



Dynamic Organization of Large-scale Functional Brain Networks Supports Interactions Between Emotion and Executive Control

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Abstract Emotion and executive control are often conceptualized as two distinct modes of human brain functioning. Little, however, is known about how the dynamic organization of large-scale functional brain networks that support flexible emotion processing and executive control, especially their interactions. The amygdala and prefrontal systems have long been thought to play crucial roles in these processes. Recent advances in human neuroimaging studies have begun to delineate functional organization principles among the large-scale brain networks underlying emotion, executive control, and their interactions. Here, we propose a dynamic brain network model to account for interactive competition between emotion and executive control by reviewing recent resting-state and task-related neuroimaging studies using network-based approaches. In this model, dynamic interactions among the executive control network, the salience network, the default mode network, and sensorimotor networks enable dynamic processes of emotion and support

flexible executive control of multiple processes; neural oscillations across multiple frequency bands and the locus coeruleus–norepinephrine pathway serve as communicational mechanisms underlying dynamic synergy among large-scale functional brain networks. This model has important implications for understanding how the dynamic organization of complex brain systems and networks empowers flexible cognitive and affective functions.

Keywords Dynamic brain network · Emotion · Executive control · Salience network · Executive control network · Default mode network

Introduction

William James asserted that conscious experience in humans fluctuates over time in “an alternation of flights and perchings” [1]. As essential ingredients of conscious experience,

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emotion, and executive control are especially dynamic. Emotional processing is fundamental for animals and humans; it supports the basic survival of individuals and advanced communications in society. Executive control involves a series of essential high-level cognitive processes, including attention control, conflict resolution, and goal maintaining and switching [2]. In terms of dynamics, our subjective emotional experiences often undergo rapid changes over time, while executive control intrinsically enables the dynamic allocation of cognitive resources according to internal and external demands. Interactive influences between emotion and executive control have been linked to the dynamic adaptation of large-scale functional brain networks in order to meet ever-changing environmental and cognitive demands [3].

The Dynamic Nature of Functional Brain Networks in Support of Emotion and Cognition

In past decades, the neural mechanisms underlying human emotion and executive control have been widely explored by using functional magnetic resonance imaging (fMRI) [3–5]. These studies have shown that the amygdala, insula, and anterior cingulate cortex (ACC) are activated during the processing of negative emotions, with hyperactivation in individuals with high levels of anxiety [6, 7]. In parallel, brain regions including the dorsolateral prefrontal cortex (dlPFC) and posterior parietal cortex are involved in executive control including goal-oriented attention and top-down control [2, 8]. These findings from functional brain localization studies provide important evidence for the development of neurocognitive theories of emotion and executive control. However, a mainstay of conventional fMRI studies focusing on the functional localization of emotion processing and executive control provides insufficient evidence for functional interactions among brain networks. Thus, novel approaches are required to uncover functional segmentation and integration of the brain fundamentally underpinning the interplay between emotion and cognition.

The above issues are being ameliorated by recent advances in resting-state and task-state functional connectivity and graph-based brain network approaches. Specifically, the resting-state fMRI approach focuses on the intrinsic functional connectivity among brain regions during an idle and non-task state. Raichle and colleagues found that a set of widely distributed regions become active in an idle state or a non-task resting state [9], namely the default mode network (DMN) [10], which mainly consists of the posterior cingulate cortex, the medial prefrontal cortex (mPFC) including ventral anterior cingulate cortex (vACC), and the angular gyrus in the lateral parietal cortex [11]. The brain-behavior association between resting-state functional connectivity and

out-scanner emotional/behavioral measures such as self-report anxiety score and executive control performance have been used to assess the intrinsic functional organization of large-scale brain networks linked to emotion and executive control [12–14]. Task-state functional connectivity, estimated by psychophysiological interaction analysis and time series correlation, focuses on how brain connectivity is actively engaged in emotion processing and executive control tasks [15]. By using dynamic causal modeling and dynamical systems theory, neuroimaging studies can also estimate the effective spontaneous connectivity between brain regions [16] or that induced by a specific task [17], as well as dynamic effective connectivity that changes over time [18]. More broadly, based on functional connectivity among brain regions, a graph-theory-based approach can be used to examine the integration and segmentation among brain networks during rest and cognitive processing at the whole-brain level [19].

