact of depression and culture on responses to intrusive autobiographical memories: Cognitive appraisals, cognitive avoidance, and brooding rumination. *British Journal of Clinical Psychology*, 59(1), 66–79.

Morrow, J., & Nolen-Hoeksema, S. (1990). Effects of responses to depression on the remediation of depressive affect. *Journal of Personality and Social Psychology*, 58(3), 519–527.

Nejad, A. B., Fossati, P., & Lemogne, C. (2013). Self-referential processing, rumination, and cortical midline structures in major depression. *Frontiers in Human Neuroscience*, 7, 666.

Nejad, A. B., Rotgé, J. Y., Valabregue, R., Guérin-Langlois, C., Hoertel, N., Gorwood, P., Dubertret, C., Limosin, F., Fossati, P., & Lemogne, C. (2019). Medial prefrontal disengagement during self-focus in formerly depressed patients prone to rumination. *Journal of Affective Disorders*, 247, 36–44.

Nejati, V., Majdi, R., Salehinejad, M. A., & Nitsche, M. A. (2021). The role of dorsolateral and ventromedial prefrontal cortex in the processing of emotional dimensions. *Scientific Reports*, 11(1), 1971.

Nolen-Hoeksema, S. (1987). Sex differences in unipolar depression: Evidence and theory. *Psychological Bulletin*, 101(2), 259–282.

Nolen-Hoeksema, S. (1991). Responses to depression and their effects on the duration of depressive episodes. *Journal of Abnormal Psychology*, 100(4), 569–582.

Nolen-Hoeksema, S. (2000). The role of rumination in depressive disorders and mixed anxiety/depressive symptoms. *Journal of Abnormal Psychology*, 109(3), 504–511.

Nolen-Hoeksema, S., Wisco, B. E., & Lyubomirsky, S. (2008). Rethinking rumination. *Perspectives on Psychological Science*, 3(5), 400–424.

Peters, S. K., Dunlop, K., & Downar, J. (2016). Cortico-striatal-thalamic loop circuits of the salience network: A central pathway in psychiatric disease and treatment. *Frontiers in Systems Neuroscience*, 10, 104.

Petersen, S. E., & Sporns, O. (2015). Brain networks and cognitive architectures. *Neuron*, 88(1), 207–219.

Price, R. B., Lane, S., Gates, K., Kraynak, T. E., Horner, M. S., Thase, M. E., & Siegle, G. J. (2017). Parsing heterogeneity in the brain connectivity of

depressed and healthy adults during positive mood. *Biological Psychiatry*, 81(4), 347–357.

Provenzano, J., Fossati, P., Dejonckheere, E., Verduyn, P., & Kuppens, P. (2021). Inflexibly sustained negative affect and rumination independently link default mode network efficiency to subclinical depressive symptoms. *Journal of Affective Disorders*, 293, 347–354.

Reed, A. E., Chan, L., & Mikels, J. A. (2014). Meta-analysis of the age-related positivity effect: Age differences in preferences for positive over negative information. *Psychology and Aging*, 29(1), 1–15.

Ricarte Trives, J. J., Navarro Bravo, B., Latorre Postigo, J. M., Ros Segura, L., & Watkins, E. (2016). Age and gender differences in emotion regulation strategies: Autobiographical memory, rumination, problem solving and distraction. *The Spanish Journal of Psychology*, 19, E43.

Rosenbaum, D., Haipt, A., Fuhr, K., Haeussinger, F. B., Metzger, F. G., Nuerk, H. C., ···Ehlis, A. C. (2017). Aberrant functional connectivity in depression as an index of state and trait rumination. *Scientific Reports*, 7(1), 2174.

Rosenbaum, D., Thomas, M., Hilsendegen, P., Metzger, F. G., Haeussinger, F. B., Nuerk, H.-C., Fallgatter, A. J., Nieratschker, V., & Ehlis, A.-C. (2018). Stress-related dysfunction of the right inferior frontal cortex in high ruminators: An fNIRS study. *NeuroImage: Clinical*, 18, 510–517.

Rosenbaum, D., Maier, M. J., Hudak, J., Metzger, F. G., Wells, A., Fallgatter, A. J., & Ehlis, A. C. (2018). Neurophysiological correlates of the attention training technique: A component study. *NeuroImage: Clinical*, 19, 1018–1024.

Sanchez, A., Vanderhasselt, M. A., Baeken, C., & De Raedt, R. (2016). Effects of tDCS over the right DLPFC on attentional disengagement from positive and negative faces: An eye-tracking study. *Cognitive, Affective & Behavioral Neuroscience*, 16(6), 1027–1038.

