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Decoupling of large-scale brain networks supports the consolidation of durable episodic memories

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ABSTRACT

At a large scale, the human brain is organized into modules of interconnected regions, some of which play opposing roles in supporting cognition. In particular, the Default-Mode Network (DMN) has been linked to operations on internal representations, while task-positive networks are recruited during interactions with the external world. Here, we test the hypothesis that the generation of durable long-term memories depends on optimal recruitment of such antagonistic large-scale networks. As long-term memory consolidation is a process ongoing for days and weeks after an experience, we propose that individuals characterized by strong decoupling of the DMN and task-positive networks at rest operate in a mode beneficial for the long-term stabilization of episodic memories. To capture network connectivity unaffected by transient task demands and representative of brain behavior outside an experimental setting, 87 participants were scanned during rest before performing an associative encoding task. To link individual resting-state functional connectivity patterns to time-dependent memory consolidation processes, participants were given an unannounced memory test, either after a brief interval or after a retention period of ~6 weeks. We found that participants with a resting state characterized by high synchronicity in a DMN-centered network system and low synchronicity between task-positive networks showed superior recollection weeks after encoding. These relationships were not observed for information probed only hours after encoding. Furthermore, the two network systems were found to be anticorrelated. Our results suggest that this memory-relevant antagonism between DMN and task-positive networks is maintained through complex regulatory interactions between the systems.

Introduction

Episodic long-term memory consolidation is a process that progresses over time, starting immediately following the encoding of an event and continuing through days and nights, months and possibly years (Dudai et al., 2015). Recent efforts in human neuroimaging have shed light on brain processes during the initial post-encoding interval that are relevant for early consolidation and subsequent memory performance, either by investigating post-stimulus activity time-locked to the offset of encoding events (Ben-Yakov et al., 2014, 2013; Ben-Yakov and Dudai, 2011), or intrinsic network activity during post-encoding rest periods (Schlichting and Preston, 2014; Stevens et al., 2010; Tambini et al., 2010; Tambini and Davachi, 2013; van Kesteren et al., 2010). These studies have elegantly demonstrated that the representational state of memory traces immediately following encoding is linked to retrieval success after short periods of retention.

There is a however also a strong consensus that systems consolidation – i.e. the transformation of labile representations into enduring *long-term* memories (Nadel and Moscovitch, 1997; Squire and Alvarez, 1995) – depends on repeated replay, and thus strengthening, of internal representations over extended periods of time, involving periods of sleep (Diekelmann and Born, 2010; Stickgold, 2013). On a neuronal level, this repeated accessing of labile representations is suggested to occur through recurrent communication during sleep and awake rest between the hippocampus and neocortical networks (Dudai et al., 2015). Much evidence show that such neocortical networks can exist in antagonistic relationships: introspection and the recruitment of networks involved in internally oriented cognition suppresses networks supporting interactions with external representations, and vice versa (Daselaar et al., 2009; Kim, 2011; Raichle et al., 2001). Efficient decoupling between the brain systems recruited during the two attentional modes – internal mentation and operations on external

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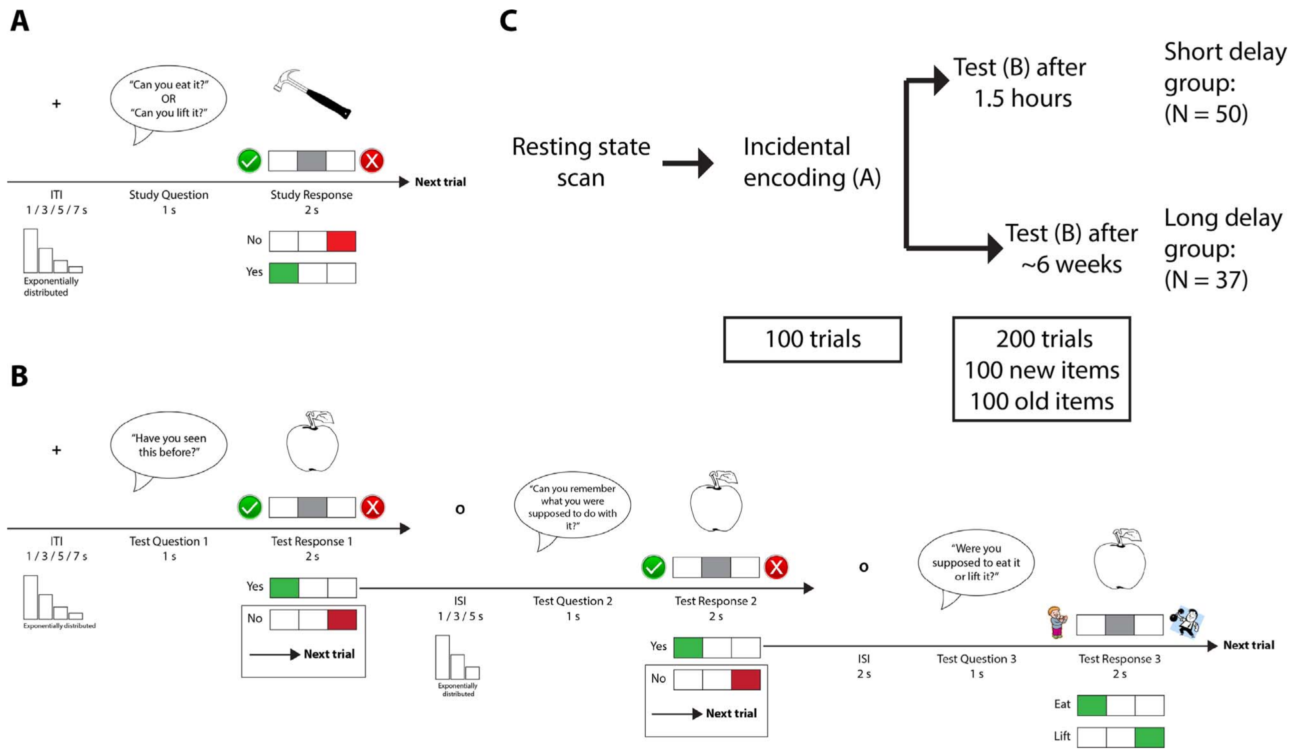

