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Brains striving for coherence: Long-term cumulative plot formation in the default mode network

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ABSTRACT

Many everyday activities, such as engaging in conversation or listening to a story, require us to sustain attention over a prolonged period of time while integrating and synthesizing complex episodic content into a coherent mental model. Humans are remarkably capable of navigating and keeping track of all the parallel social activities of everyday life even when confronted with interruptions or changes in the environment. However, the underlying cognitive and neurocognitive mechanisms of such long-term integration and profiling of information remain a challenge to neuroscience. While brain activity is generally traceable within the short time frame of working memory (milliseconds to seconds), these integrative processes last for minutes, hours or even days. Here we report two experiments on story comprehension. Experiment I establishes a cognitive dissociation between our comprehension of plot and incidental facts in narratives: when episodic material allows for long-term integration in a coherent plot, we recall fewer factual details. However, when plot formation is challenged, we pay more attention to incidental facts. Experiment II investigates the neural underpinnings of plot formation. Results suggest a central role for the brain's default mode network related to comprehension of coherent narratives while incoherent episodes rather activate the frontoparietal network. Moreover, an analysis of cortical activity as a function of the cumulative integration of narrative material into a coherent story, points to linear modulations of right hemisphere posterior temporal and parietal regions. Together these findings point to key neural mechanisms involved in the fundamental human capacity for cumulative plot formation.

Introduction

Humans live complicated lives. Compared to even our nearest primate relatives, we have become reliant on hugely distributed and multileveled social and cultural structures and organization. Yet humans seem remarkably capable of navigating and keeping track of all the complex and interwoven narratives of life (ex. intrigues at the working place, international politics, fictional movies or family relations) while sustaining focus across changes in their environments. It takes sustained neurocognitive processing to engage in the extended, long-term and complex social activities and relations of human society. Although neural activity is generally traceable within the relatively short time frame of working memory, it is not clear how the brain can sustain a longer term focus, while continuously integrating new experiential content into a coherent representational structure or situation model (Zwaan, Langston, and Graesser, 1995).

An example of a task that requires such sustained attention is listening to a story (Smallwood, McSpadden, and Schooler, 2008). Despite interruptions or major changes in the environment surrounding the listener, the focus can be maintained—in principle for hours—and the thematic content can be continuously updated, integrated and synthesized into a coherent cognitive model. Often the length of such interactions far exceeds the assumed limits of working memory (Baddeley, 2003). Likewise, the dynamic and continuous nature of the process lends itself uneasily to the ideas of encoding, consolidation and retrieval characteristic of most models of long-term memory (Blumenfeld and Ranganath, 2007). This kind of "slow" processing (Donald, 2007) is especially important in the comprehension of social events that extend over significant periods of time. Such events can last for minutes, hours, or days and present a challenge for the basic theory of nervous activity: how and where in the brain is the longer-term synthesis of complex stimulus material achieved?

Recent developments in the study of the brain's default mode network can supply some initial intuitions. The default mode network comprises areas along the anterior and posterior midline, the lateral parietal cortex, prefrontal cortex, and the medial temporal lobe. It was originally

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found to activate when experimental participants were not focusing attention on the here-and-now immediacy of a task and was thus thought to reflect the 'resting brain' (Esposito et al., 2006; Raichle et al., 2001) or 'spontaneous, unconstrained thought' (Andrews-Hanna et al., 2010a, 2010b; Buckner, Andrews-Hanna, and Schacter, 2008; Harrison et al., 2008; Mason et al., 2007; Smallwood, Brown, Baird, and Schooler, 2011). However, over the last decade, researchers have been reconsidering the possible cognitive adaptations of the default mode network (Andrews-Hanna et al., 2010a, 2010b). Recent studies suggest that it is also associated with more goal-oriented and constructive processes of multi-episode integration, imagining the future and mental scene construction (Hassabis and Maguire, 2007; D. L. Schacter and Addis, 2007; Spreng, Mar, and Kim, 2009), requiring participants to attend beyond the immediacy of current perceptions (Smallwood, 2013; Smallwood et al., 2013). Furthermore, findings suggest that the default mode network flexibly couples with other networks to accomplish memory-related functional goals. For instance, it has been found that a network of areas in lateral prefrontal and parietal cortex, termed the *frontoparietal control network*, coactivate with the default mode network as a function of increased task demands (Meyer, Spunt, Berkman, Taylor, and Lieberman, 2012; D.L. Schacter et al., 2012; Summerfield, Hassabis, and Maguire, 2010), possibly associated with the extent to which constructive processes rely on memory (Baird, Smallwood, Gorgolewski, and Margulies, 2013).