Neuroimaging studies have focused on how brain networks dynamically (re)configure to support the flexible interplay of emotion and executive control in response to ever-changing environmental demands. These studies have also shown the topological organization of brain networks and spontaneous fluctuations in the resting state. These fluctuations can be characterized by alternations between integration and segmentation, which are proposed to be associated with cognitive engagement and disengagement [20], as well as being responsible for dynamic processes of emotion [21, 22]. During the task state, according to cognitive goals and external environment demands, there are also dynamic reorganizations of the topology of brain networks [23, 24]. In the present review paper, we focus on the dynamic brain networks underlying the flexible interplay between executive control and emotion processing, by summarizing neuroimaging studies exploring dynamic brain networks during resting and task states. Here we propose a neurocognitive model of dynamic brain networks to account for the interactive influence between emotion and executive control, which provides new insights into future research and clinical applications.

Dynamic Organization of Functional Brain Networks Involved in Emotional Processing

At the large-scale network level, Seeley and colleagues [12] used independent component analysis of resting-state fMRI data to identify the ACC, the anterior insula (AI), the amygdala, and the caudate as anchored into the salience network (SN), and the dorsolateral prefrontal and parietal regions as anchored into the executive control network (ECN). In this study, connectivity within the SN was positively associated with anxiety levels, while connectivity in the ECN was positively linked to performance in the executive control

task. The above findings suggest that the SN and ECN are spatially separated during the resting state, while the SN is more important for emotional processing, and the ECN is more involved in executive control. Recent research has suggested that functional coordination among regions within the SN plays a critical role in emotional processing, which is driven by multiple neuromodulator systems, especially the locus coeruleus (LC) and the norepinephrine system (NE). Specifically, Hermans *et al.* [25] found that during exposure to stressful conditions, connectivity within the SN increases when the physiological response is enhanced. More importantly, blocking the activity of the NE system was found to weaken connectivity within the SN and reduce the emotional response to aversive stimuli. This supports the theory that NE serves as an important neuromodulator released by the LC and its projection into a wide range of brain regions including the prefrontal cortex and limbic system such as the amygdala and hippocampus [26].

Dynamic interactions between regions of the SN are crucial for tracking the process of emotional stimuli and events. This notion has been supported by several studies which found that the dynamics of SN, under a variety of resting states and cognitive tasks, is highly synchronous with the changes in the physiological indices of emotional processing (Fig. 1). For instance, Chang and colleagues applied a sliding window approach to resting-state fMRI data with heart rate variability (HRV), which is a physiological indicator of emotional state in humans, and found functional connectivity among the amygdala, dACC, thalamus, and dynamically tracked levels of HRV [21]. Dynamic representation of the emotional state in the SN has also been found during real-time emotion processing. Baczkowski and colleagues used a fear learning paradigm and sliding window approach and found that functional connectivity of the amygdala varied with the skin conductance level (SCL) evoked by a fear

conditioning cue [22]. Specifically, increased connectivity of the amygdala with the insula and the mPFC was found when SCL increased. The effectiveness of the connectivity of the amygdala with different networks, such as the ECN, sensorimotor network, and DMN, has been shown to contribute to the processing of different types of basic emotions [27], and there is also evidence showing that effective connectivity from the amygdala to the hippocampus (part of the DMN) is modulated by emotional arousal, regardless of its valence [28]. A recent meta-analysis systematically reviewed studies of functional and effective connectivity during emotion perception and regulation and highlighted the context-dependent dynamic modulatory role of the ECN on the SN and sensorimotor networks [29].

Dynamic reconfiguration within and between the SN and other networks including the ECN and emotion system (e.g., the amygdala and bed nucleus of the stria terminalis [BNST]) has been linked to the real-time process of anticipated anxiety. Bottom-up signals from the amygdala to the dACC (core node of the SN) [30] and the dlPFC (core node of the DCN) [31] have been shown in anxiety during emotional decision-making. Input signals from the temporoparietal junction to the dACC of the SN have also been shown to be involved in fear-biased adaptation to environmental volatility [32]. Such results suggest that the SN is responsible for continuous and real-time processing of anticipated anxiety under conditions of uncertainty. In a similar paradigm [33], network efficiency in the SN was reduced during the initial phase and increased during the continuous phase of anticipation of threat, while network efficiency of the ECN decreased during the initial phase; the centrality of the amygdala and BNST was increased during both phases. These results suggest that during anticipated anxiety, the functional organization of brain networks undergoes dynamic changes in different stages of emotional processing.

