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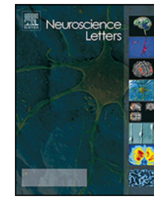

Default mode network gates the retrieval of task-irrelevant incidental memories

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ABSTRACT

Episodic memories can be retrieved by an intentional search for certain information. Alternatively, a past episode may enter our consciousness without any intention to retrieve it, prompted by a stimulus in our surroundings. Incidental retrieval does not occur upon each encounter with a familiar stimulus, suggesting that a gating mechanism exists which regulates incidental retrieval activity. We analyzed data from a functional magnetic resonance imaging study on incidental retrieval in healthy young adults and found that failure to incidentally retrieve was selectively associated with reduced activation of lateral and medial parietal regions as well as ventromedial frontal cortex, areas implicated in default mode network. This is the first demonstration that relative deactivation of the brain regions associated with the default mode gates the consciousness from currently irrelevant memories.

During episodic retrieval several brain regions collaborate to bring an episode from our personal past to our consciousness. At times, a specific memory must be actively sought after, at other times a recollection may occur spontaneously, upon encountering a familiar stimulus. We have previously shown [9] that there is considerable overlap between the brain areas that are engaged when the memory is actively sought after and when it comes to mind incidentally. In particular, hippocampus and precuneus are associated to successful retrieval in both controlled and incidental episodic retrieval, whereas specific early-stage oldness assessment in occipito-temporal regions, not found during controlled retrieval, triggers incidental retrieval [9]. However, incidental retrieval does not happen on all occasions when we see familiar stimuli, suggesting that there must exist a gating mechanism which controls when the cognitive processing can be directed to recollecting an episode associated to the currently active mental representation. Understanding the neural mechanisms which prevent incidental retrieval from happening can be beneficial for individuals who experience unwanted, intrusive recollections of unpleasant experiences.

Behavioural studies have suggested that incidental retrieval frequently happens when the mind is idle, such as during a monotonous, non-demanding task [16]. In fMRI studies during simple ('baseline') tasks, co-activation of specific brain regions in medial frontal and parietal as well as lateral parietal cortex has been found. These regions, which typically show relative decrease in activation levels as the cognitive demands increase, form the so-called "default mode network", suggested to support the internally oriented, self-reflective processing [8,14]. This network seems to have strong relationships with episodic memory system [1,17,18], with association between the default mode activity in parietal and ventromedial frontal brain regions and hippocampus [6,7,20]. Further, deactivation of the default mode network seems to be related to disruption of task-irrelevant thoughts [12]. It therefore appears plausible that the occasions when a familiar stimulus does not lead to incidental recollection may be associated to decreased activation in the default mode network and increased activation in the brain regions associated to task-related effort.

In order to test this hypothesis, we analyzed functional magnetic resonance data from healthy young adults performing an incidental retrieval task described in [9], concentrating on the brain activity specifically expressed during instances of incidental retrieval failure, compared to incidental retrieval as well as processing of novel items.

The subjects were 14 healthy young adults (mean age 24.1 years, SD 4.5 years), native Swedish speakers, right-handed by self-report, with normal or corrected-to-normal visual acuity. The subjects gave informed consent. The study was approved by the ethics committee of the University Hospital of Northern Sweden.

We used a novel incidental retrieval task (see [9,15] for more details). Approximately 24 h before the fMRI session, the subjects intentionally encoded 40 naturalistic sounds and 40 colour photographs of common, everyday objects. During the fMRI session, the subjects were visually presented with concrete and abstract words ($n = 240$, presentation duration 2500 ms, word order pseudo-randomized). The subjects performed an intentional and an

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incidental retrieval task, each with 120 words. The tasks were performed in fixed order, to minimize the deliberate retrieval attempts during the incidental retrieval. In the intentional task the subjects were asked to identify the words denoting the objects which were presented during the encoding session (without indicating the presentation modality). In the incidental task they were asked to categorize the words as concrete and abstract. In the intentional condition the subjects additionally had to categorize each word as concrete or abstract, whereas in the incidental condition they were asked to indicate in case a word happened to spontaneously elicit a memory of encountering that object during the encoding session. The order of the “remember” and “categorize” responses was not fixed, the subjects were encouraged to report retrieval as soon as it occurred in both conditions. In both conditions the subjects were instructed to concentrate on the primary task and attempt to maximise their performance (retrieval or categorization, respectively). The proportion of new concrete, matching concrete, and abstract words was identical in both conditions, with 40 instances of each category. The subjects gave their responses with three fingers of the dominant hand (index finger – concrete, middle finger – abstract, ring finger – remember). Due to the response instructions, the matching concrete words which the subjects failed to identify as old were treated behaviourally identically as the new concrete words, i.e., the subjects gave only the categorization response.

