

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/neuroimage



Schema benefit vs. proactive interference: Contradicting behavioral outcomes and coexisting neural patterns



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ARTICLE INFO

Keywords: Inter-subject correlation Dual task fMRI Movie Posterior cingulate cortex

ABSTRACT

Prior knowledge can either assist or hinder the ability to learn new information. These contradicting behavioral outcomes, referred to as schema benefit and proactive interference respectively, have been studied separately. Here we examined whether the known neural correlates of each process coexist, and how they are influenced by attentional loading and aging. To this end we used an fMRI task that affected both processes simultaneously by presenting pairs of related short movies in succession. The first movie of each pair provided context for the second movie, which could evoke schema benefit and/or proactive interference. Inclusion of an easy or hard secondary task performed during encoding of the movies, as well as testing both younger (22-35y) and older (65-79y) adults, allowed examining the effect of attentional load and older age on the neural patterns associated with context. Analyses focused on three predefined regions and examined how their inter-subject correlation (inter-SC) and functional connectivity (FC) with the hippocampi changed between the first and second movie. The results in the medial prefrontal cortex (mPFC) and posterior cingulate cortex (PCC) matched and expanded previous findings: higher inter-SC and lower FC were observed during the second compared to the first movie; yet the differentiation between the first and second movies in these regions was attenuated under high attentional load, pointing to dependency on attentional resources. Instead, at high load there was a significant context effect in the FC of the left ventrolateral prefrontal cortex (vIPFC), and greater FC in the second movie was related to greater proactive interference. Further, older adults showed context effect in the PCC and vIPFC. Intriguingly, older adults with inter-SC mPFC patterns similar to younger adults exhibited schema benefit in our task, while those with inter-SC PCC patterns similar to younger adults showed proactive interference in an independent task. The brainbehavior relationships corroborate the functional significance of these regions and indicate that the mPFC mainly contributes to schema benefit, while the left vIPFC and PCC contribute to proactive interference. Importantly, our findings show that the functions of the regions are retained throughout the lifespan and may predict the predominant behavioral outcome.

1. Introduction

A major challenge when encountering and encoding a new event is to

simultaneously incorporate it into and distinguish it from previously stored information. Prior knowledge, or context, may serve as a schema that aids in the understanding and facilitates memory of new

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information, a phenomenon termed schema benefit (Preston and Eichenbaum, 2013). But prior knowledge can also hinder the ability to remember new content, as in the case of proactive interference (Jonides and Nee, 2006). While the former enhances memory, the latter causes forgetting and may be one of the main reasons for limited memory capacity (Keppel and Underwood, 1962). To date, context has been used to study either schema benefit or proactive interference, highlighting different regions and portraying distinct neural patterns in each. Yet in real life there is no such artificial distinction and the two processes can co-occur. It is therefore not known what will be the neural dynamics in a complex ecological condition which prompts schema benefit and proactive interference simultaneously, and whether these neural dynamics can predict the behavioral outcome (i.e., benefit or interference). The current study aims to answer these questions, as well as to investigate the strength of these dynamics under conditions of attentional loading and aging.

Schema is broadly defined as a network of internal representations that aids in remembering new related information and can be modified by it (Preston and Eichenbaum, 2013). Human behavioral studies evaluating schema have yielded contradicting results. Some studies have shown an advantage for retrieval of schema-consistent information as compared to schema-inconsistent information (i.e., schema benefit; e.g., (Bransford and Johnson, 1972; Hulme et al., 1991)), while others have not (e.g., Badham and Maylor, 2016). The underlying neural patterns that support schema benefit were studied in both animals and humans. Animal studies showed that schema benefit depends on the medial prefrontal cortex (mPFC) (Tse et al., 2011). Functional magnetic resonance imaging (fMRI) studies in humans showed that relative to an unintelligible condition, a comprehensible schema during encoding was associated with increased synchronization across participants in the mPFC (Ames et al., 2015; Chen et al., 2016; van Kesteren et al., 2010). Synchronization has been quantified through the use of inter-subject correlation (inter-SC) (Hasson et al., 2004, 2010). Increased inter-SC indicates more unity in the participants' mental state and greater coupling between the region's activity and the ongoing stimulus (van Kesteren et al., 2010). In the van Kesteren study (2010), the schema condition was also associated with decreased functional connectivity (FC) between the mPFC and the hippocampi, while in the unintelligible conditions, lower FC between the two regions predicted greater comprehension of the movie. These findings corroborate the central role of the mPFC in accommodating new information into existing schema (Preston and Eichenbaum, 2013).