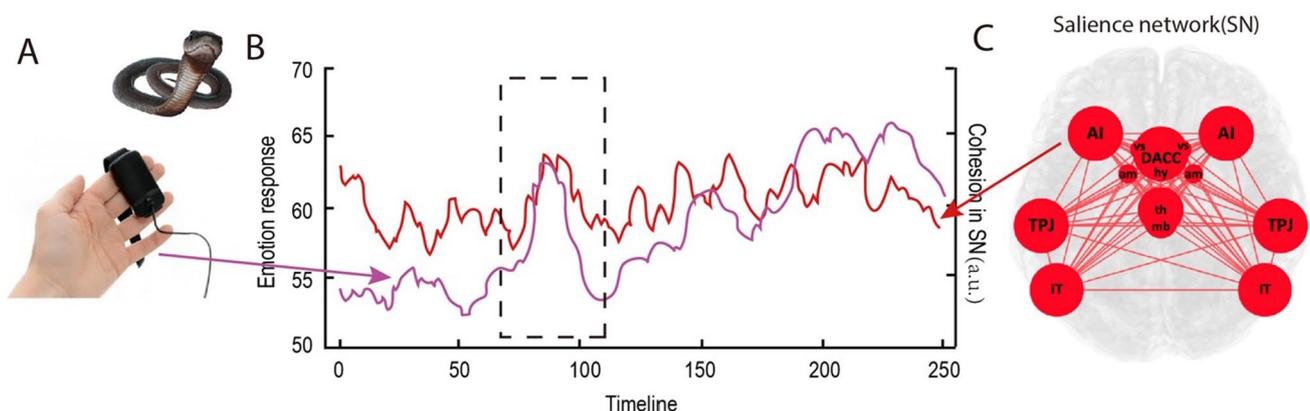


Fig. 1 The salience network tracking the dynamics of the physiological signal of emotion. **A** and **B** A participant's emotional response (e.g., skin conductance, in magenta) to a stressor (e.g., a picture of a

snake). **C** The response and connectivity of the salience network to a stressor (in red).

Specifically, the SN plays a key role in the initial integration of information, which declines over time, while the amygdala and BNST take over in the continuous phase. These findings remind us that when exploring the brain network mechanisms underlying emotion processing, it is necessary to characterize the dynamic changes of network organization over time, rather than considering emotion as a static process.

The DMN has long been involved in emotional processing (see [34] for a review). Altered functional connectivity of the DMN has been shown in anxiety disorders [35, 36], social phobia [37], panic disorder [38], and depression [39, 40]. The DMN also plays an important role in normal [41] and abnormal development [42–44]. The connectivity of the DMN also contributes to the classification of depression [45], prediction of anhedonia [46], and anxiety [47, 48]. Given the dynamic nature of emotional processes, recent evidence has shown the important role of the dynamic interactions of the DMN with other brain networks during emotional processing. By using a natural scene-viewing task, recent studies have examined the brain network during dynamic sustained naturalistic emotional experience and found that the functional connectivity of the DMN is dynamically increased with emotional arousal [49] and contributes to a classification that can accurately distinguish between sustained happiness and sadness [50]. Abnormal dynamic connectivity of the DMN has also been found in anxious individuals [51]. The accumulating evidence jointly suggests the important role of the dynamic DMN characteristics in rapid emotional experience.

Dynamic Organization of Functional Brain Networks Involved in Executive Control

Dynamic Interactions Between the ECN and Sensorimotor Networks in Executive Control

As one of the higher-order cognitive functions, executive control is responsible for flexibly coordinating and manipulating information and resources to achieve an internal goal in response to a changing environment. Executive control consists of several key components, including attention, maintaining goals, and suppressing inappropriate responses [52, 53]. The conventional view of executive control is focused on the role of the PFC [2]. However, current theories propose that, beyond the PFC, the dynamics of brain networks enable multiple executive control functions. In support of this idea, recent evidence of brain networks has suggested that dynamic interactions within and between the core networks are crucial for complex executive control [4].