Santa Maria, A., Reichert, F., Hummel, S. B., & Ehring, T. (2012). Effects of rumination on intrusive memories: Does processing mode matter? *Journal of Behavior Therapy and Experimental Psychiatry*, 43(3), 901–908.

Smallwood, J., Bernhardt, B. C., Leech, R., et al. (2021). The default mode network in cognition: A topographical perspective. *Nature Reviews Neuroscience*, 22(8), 503–513.

Smith, K. E., Mason, T. B., & Lavender, J. M. (2018). Rumination and eating disorder psychopathology: A meta-analysis. *Clinical Psychology Review*, 61, 9–23.

Steinfurth, E. C., Alius, M. G., Wendt, J., & Hamm, A. O. (2017). Physiological and neural correlates of worry and rumination: Support for the contrast avoidance model of worry. *Psychophysiology*, 54(2), 161–171.

Sporns, O. (2014). Contributions and challenges for network models in cognitive neuroscience. *Nature Neuroscience*, 17(5), 652–660.

Spreng, R. N., Mar, R. A., & Kim, A. S. (2009). The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: A quantitative meta-analysis. *Journal of Cognitive Neuroscience*, 21(3), 489–510.

Sridharan, D., Levitin, D. J., & Menon, V. (2008). A critical role for the right fronto-insular cortex in switching between central-executive and default-mode networks. *Proceedings of the National Academy of Sciences of the United States of America*, 105(34), 12569–12574.

Topper, M., Emmelkamp, P. M., Watkins, E., & Ehring, T. (2017). Prevention of anxiety disorders and depression by targeting excessive worry and rumination in adolescents and young adults: A randomized controlled trial. *Behaviour Research and Therapy*, 90, 123–136.

Tozzi, L., Zhang, X., Chesnut, M., Holt-Gosselin, B., Ramirez, C. A., & Williams, L. M. (2021). Reduced functional connectivity of default mode network subsystems in depression: Meta-analytic evidence and relationship with trait rumination. *NeuroImage: Clinical*, 30, 102570.

Valenas, S. P., Szentagotai-Tatar, A., Grafton, B., Notebaert, L., Miu, A. C., & MacLeod, C. (2017). Prediction of pre-exam state anxiety from ruminative disposition: The mediating role of impaired attentional disengagement from negative information. *Behaviour Research and Therapy*, 91, 102–110.

Vecchio, F., Miraglia, F., & Maria Rossini, P. (2017). Connectome: Graph theory application in functional brain network architecture. *Clinical Neurophysiology Practice*, 2, 206–213.

Wagner, G., Koch, K., Schachtzabel, C., Peikert, G., Schultz, C. C., Reichenbach, J. R., Sauer, H., & Schlösser, R. G. (2013). Self-referential processing influences functional activation during cognitive control: An fMRI study. *Social Cognitive and Affective Neuroscience*, 8(7), 828–837.

Watkins, E., Moberly, N. J., & Moulds, M. L. (2008). Processing mode causally influences emotional reactivity: Distinct effects of abstract versus concrete construal on emotional response. *Emotion*, 8(3), 364–378.

Yang, Y., Cao, S., Shields, G. S., Teng, Z., & Liu, Y. (2017). The relationships between rumination and core executive functions: A meta-analysis. *Depression and Anxiety*, 34(1), 37–50.

Yeo, B. T., Krienen, F. M., Sepulcre, J., Sabuncu, M. R., Lashkari, D., Hollinshead, M., ···Buckner, R. L. (2011). The organization of the human cerebral cortex estimated by intrinsic functional connectivity. *Journal of Neurophysiology*, 106(3), 1125–1165.

Zhang, R., Kranz, G. S., Zou, W., Deng, Y., Huang, X., Lin, K., & Lee, T. M. C.

(2020). Rumination network dysfunction in major depression: A brain connectome study. *Progress in Neuro-Psychopharmacology and Biological Psychiatry*, 98, 109819.

Zhou, H. X., Chen, X., Shen, Y. Q., Li, L., Chen, N. X., Zhu, Z. C., ···Yan, C. G. (2020). Rumination and the default mode network: Meta-analysis of brain imaging studies and implications for depression. *NeuroImage*, 206, 116287.

Zhu, X., Zhu, Q., Shen, H., Liao, W., & Yuan, F. (2017). Rumination and default mode network subsystems connectivity in first-episode, drug-naive young patients with major depressive disorder. *Scientific Reports*, 7, 43105.

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