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Forum

Default Network and Aging: Beyond the Task-Negative Perspective

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During cognitive tasks requiring externally directed attention, activation in the default-network (DN) typically decreases below baseline levels ('deactivation'). Healthy aging is associated with reduced deactivation, which is usually attributed to a failure to suppress DN processes. Recent evidence instead suggests that older adults may be more reliant on DN than young adults when performing these tasks.

Introduction

In one moment a student may be directing her attention to a professor's lecture, while in the next she may be directing attention to making dinner plans for the evening. These examples illustrate the distinction

between externally directed attention (attention to stimuli and events in the environment) and internally directed attention (attention to thoughts and feelings). In recent years, fMRI studies have indicated that specific brain networks—the dorsal attention network, which includes the superior parietal lobes and frontal eye fields, and the DN, which includes the medial prefrontal and medial temporal cortex, posterior cingulate cortex, inferior parietal lobes, and lateral temporal cortices—are associated with externally and internally directed attention, respectively. Moreover, in young adults there is now extensive evidence that these two networks often work in opposition [1]. Specifically, as requirements for externally directed attention increase, activation in the dorsal attention network increases whereas activation in the DN decreases below baseline levels. Such deactivations in regions of the DN are thought to reflect suppression of task-irrelevant internal processes (e.g., thinking of dinner plans) [1].

Healthy (non-demented) older adults aged 60 years and above often exhibit reduced deactivation compared with young adults during tasks requiring externally directed attention, such as tasks assessing episodic memory encoding and working memory [2–7]. These effects have often been interpreted as failure of task-induced deactivation with age [2,4,6], although the precise mechanisms underlying this effect have remained elusive.

In one of the first studies [5] to assess age-related differences in deactivation, young adults, healthy older adults, and Alzheimer's disease (AD) patients performed a semantic classification task intermixed with passive fixation (baseline). Results indicated that during semantic classification versus baseline, young adults exhibited the most deactivation in the posterior cingulate cortex, older adults exhibited an intermediate level of deactivation, and AD patients exhibited the least (for further discussion of the association between deactivation and AD-related pathology, see

Box 1). Subsequent studies indicated that reduced deactivation occurs not only when contrasting activation in a task versus baseline contrast but also when comparing between-group differences in two tasks (e.g., hard versus easy working memory task [7]). This observation is important because, whereas age-related differences in a task–baseline contrast could be attributable to baseline differences in cerebral blood flow or neurovascular coupling, age-related differences in a contrast between two experimental tasks (an age-group-by-task interaction) are more likely to be attributable to age-related differences in neural activity associated with cognitive processes tapped by different experimental tasks [8]. It is these age-group-by-task interactions in the DN that are of interest in this Forum article.

When Do Older Adults Exhibit Reduced Deactivation?

There are two experimental paradigms in which age-group-by-task interactions in deactivation have consistently been observed. First, in studies that include manipulation of task difficulty (e.g. a hard and an easy working memory task) [7], young and older adults typically exhibit similar levels of deactivation in the easy task but older adults exhibit reduced deactivation in harder tasks. Thus, age-related reductions in deactivation occur primarily when cognitive resources are taxed [7]. However, these studies have rarely correlated brain activation with task performance, making it hard to determine whether decreased deactivation in aging contributes to or impairs task performance.

The second paradigm in which age-group-by-task interactions in deactivation have consistently been observed is the subsequent memory paradigm. Here, activation is contrasted between encoding items (e.g., words, pictures) that are remembered versus forgotten in a later memory test. Subsequent memory studies have used two complementary types of brain–behavior association. First, the subsequent memory contrast allows identification of

regions that are more active when individuals successfully versus unsuccessfully encode information. Second, across-individual correlations between activation and task performance reveal brain regions that are activated in individuals performing the best overall. The brain regions identified as supporting performance in these two analyses need not correspond. For instance, consider an experimental task that can be performed using two distinct strategies, one of which is more efficient and will lead to higher performance than the other. In this scenario, brain regions involved in the less effective strategy may be more active during successful versus unsuccessful task performance (because this is one way to do the task) and negatively correlated with overall task performance (because this is not the optimal strategy) [9].