The coupling between the ECN and lower-level sensorimotor networks is dynamically adjusted in response to changes in cognitive goals and task demands. A core

function of executive control is to dynamically adjust neurocognitive resources to optimize task performance to reach cognitive goals. Dynamic reorganization of functional brain networks is responsive to this adjustment. Indeed, during preparation for sensory/motor preparation, the brain activity was found to be decomposed into two separate networks, the core network (located in the ECN) critical for integrating with other networks, and the periphery network (located in the sensorimotor network) responsible for specific perception and motion processing [54]. With a change in task goals, functional connectivity between the core and peripheral networks is dynamically adjusted. For instance, when the task goal is to discern a visual stimulus, the core network is integrated with the visual network and separated from the motor network; while if the task goal is to discern a moving stimulus, the core network is integrated with the motor network, and separated from the visual network. These results suggested that interactions between the core network and the periphery networks are reconfigured according to real-time cognitive goals, in order to optimize the specific task performance at hand. Interestingly, during a task of transition from conscious control processing to automated motion processing [55], the involvement of the prefrontal control network gradually decreases, the sensorimotor networks gradually increase, and the interaction between the prefrontal control and sensorimotor networks gradually decreases.

Goal-oriented attention, another important component of executive control, is theoretically accomplished through the modulation of sensory cortex activity by top-down signals from the prefrontal cortex [56]. Recently, studies of large-scale brain networks have extended the theory from activity to connectivity and indicate that the ECN flexibly connects to the visual network depending on attentional goals, and thus modulates connectivity within the visual system to enable goal-directed executive functions. One study has found that goal-directed attention can dynamically adjust the functional connectivity between lower- and higher-level visual regions, while the ECN is involved in the modulation of this dynamic adjustment [57]. In particular, participants completed attentional switching between the images of faces and buildings: when they paid attention to faces according to the task goal, connectivity between V1-V4 and the fusiform face area (FFA) increased; when they attended to building, the connectivity of V1-V4 with para-hippocampus area (PPA) increased. These results suggest that a specific goal modulates synchronization within the visual network to prioritize goal-related visual information processing. Hwang, *et al.* [58] used a similar paradigm and replicated the above findings that attentional goal selectively strengthens specific functional connectivity (faces: v1-FFA, building: v1-PPA). Importantly, activation in core regions of the ECN was found to provide top-down signals of modulation, depending on the

attention goal, to dynamically modify functional connectivity in the visual networks.

Dynamic Interactions Among the ECN, DMN, and SN During Execution Control

The ECN, DMN, and SN, three core higher-order functional brain networks, play critical roles in support of executive functions including selective attention and working memory, through their interactions with lower-order sensorimotor networks. Besides the above dynamic interactions of the ECN with sensory and motor networks, the DMN also plays a key role in the dynamic integration of information during working memory. Indeed, previous studies have found that the brain becomes integrated with the increase of cognitive load. Functional connectivity between the DMN and other networks including visual and motion networks is increased, which is likely to drive the dynamic integration of the whole brain [59–61]. In addition, the SN is closely related to executive control and cognitive flexibility. The SN shows the highest flexibility and centrality among all the networks, and the connectivity of the SN with other networks including visual and motor networks shows high temporal flexibility [62]. Temporal flexibility is highly correlated with cognitive flexibility, which is important for executive control. Granger causal analyses (GCA) have also been used to estimate the effective connectivity among nodes of the SN, DMN, and ECN in previous studies, demonstrating a gatekeeper role of the AI in executive control by dynamically integrating with the ECN and DMN [63, 64].

Functional interactions among these three core networks are also flexibly involved in executive control. In the conventional models, the ECN and SN are often considered to be uniquely identical and relatively independent [12, 53, 65, 66]. Interestingly, the ECN/SN and DMN are antagonistic, and the ECN/SN suppresses the DMN during tasks. For instance, effective inhibitory control has been associated with de-activation of the DMN [67]. In patients with brain damage, the degree of damage in the connectivity of the SN can predict the degree of failure in suppressing the activation of the DMN. Furthermore, Chen, *et al.* [68] used transcranial magnetic stimulation (TMS) to stimulate regions in the ECN and found that excitement of the ECN causes negative connectivity between the ECN and DMN, while suppression of the ECN causes increased activity of the DMN from low to high frequencies, suggesting that the ECN suppresses the DMN.

Accumulating evidence of dynamic brain networks now poses challenges to the traditional triple networks model and suggests that network architecture, and interactions among these three networks, dynamically change according to task goals and demands. For instance, the ECN and SN are not statically independent but they are dynamically integrated.