Fig. 1. A) Encoding trial example. B) Test trial example. C) Design overview.

stimuli – has been associated with optimal behavioral performance on a variety of tasks (Eichele et al., 2008; Fox et al., 2005; Kelly et al., 2008). Thus, an intriguing hypothesis is that the prolonged accessing of internal representations – thought to underlie successful systems consolidation – is supported by the combined up- and down-regulation of antagonistic neocortical systems.

A strong neocortical candidate for long-term memory-relevant processing is the Default-Mode Network (DMN), as it is closely connected to the medial temporal lobes (MTL; Buckner et al., 2008) and is functionally coupled to processes involved in attention to internal representations (Andrews-Hanna et al., 2014; Konishi et al., 2015; Smallwood et al., 2013; Spreng et al., 2014). Moreover, the retrieval of remote memories recruits DMN nodes more strongly than does retrieval of information encoded the same day (Frankland and Bontempi, 2005; Gais et al., 2007; Takashima et al., 2007; Wiltgen et al., 2004), suggesting that DMN regions are particularly central in accessing information after prolonged retention intervals. The DMN is commonly found to be decoupled with sensory and perceptual brain regions (Sadaghiani et al., 2015; Schooler et al., 2011), as well as the external attention system (EAS) consisting of several task-positive networks including the dorsal attention, the cingulo-opercular, and the fronto-parietal network (Anticevic et al., 2012; Fox et al., 2005). From this, we would expect that individuals recruiting the DMN while at the same time disengaging task-positive networks operate in a mode beneficial for the long-term stabilization of episodic memories.

In the present study, using functional magnetic resonance imaging (fMRI) and an individual differences approach, we investigate how brain network communication may support the formation of durable long-term memories. Rather than focusing on post-encoding rest periods that reflect state-dependent brain processes likely active only until a new encoding situation is encountered, we aimed at capturing task-independent network interactions reflective of the brain's default behavior outside an experimental setting. We therefore measured rsFC *pre*-encoding, i.e. before two groups of participants performed an associative encoding task followed by an unannounced memory test. For one group, we estimated episodic memory capacity over commonly used short retention intervals (hours) between encoding and test. Crucially, to investigate associations between brain network interactions and capacity to form durable long-term memories, we used a delay interval of several weeks in the second group of participants. As the effect of encoding and retrieval processes on performance should be unaffected by manipulations of retention intervals, this made it possible to separate connectivity patterns enabling efficient consolidation from encoding and retrieval influences.

Materials and methods

Participants

Eighty-nine participants (female n=60; age range 19.5–38.6; mean age 25.4) gave written informed consent and took part in the study, which was approved by the Regional Ethical Committee of South Norway. Participants reported no history of neurological or psychiatric disorders, chronic illness, premature birth, learning disabilities, or use of medicines known to affect nervous system functioning. They were further required to be right-handed, speak Norwegian fluently and have normal or corrected to normal hearing and vision. Moreover, participants were required to score ≥26 on the Mini Mental State Examination (Folstein et al., 1975), and have a Beck Depression Inventory (Beck and Steer, 1987) score ≤16. At scanning a separate clinical sequence (T2-FLAIR) was included for neuroradiological evaluation by a neuroradiologist, and the scans were required to be deemed free of significant injuries or conditions. One person was excluded due to an incidental MRI finding, and one due to excessive motion (> 1.5 mm) during the resting state fMRI (rsfMRI) scan. Participant demographics are summarized in Supplementary Table 1.

Experimental design

Participants were scanned at rest (eyes closed) using BOLD fMRI