In the subsequent memory paradigm, young adults typically exhibit greater deactivation for subsequently remembered versus forgotten encoding items in DN regions, suggesting that deactivation in DN regions contributes to successful encoding in young adults [3,6]. Compared with young adults, older adults exhibit decreased deactivation in DN regions while encoding items they will later remember. This results in a group-by-task interaction in which older adults exhibit a reduced difference in activation between forgotten and remembered events compared with young adults in some studies or even a reversal of the young adult effect in other studies, such that there is less deactivation for remembered versus forgotten items in older adults [3,6,9] (Figure 1). Furthermore, those older adults who exhibit the most deactivation during successful encoding tend to perform worst on the task overall [3,6,9]. Thus, DN regions contribute to task performance primarily in lower-performing older adults. Furthermore, subsequent memory and task-difficulty paradigms both suggest that age-related reduction in deactivation occurs primarily when cognitive resources are taxed (in a harder versus

Box 1. Association between Deactivation and Beta-Amyloid Deposition

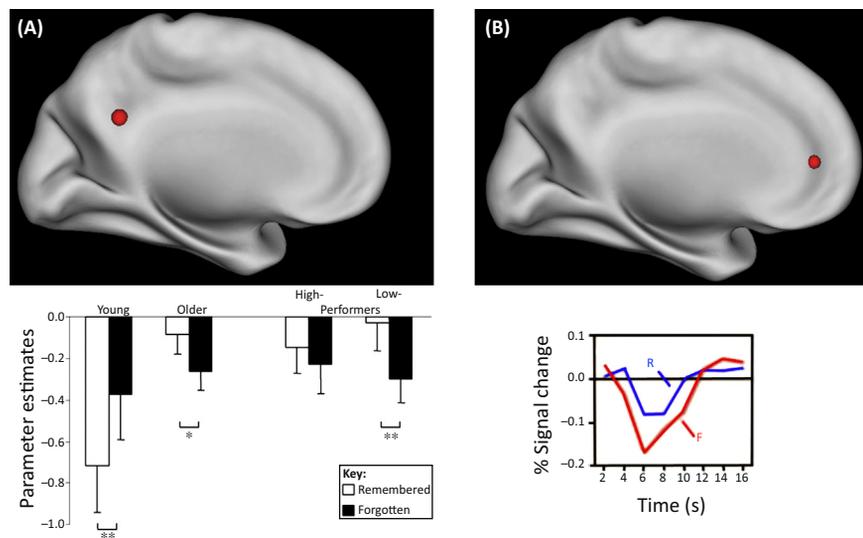
At around the same time that interest grew in age-related differences in deactivation, new technology allowed *in vivo* measurement of beta-amyloid deposition, a biomarker for AD. Studies using this technology indicated that amyloid deposition is detectable before any behavioral symptoms in a significant percentage (20–33%) of non-demented individuals [4]. Additionally, amyloid is present in DN regions, and higher rates of amyloid correlate with decreased deactivation in DN regions [4]. These results raised the possibility that previous reports of reduced deactivation in samples of older relative to young adults are primarily or entirely attributable to individuals with high amyloid in the older sample. However, recent studies that can dissociate the effects of age and amyloid deposition on age-group-by-task interactions in the DN have indicated that deactivations are present even in older adults with no evidence of amyloid deposition [13,14] (although it remains possible that subthreshold levels of amyloid or other AD-related pathology contribute to these results). Moreover, whereas there is often an *a priori* focus of amyloid–DN associations, it is important to note that amyloid sometimes has a larger impact on task-related activation in regions outside the DN that are activated above baseline [13].

an easy task or in individuals performing more poorly on the task).