When the complexity of the task increases during an executive control task, the ECN and SN become more integrated, with dynamically enhancing connectivity between the insula/dACC and dlPFC [69]. In addition, the antagonism between the ECN/SN and DMN appears depending on which cognitive processes are involved. During self-related information processing in control tasks, for instance, this antagonism between the two networks switches into a positive synergy [70]. Together, the human brain shows great cognitive flexibility according to external and internal goals, and this flexibility is closely related to dynamic cooperation and antagonism between core brain networks among the ECN, SN, and DMN. In future studies, it would be very promising to directly characterize how task demands and cognitive goals drive dynamic reconfiguration among core large-scale networks.

Revised Flexible Hub Theory

Although the above findings strongly support the flexible hub theory [4, 8], some significant issues remain unresolved (Fig. 2). The flexible hub theory is an expansion of the guided activation framework which proposes that top-down signals from the prefrontal cortex are crucial in modulating perceptual brain regions, thereby enabling executive control. The flexible hub theory extends the guided activation framework from the perspective of dynamic brain networks in two aspects (Fig. 2A). First, not only a single brain region (i.e., the prefrontal cortex) but also the ECN, including multiple brain regions (e.g., the frontoparietal areas), enable top-down control according to different task goals by dynamically changing the functional connectivity of the ECN with other networks. Second, the theory proposes a novel concept of compositional coding, hypothesizing that the functional connectivity patterns of brain networks can represent specific cognitive processing components. For instance, the connectivity of the visual network represents and processes visual information, while the connectivity of the motor network represents and processes motor responses. Cole and colleagues [4] have found that the connectivity of the ECN with other brain networks dynamically switches according to different task goals in a goal-switching task, providing direct evidence in support of flexible hub theory. It has also been shown that the higher-order ECN and lower-order visual and motion networks are dynamically reorganized according to task goals across many tasks of executive control, including task preparation [54], motor learning [55], and goal-directed attention [57, 58]. Therefore, the connectivity of the ECN with the lower-level networks is responsible for the transmission of the top-down control signals, while the low-level visual and motion networks are responsible for specific task-specific information representation (i.e., compositional coding).

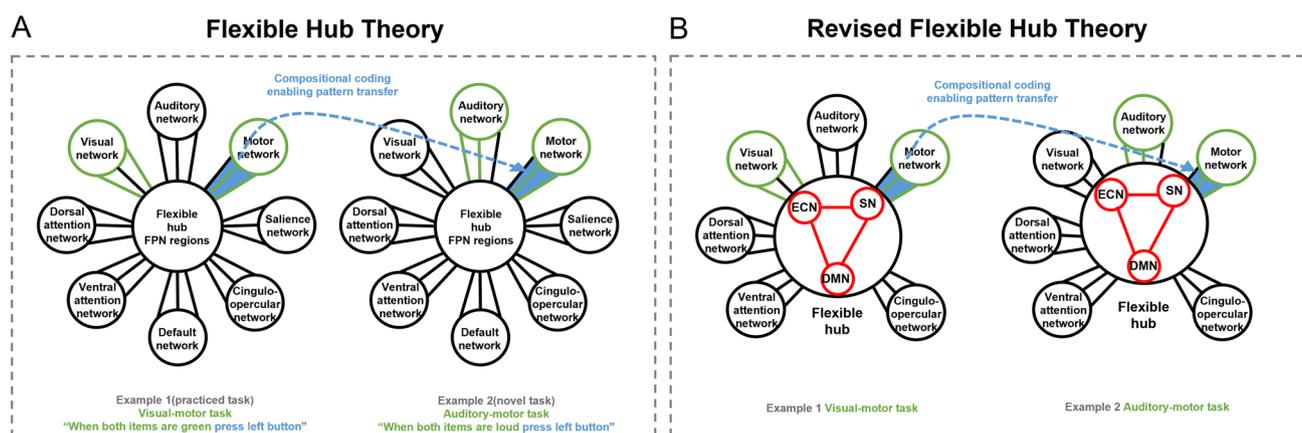


Fig. 2 The revised flexible hub theory. **A** Flexible hub theory proposes not only a single brain region but also the executive control network (ECN) including the prefrontal and posterior parietal cortex enable top-down control. Compositional coding is enabled by the functional connectivity patterns of brain networks that represent spe-

cific cognitive processing components. **B** Revised flexible hub theory suggests that not only the ECN but other key brain networks including the salience network (SN) and default mode network (DMN) are involved in the control processing.

