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Opinion

A Neural Model of Mind Wandering

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The role of the default-mode network (DMN) in the emergence of mind wandering and task-unrelated thought has been studied extensively. In parallel work, mind wandering has been associated with neuromodulation via the locus coeruleus (LC) norepinephrine (LC-NE) system. Here we propose a neural model that links the two systems in an integrative framework. The model attempts to explain how dynamic changes in brain systems give rise to the subjective experience of mind wandering. The model implies a neural and conceptual distinction between an off-focus state and an active mind-wandering state and provides a potential neural grounding for well-known cognitive theories of mind wandering. Finally, the proposed neural model of mind wandering generates precise, testable predictions at neural and behavioral levels.

Trends

Large-scale brain networks are important for goal-directed cognition. The default mode network (DMN) is central to mind wandering.

The locus coeruleus norepinephrine (LC-NE) system is a potential neural modulator of mind wandering. The LC-NE system adaptively gates the transition between exploring new avenues and exploiting existing ones, known as the exploration–exploitation tradeoff.

We propose that the DMN and LC-NE systems interact to give rise to the subjective phenomenon of mind wandering.

Mind Wandering and the Brain

Mind wandering, or engaging in trains of thought that are unrelated (or unhelpful) to current task goals, is common in daily life [1]. In recent years mind wandering has received considerable attention in the cognitive neurosciences, with a particular focus on uncovering its neural origins. Because mind wandering appears to be a pervasive state of mental functioning, exploring its underlying mechanisms may tell us much about the human brain. In particular, understanding the causes of the attentional fluctuations that underlie mind wandering can help to identify separate brain states in which information processing is differentially affected.

The **DMN** (see Glossary) is strongly implicated in mind wandering [2–4]. The DMN is one of the most widely studied intrinsic connectivity networks (ICNs) [5] and includes nodes such as the medial prefrontal cortex (mPFC), the parietal cingulate cortex (PCC), the precuneus, and both angular gyri. These regions are reliably activated in the absence of a task (i.e., resting-state fMRI sessions; for a review see [6]), although it is unlikely that the DMN is a purely task-negative network [7–9]. The DMN is also involved in autobiographical planning and internally guided thoughts [10,11]. Generally, activity in the core DMN nodes is positively related to mind wandering as indicated by introspective thought sampling and attentional lapses in the form of behavioral errors [3,12,13]).

Simultaneously, a second neural system – the LC-NE system – has also been studied as a potential neural modulator of mind wandering [4,14,15]. Norepinephrine is assumed to control an alerting system that produces and maintains optimal levels of vigilance and performance [16,17]. A great deal of research has investigated the role of norepinephrine within the LC-NE system in supporting sustained attention (for reviews see [18,19]) or attentional lapses [20]. The dynamics of the LC-NE system are commonly separated into slow, tonic fluctuations and fast, phasic responses to stimuli that are connected via an inverse U-shape relationship: When tonic LC activity is low or high, performance-relevant phasic responses are attenuated. Measuring these dynamics is difficult because of the small size of the LC (Box 1). Instead, activity of the LC-NE

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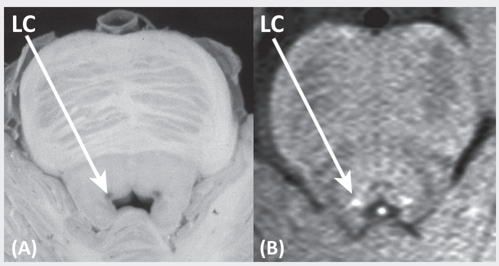
Box 1. High-Fidelity Imaging of the LC

The LC is a pontine nucleus comprising a small group of cells with widespread projections throughout the central nervous system. Because of its small size and location deep within the brain, signal from the LC is difficult to acquire. Using structural MRI, the LC cannot be seen on standard structural scans [54]; LC-tailored MRI structural sequences are required to accurately localize the LC. Recently, the first *in vivo* anatomical map of the human LC in standard space was created [55] using a T1 turbo spin echo (TSE) sequence [54] that exploited the increased contrast that the presence of neuromelanin in the LC offers. This method was later validated with postmortem scans and histology [56] (Figure I).