Cognitive Processes Associated with Reduced Deactivation in Aging

What are the cognitive processes associated with age-group-by-task interactions in deactivation in DN regions? One

influential perspective is that healthy older adults exhibit reduced deactivation because they are less able than young adults to suppress task-irrelevant processes (e.g., [2]). Yet this proposal is inconsistent with the findings reviewed above indicating that age-related differences in deactivation occur when participants are successfully doing the task.



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Figure 1. Reduced Deactivation during Events Later Remembered versus Forgotten. (A) A representative example of an age-group-by-subsequent-memory interaction in a deactivated region. Adapted from [3]. The bar graph displays parameter estimates in the posterior cingulate cortex for encoding events subsequently remembered and forgotten in young adults, older adults, and subgroups of high-performing and low-performing older adults. A reversal in subsequent memory effects with age (forgotten > remembered in young, remembered > forgotten in old) was observed that is particularly evident in low-performing older adults. This interaction is attributable primarily to a difference in activation for remembered (rather than forgotten) events. See [9] for a meta-analysis indicating that such effects are consistently observed. (B) Young adults, under certain conditions, can also exhibit reduced deactivation in a region that contributes to successful task performance. Adapted from [15]. A region in the medial prefrontal cortex was less deactivated for remembered (R) than forgotten (F) events. The encoding task was to judge the self-descriptiveness of adjectives, a task that differs from traditional semantic encoding tasks such as the animate/inanimate task used in [3].

Further evidence against this proposal comes from behavioral studies that have consistently revealed that older adults exhibit a reduction in self-reported task-irrelevant thoughts during a variety of tasks [10]. Moreover, older adults sometimes outperform young adults in monotonous sustained-attention tasks, providing objective evidence to corroborate self-reports. However, behavioral studies take place in quiet and comfortable environments, which differs from the noisy and less comfortable fMRI environment. It is possible that, in this latter setting, older adults exhibit a higher frequency of task-irrelevant thoughts (e.g., because they are distracted by the scanner environment). Inconsistent with this idea, a recent study [11] found no significant age-related differences in online self-reports of task-irrelevant thoughts (personal thoughts, thoughts about the scanner environment, and worries about task performance) during an fMRI episodic encoding task; task-unrelated thoughts were numerically lower in older versus young subjects, consistent with behavioral studies. It is thus unlikely that age-related reduction in deactivation is attributable to increased task-unrelated thoughts.

Instead, we suggest that when cognitive resources are taxed, older adults increasingly rely on cognitive processes mediated by the DN (see also [7,9]). The critical aspect of this proposal is that age-related reductions in the DN represent task-relevant processes rather than task-irrelevant ones. Importantly, we are not suggesting that recruitment of the DN in older adults is compensatory in the sense that those older adults that recruit the DN the most

will perform the best (as discussed earlier, the opposite seems to be true).

The precise corresponding cognitive processes engaged by older adults remain to be elucidated and may differ based on the task. For example, whereas current evidence suggests that older adults do not mind-wander more than young adults during cognitive tasks (thoughts that have nothing to with and were not triggered by any stimulus in the current task, such as dinner plans), one possibility is that they exhibit more task-related thoughts and feelings (thoughts/feelings triggered by stimuli in the task itself, such as a picture of a sofa triggering a thought about how it looks similar to the one in my living room) [12]. Distinguishing which thoughts are task-related/unrelated is a thorny issue and may vary based on the specific requirements of a task. Another possibility is that older adults rely more on prior knowledge, experience, and schemas that they have accumulated over their longer lifespan (i.e., semantic memory) [7]. The suggestion that older adults sometimes use their greater knowledge in the face of declining cognitive efficiency is not new; however, these ideas have not yet been widely discussed by neuroimaging researchers in relation to age-related differences in DN activation. Our hope is that this Forum article brings attention to these possibilities and stimulates research assessing their validity.

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