However, possible revision and extension of the flexible hub theory are noteworthy. On one hand, besides the ECN, there is emerging evidence that the SN and DMN, as well as dynamic interactions among these three networks, are also involved in implementing flexible executive control. For instance, as discussed above, highly flexible functional connectivity of the SN is positively correlated with cognitive flexibility [62]; functional connectivity of the DMN with other networks including visual and motion networks dynamically changes in response to the cognitive loads of working memory [60, 61]; and connectivity among these three core networks is also dynamically reconfigured in response to changes in task goals and demands [66].

On the other hand, these brain networks are not only involved in executive control but also play crucial roles in emotion processing and their interactions. Emotion processing involved in threat, stress, and anxiety can actively modulate executive control by engaging the SN to weaken the ECN (Fig. 3B). Threat processing is thought to occupy core neural resources shared by different components of execution control [5]. The candidates, possibly serving as these core resources, include the dlPFC, mPFC, ACC, and AI, which are extensively overlapped with the SN and ECN, suggesting that the SN and ECN play key roles in the modulation of executive control by emotion. Hermans *et al.* [3] proposed a dynamic brain network model of how stress impacts executive control. They proposed that under stress, cognitive resources are assigned to the SN, and alertness and fear processing are enhanced, by weakening the executive function of the ECN. After stress subsides, the allocation of cognitive resources is reversed, emotional responses return to baseline levels, and executive control functions recover. Excessive stress enhances dynamic internal reorganization within the

SN and inhibits the ECN by the connection between the SN and ECN, leading to the failure to suppress the DMN. Our previous study showed that stress weakens the activity of the ECN, with a failure of suppression of DMN activity during working memory [71].

Several interesting and important questions emerge if the SN and DMN also serve as flexible hubs. Why are not only the ECN but also other networks necessary and critical for emotion and executive control? What specific and unique roles do the SN and DMN play? Do the three networks serve as flexible hubs simultaneously or separately? Previous studies have suggested that the triple networks play distinct roles in emotion and executive control: (1) The SN is involved in both emotion processing and salience-driven goal-directed control. The SN is proposed to be involved in the calculation of decision value to further trigger the execution of control by engaging the ECN [72]. (2) The ECN interacts with lower-order sensorimotor networks to enable flexible cognitive and affective computation, as suggested by the flexible hub theory. (3) The DMN serves as an integrative hub, which can gather multiple resources from the whole brain to support cognitive and affective computation in the SN and ECN [60, 61, 72, 73]. Therefore, the three networks serve as different flexible hubs in emotion processing and executive control, which can be compatible with the flexible hub theory and previous triple network models [66, 74].

Thus, we propose that the SN, ECN, and DMN together as the core flexible hubs enable network flexibility, meanwhile lower-level visual, auditory, and motor networks are responsible for compositional coding. Dynamic configuration of the three core networks and sensorimotor networks accomplishes specific goal-oriented functions (Fig. 2B). Although this hypothesis is supported by multiple streams