Proactive interference is defined as the tendency of previously learned material to hinder subsequent learning, since the new incoming information must compete with the existing representations of past events (Jonides and Nee, 2006). Most fMRI studies of proactive interference explored tasks in which the participant is asked to monitor and retain a set of still stimuli and indicate whether the current probe matches one of the items from the previous target set. Activation in the left ventrolateral prefrontal cortex (vIPFC) related to interference was found in these studies (for reviews see (Irlbacher et al., 2014; Jonides and Nee, 2006)). Specifically, the left vIPFC was activated when the current probe was not part of immediately preceding target set, but was presented in an earlier target set (Badre and Wagner, 2007; Nee et al., 2007a; Oren et al., 2017). In the case of proactive interference, the higher-order visual regions simultaneously process the new, relevant information and reactivate stored representations of the old, competing, irrelevant information (Kuhl et al., 2011; Oztekin and Badre, 2011), while the left vlPFC selects the former and inhibits the latter (Fletcher et al., 2000; Thompson-Schill et al., 1999). Although the left vIPFC activation profile is well characterized via studies with still stimuli, the effect of proactive interference evoked by dynamic, real-life stimuli has not been studied thus far. Regarding FC, it has been shown that proactive interference is associated with increased FC between the left vIPFC and the hippocampus (Nee et al., 2007a). Interestingly though, the left vIPFC is associated not only with interference but also with facilitation. For example, the left

vlPFC was activated in response to a repeated presentation of a probe that previously appeared as a distractor and currently as a target (Badre and Wagner, 2007; Jonides and Nee, 2006). Facilitation has much in common with schema benefit, suggesting that the left vlPFC may support both proactive interference and schema benefit, depending on the design of the paradigm and the task.

A third region that is related to both schema and interference is the posterior cingulate cortex (PCC). Like the mPFC, inter-SC of the PCC increases when there is a prior schema, relative to a non-schema condition (Ames et al., 2015; Chen et al., 2016). Similar to the left vlPFC, the PCC was also activated in conditions related to facilitation (Nee et al., 2007a). In contrast, the PCC emerges in various conditions that create interference (e.g., Oren et al., 2017), including retrieval of information that is incongruent with an established schema (Brod et al., 2015) and inter-SC levels in the PCC predict memory interference due to attentional loading (Oren et al., 2016). Additionally, expert mediators that display higher levels of attention and concentration show improved regulation of PCC function, and the PCC is the target for neurofeedback training that aims, among other things, to reduce distractibility (Brewer and Garrison, 2014). Hence, like the left vlPFC, the PCC seems to be related to both schema benefit and proactive interference.

Attentional load and aging are known to influence schema benefit and proactive interference and to modulate the function of the three aforementioned regions of interest (ROIs). Attentional loading increases the effect of proactive interference, especially in younger adults with high working memory capacity (Kane et al., 2000). Attentional loading may hinder creation of schemas and reduce schema benefit, since the construction of schemas requires investment of cognitive effort (Sweller et al., 1998). At the neural level, attentional loading is associated with higher levels of inter-SC in all three ROIs (Oren et al., 2016) and alterations in FC (Newton et al., 2011; Oren et al., 2016). Aging is generally associated with lower performance in memory tasks (Craik et al., 2010), yet schema may alleviate age-related deficits for material consistent with schematic knowledge ((Umanath and Marsh, 2014); also see (Badham and Maylor, 2016)). Older adults are also susceptible to proactive interference (Ebert and Anderson, 2009; Loosli et al., 2014), and this susceptibility can predict progression to dementia (Loewenstein et al., 2007). At the neural level, older age is associated with a general tendency to reduced levels of inter-SC (Campbell et al., 2015) and FC (Ferreira and Busatto, 2013). Hence, both attentional loading and advanced age have the potential to alter the behavioral outcomes of prior knowledge and context, as well as the underlying neural patterns. Notably, these two factors are different in terms of the duration and the width of their impact. Attentional loading in younger adults has a transient and specific influence, meaning that it specifically burdens the attentional mechanisms for definite period of time. Aging is the result of long lasting and widespread changes in the nervous and cognitive systems, and thus has enduring and non-specific consequences (Grady, 2012). Moreover, in aging, the persistent decrease in attentional resources is merely one of several cognitive changes. Hence, attentional loading and aging model two distinct challenges (Craik et al., 2010). Here we examined how these challenges influenced the neural dynamics related to schema benefit and proactive interference.

The current study aims are thus twofold. First, we aimed to characterize the roles of the mPFC, left vlPFC and PCC during coexisting schema benefit and proactive interference effects. Second, we aimed to test whether these regions continued to display similar neural patterns under attentional loading and aging. To this end, participants watched pairs of short related movies during the encoding phase. The first movie of a pair provided context for the second movie that followed, thus potentially eliciting both schema benefit and proactive interference. Loading was introduced by a secondary, non-mnemonic linguistic task that was performed during encoding and had two difficulty levels. Aging effects were examined by evaluating task performance and characterizing neural dynamics in both younger and older adults.

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