Based on these observations, we hypothesize that the default mode network could subserve long-term, time-dependent cumulative synthesis of episodic information, henceforth *plot formation*. While most psychological experiments require us to momentarily focus attention on the subtleties of immediate perception within the short duration of an experimental trial, our everyday engagements in tasks, conversations and narratives only become meaningful to the extent that we can integrate and profile local information in relation to larger coherent situation models and story plots. We argue that this might be one of the main cognitive roles of the default mode network.

In the following, we address the role of the default mode network in the continuous cumulative synthesis of complex verbal stimuli into coherent plot structures. We define *plot information* as content crucial for the understanding of the subsequent events in the stories. Often the plot comprises characters' motives or attitudes, incidents with fatal implication, or other aspects of causal relevance. In contrast, *incidental facts* are descriptive material that have no causal relevance for the subsequent events and often consist of characters' age, hair color, brand of car, etc. In two experiments, a behavioral and an fMRI brain imaging study, participants listened to crime stories divided into a series of short episodes. However, these episodes were interleaved with randomly chosen episodes from a set of distractor stories that did not allow for integration into a coherent plot (see Fig. 1). The experimental design allows us to study behavioral and brain components of our experience of stimuli affording long-term cumulative plot formation in contrast to stimuli that resist such integration and merely require local attention and processing.

Experiment I targeted participants' memory for plot-related information and incidental facts in the crime stories. When listening to a story, we continuously attribute differential significance to various pieces of information in anticipation of their role in the overall plot of the story (cf. 'foregrounding', Gernsbacher, Robertson, Palladino, and Werner, 2004; Talmy, 2000; Zwaan et al., 1995). To the extent that a story allows for cumulative integration of information into a coherent

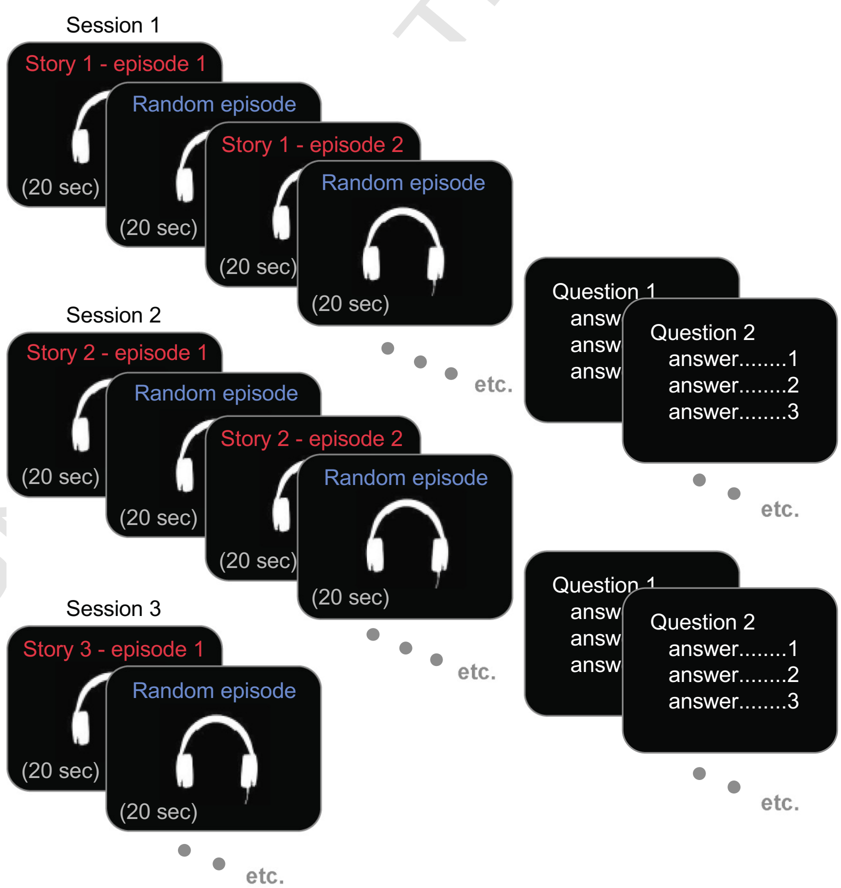

Fig. 1. Schematic depictions of the stimulus presentation design: through five sessions, participants listened to stories divided into 20 sec episodes. Six episodes together constituted a coherent story. However these episodes were interleaved with randomly chosen episodes from a set of distractor stories.

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