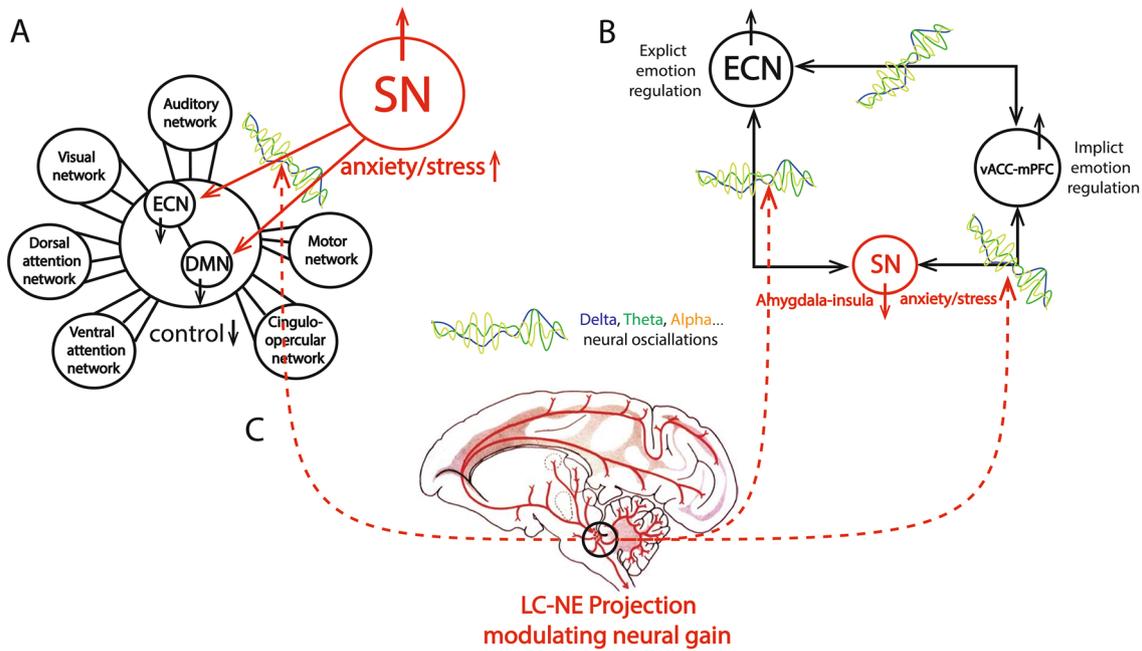


Fig. 3 The dynamic brain network model of interaction between emotion and executive control. **A** The activation of the salience network (SN) increases and the activation of the other two networks, the executive control network (ECN) and the default mode network (DMN), decreases while facing stressors. **B** When regulating the emotional response to stressors, the ECN, ventral anterior cingulate

cortex(vACC), and medial prefrontal cortex show increased activation and the SN shows decreased activation. **C** Locus coeruleus (LC)-norepinephrine (NE) is proposed to enable neural gain modulation to support neural oscillations and the dynamic interactions between large-scale brain networks.

of evidence, it still requires direct evidence that simultaneously links emotion and executive control with network flexibility of the SN, ECN, and DMN. We used an emotional working memory task (i.e. n-back) and found that during low task demand, activation in the SN increased in the fear condition, but when task demand increased, the hyper-activation of the SN reversed, which indicates that the modulation of executive control by the SN is also mediated by task demands [75]. In addition, one task-state connectivity study has shown a monotonically increasing correlation between heart rate variance and dynamic changes in coherence in the SN while participants view negative pictures, indicating that the coherence within the SN can dynamically track the emotional states [49]. More importantly, the dynamic change of connectivity between SN and ECN is associated with the biological measurement of emotion in the manner of an inverted U-shaped curve. That is, under moderate levels of emotional responses, SN–ECN connectivity reaches a maximum.

Neural Oscillations Enable Flexible Communications Among Large-Scale Functional Brain Networks

Neural oscillations have been widely used to establish the synergy of neural responses in the central nervous system.

Such oscillations may serve as an important mechanism underlying how large-scale network synchronization scaffolds a complex interplay between affective and cognitive functions [76] (Fig. 3B, C). Recent studies using electroencephalography (EEG), magnetoencephalography (MEG), and fMRI provide important insights into the relationship between the functional connectivity measured by fMRI and the neural oscillations measured by EEG/MEG, particularly in emotion processing and executive control. One resting-state fMRI study with concurrent EEG recording found that functional connectivity between the ECN and DMN is significantly associated with the strength of alpha oscillation [77]. Another study found that during the resting state, alpha oscillation in the posterior electrode is linked to functional connectivity within and between visual networks [78]. Moreover, while watching movies, synchronization between visual networks and language networks increases in the theta and delta bands, and synchronization between the DMN and language networks increases in the gamma band, are consistent with increased brain network connectivity found in previous fMRI studies using similar cognitive paradigms. These findings demonstrate the relationship between neural oscillations and fMRI functional connectivity, suggesting that neural oscillations may be an important neurophysiological mechanism underlying the functional organization of brain

networks observed in fMRI studies of emotion, executive control, and their interactions.