Probabilistic maps of the LC in standard space can be used to provide an accurate region of interest (ROI) for the investigation of LC signal. However, the position of the LC might vary between individuals to such an extent that standard-space probabilistic LC maps may not provide sufficient spatial precision. This problem is exacerbated by other factors such as age-related alterations in LC signal [54]. To obtain a more precise ROI of the LC, future studies would benefit from acquiring an individual, LC-tailored (e.g., the T1 TSE) sequence for each participant.



Trends in Cognitive Sciences

Figure I. Axial View of the Human Locus Coeruleus (LC). The LC is depicted in (**A**) a postmortem histological brainstem section and (**B**) an *in vivo* T1 turbo spin echo (TSE) scan. LC-tailored MRI scanning of this area was performed and the position of the LC was validated using a histological approach [55]. Reproduced, with permission, from [55].

system is commonly operationalized with measures derived from the pupil diameter. This operationalization is based on correlations between simultaneously recorded neural activity and pupil diameter [18], and although this link has been somewhat speculative [21,22] the relationship between LC-NE system activity and pupil diameter was recently substantiated with electrophysiological measures in nonhuman primates [23]. In addition, several studies have investigated pupil diameter in a mind-wandering context: an increase in tonic pupil diameter precedes mind wandering-related errors [14] and a decrease in the phasic pupil response to stimulation is observed during episodes of mind wandering [4]. These findings have been taken as evidence for a role of the LC-NE system in mind wandering.

An intermediate level of tonic LC activity is likely to be required for optimal information processing; decreased or increased tonic levels are counterproductive in the sense that performance on a primary task suffers. The role of tonic LC-NE activity has been conceptualized in terms of an **exploration–exploitation** tradeoff [18]. In this framework, intermediate levels of tonic norepinephrine help to efficiently solve the task at hand because transient bursts of norepinephrine allow efficient selection of the most salient action in a multilayered neural network [24]. In this sense, intermediate levels of LC-NE activity are optimal. If tonic LC-NE levels increase relative to the optimum, the brain enters an exploratory mode where incidentally high activations can evoke response patterns that otherwise would not be strong enough to cross the threshold.

Functional connectivity and gain modulation of the LC-NE system may also be linked. Using large-scale simulations, a recent paper [25] showed that increases in **neural gain** entailed stronger functional connectivity. This finding was validated experimentally: blocks with increased baseline pupil diameter had stronger functional connectivity between brain regions. As neural gain increases there is a shift from widely distributed patterns of neural processing to tightly clustered patterns dominated by the strongest connections. Because this high-gain mode has

Glossary

Component process theory of mind wandering: the component process account describes a set of psychological constructs that are thought to mutually interact to give rise to mind wandering.

Default-mode network (DMN): a large-scale brain network comprising PCC and mPFC core nodes and two functionally distinct subnetworks, the MTL subsystem and the DM subsystem. The DMN is consistently activated in resting-state scans but has also been shown to play a role in the coordination of different cognitive tasks [7–9].

Exploration–exploitation: brain states during which new behavioral patterns are investigated (exploration) or an existing behavioral goal is pursued (exploitation). Transitions between states of exploration and exploitation are modulated by the LC-NE system.

Functional connectivity: distinct brain areas that show a similar (correlated) time evolution of neural activity are functionally connected. Often brain areas that are functionally connected also share an anatomical connection but this is not strictly necessary.

Model-based neuroscience: a theoretical framework where abstract, formal models of cognition are related to measures of neural functioning [52,53].

Neural gain: changes the communication pattern of connected neurons. When neural gain is high, only strongly connected neurons will communicate while weak connections are blocked. When neural gain is low, weak connections have a higher probability of becoming active and strong connections are attenuated. The LC-NE system changes neural gain across a wide range of cortical and subcortical regions.