Indeed, a series of recent studies using EEG and fMRI techniques have found that neural oscillations play a key role in information synchronization during the processing of emotion and alertness. Synchronization in the delta frequency band is related to fear processing [79]. When processing negative emotional faces, participants exhibited local activity enhancement and larger small-world properties in the gamma band. During tonic alertness processing, neural oscillations in the alpha band were highly correlated with fMRI functional connectivity in the network including the dACC, insula, and thalamus [80]. Neural oscillations are also critical for executive control. In several studies of goal-oriented visual attention, functional coordination between the visual network and ECN has been found to be related to neural synchronization in the alpha band [81, 82]. In addition, when emotion and executive control interact, there is a high neural synchronization in the emotion network and ECN including the prefrontal cortex, amygdala, and hippocampus in gamma and theta [83, 84]. Together, we conclude that neural oscillations are important for emotional processing and executive control, and their interaction, may serve as oscillatory mechanisms underlying fMRI-measured connectivity between large-scale brain networks. In future research, simultaneous recording of fMRI and EEG/MEG, examining the neural oscillation mechanism of large-scale brain network interactions during ‘emotion-executive control interaction’ task states, will provide more direct evidence for this hypothesis.

Neuromodulatory Mechanisms Underlying Dynamic Network Interactions in Emotion Processing and Executive Control

One important question in human cognitive neuroscience is to understand the neurobiological mechanisms underlying the principles of the dynamic organization of brain networks in response to changes in task demands/goals. Preliminary evidence suggests that brainstem activity, particularly in the LC, plays an important role in shaping the dynamics of brain networks. These neuromodulators of the LC (NE) project to the higher-order neocortex, and widely influence higher cortical systems, as well as regulating the neural gain in local regions (Fig. 3D). Neural gain can be viewed as the relation between excitatory and inhibitory neuronal activity; this ratio dynamically modulates the probability of interaction between brain regions [26]. In goal-directed tasks, it has been shown that pupil diameter and neural gain are highly correlated, modulating the strength of functional connectivity at the large-scale brain network level [85]. These findings support the idea that the LC-NE-driven neural gain serves as a potential mechanism underlying dynamic changes in the

functional network configuration of goal-oriented attention. NE is a potential neuromodulator of the dynamic organization among key brain networks. For example, NE has been shown to play a key role in the dynamic switching of the SN-ECN network balance [3]. More directly, Shine and colleagues administered atomoxetine to suppress the activity of NE during working memory tasks to examine the causal role of NE in dynamic network organization [86]. They found that atomoxetine increases the flexibility and integration in a distributed brain network during an N-back task, suggesting that manipulating NE levels can re-organize the brain networks of working memory.

In addition, previous studies have found that individuals with anxiety and under stress exhibit persistent attention bias (alertness) to threat stimuli. This bias is thought to be the result of a competition between the amygdala-based threat evaluation system (e.g., the SN) and the prefrontal control system (e.g., the ECN), where the LC-NE plays a central role [3, 26, 87–89]. Based on the above findings on emotion and executive control, it is concluded that the NE-driven changes in neural gain may be the core neural mechanism for network reconfiguration in the interaction between emotional processing and executive control. In future research, directly operating on LC-NE in the interaction of emotions and executive control, and recording the dynamic changes of large-scale brain networks will provide direct evidence for the above inference.

Summary and Conclusions

In this review, we summarize recent progress in understanding the dynamic organization of the large-scale functional brain networks involved in emotion, executive control, and their interactions. We propose a dynamic brain network model of human emotion and executive control. The model has four aspects: (1) Functional connectivity within core regions of the SN dynamically coordinates and reconfigures to track emotional states including anxiety and stress. (2) Executive control is anchored by the ECN, SN, and DMN, and their dynamic organization among each other and interaction with lower sensorimotor networks serves various cognitive goals, to enable specific cognitive processing and information representations. (3) Brain oscillations are possible neurophysiological mechanisms underlying the dynamic organization of large-scale functional brain networks during emotional processing, executive control, and their interactions. (4) Neuromodulators (i.e., NE) can flexibly regulate neural gain, and then modulate dynamic network interactions to accomplish emotional processing, executive control, and their interactions. Altogether, there is now a newly emerging trend in human cognitive neuroscience research toward understanding the dynamic nature of

large-scale functional brain networks, while cutting-edging neuroimaging technologies with finer temporal and spatial resolution are rapidly developing and iterating to enable the goal of charting brain connectivity and network dynamics. The network neuroscience approaches in conjunction with neuropharmacological manipulations and novel cognitive paradigms as well as advanced AI-empowered analytic methods are crucial to reveal the neurobiological mechanisms underlying the dynamic coordination of large-scale functional brain networks in the cognitive processing of emotion, executive control, and their interactions.

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