The data were acquired on a 3 T Philips Achieva scanner. Functional T2*-weighted images were acquired with a single-shot gradient-echo sequence (TR = 1512 ms, TE = 30 ms, field of view = 22 cm). The images were analyzed using SPM5 software (Wellcome Trust Centre for Neuroimaging, London, UK). The functional images were realigned and unwarped, corrected for within-volume time delay due to slice-wise acquisition, normalized to the Montreal Neurological Institute EPI template provided by SPM5, and smoothed with a Gaussian kernel with 8 mm full width at half maximum. The eight experimental conditions (retrieved, failed, new concrete and abstract words in intentional and incidental tasks) were modelled with separate regressors. Each regressor was constructed using delta functions marking the stimulus onsets, convolved with the canonical hemodynamic response function. At the single-subject level, this model was estimated on a voxel-to-voxel basis. At the group level planned comparisons were performed over the single-subject beta images corresponding to the retrieved, failed and new concrete items, treated as repeated measures. These comparisons, performed separately for the intentional and incidental task, were aimed at identifying voxels which show specific response for failed items ([1 −2 1] and [−1 2 −1]). Such comparisons show the brain regions which are not associated with retrieval success (since the retrieved and new items are coded as equal) or semantic categorization (since the behaviourally equivalent failed and new concrete items are coded as non-equal), thus these regions can be assumed to support processes which are specifically associated with retrieval failure. The results were thresholded at $p < .05$, corrected for family-wise error.

As expected, the subjects retrieved more items in the intentional retrieval condition compared to the incidental retrieval condition (intentional: 61.6%; incidental: 47.4%; $t(13) = 4.1$, $p < .005$). Regarding the retrieved items, the subjects reported “remember” response as the first response (compared to the categorization response for the same item) more often in the intentional retrieval condition (intentional: 51%; incidental: 6%; $t(13) = 4.8$, $p < .005$). Correspondingly, the “remember” responses were given faster in the intentional retrieval condition (intentional retrieval: 1594 ms, incidental retrieval: 1780 ms; $t(13) = 3.8$, $p < .005$). This supports the view that the two conditions differed in the distribution of cognitive resources to retrieval and semantic categorization, respectively. We further explored the subjects’ performance by comparing the response speed for the semantic categorization responses given for the new items and failed items using factorial repeated measures analysis of variance with the factors Condition (intentional/incidental) and Stimulus (new/failed). Both main effects were significant (Condition: $F(1,13) = 31.6$; $p < .005$; Stimulus: $F(1,13) = 12.2$; $p < .005$), also the interaction between the factors was significant ($F(1,13) = 10.4$; $p = .007$). Post hoc testing, using t-tests for repeated measures, showed that this interaction stemmed from significantly slower semantic categorization responses for failed items compared to new items in the intentional retrieval condition ($t(13) = 3.9$; $p < .005$), whereas there was no difference between the speed of the semantic categorization responses for the failed and new items in the incidental retrieval condition ($t(13) = 0.6$, $p > .5$). This pattern indicates that the new and failed items were processed identically by the subjects during the incidental retrieval condition.

Table 1
The brain regions showing selectively reduced activation during incidental retrieval failure compared to incidentally retrieved and new items. BA – Brodmann area, Z – z-score of the peak voxel, and k – number of voxels in the cluster.

Region	BA	x	y	z	Z	k
Inferior parietal lobule	40	48	−54	34	6.16	482
Anterior cingulate	32	−6	36	16	5.59	170
Precuneus	7	2	−68	48	5.47	353
Angular gyrus	40	−50	−62	32	4.96	15

We found selectively reduced activation during incidental retrieval failure compared to incidentally retrieved and new items in a restricted set of brain regions, consisting of lateral and medial parietal cortex and ventromedial frontal cortex (Fig. 1, Table 1). These brain areas are consistently reported as part of the default mode network [9,15]. We did not find any brain regions which selectively increased their activation during incidental retrieval failure. For exploratory purposes we lowered the statistical threshold to $p < .0001$ (uncorrected for family-wise error) and found one cluster, situated in right putamen ($x, y, z = 30, 8, 14$; $Z = 4.44$; $k = 23$). To ensure that the results accurately reflect clusters which react specifically to incidental retrieval failures, with no substantial modulation across incidentally retrieved and new items, we exclusively masked the planned comparison with a contrast between incidentally retrieved and new items (thresholded at $p < .05$, FWE). This procedure did not have any influence on the results reported above. Finally, we examined the effect sizes (Cohen’s d for repeated measures) of the differences between three pairs of conditions. The average difference across the four clusters between incidentally recalled and failed items ($d = 2.0$) as well as new and failed items ($d = 1.3$) was substantially larger than the difference between recalled and new items ($d = 0.7$), confirming that the four clusters show reduced activation specifically during incidental retrieval failure.

We found selective deactivation in a single voxel, situated in the white matter close to parahippocampal gyrus ($x, y, z = -40, -32, -8$; $Z = 4.85$). We did not find selective increase in activation in any brain regions during intentional retrieval failure; lowering the statistical threshold to $p < .0001$, as above, did not reveal any activations.

We found that event-related relative deactivation in a certain set of brain regions selectively disrupts incidental episodic retrieval, while we did not find such selective deactivation during intentional retrieval failures. The lateral and medial parietal cortex and ventromedial frontal cortex are associated with the so-called default mode network, a set of brain regions which show spontaneous coherence in their activation during rest and relative deactivation during cognitively demanding tasks [14]. Exploratory analysis at a more lenient threshold ($p < .0001$ uncorrected) further suggested that the incidental retrieval failures are associated with selectively increased activation of right putamen, a finding consistent with

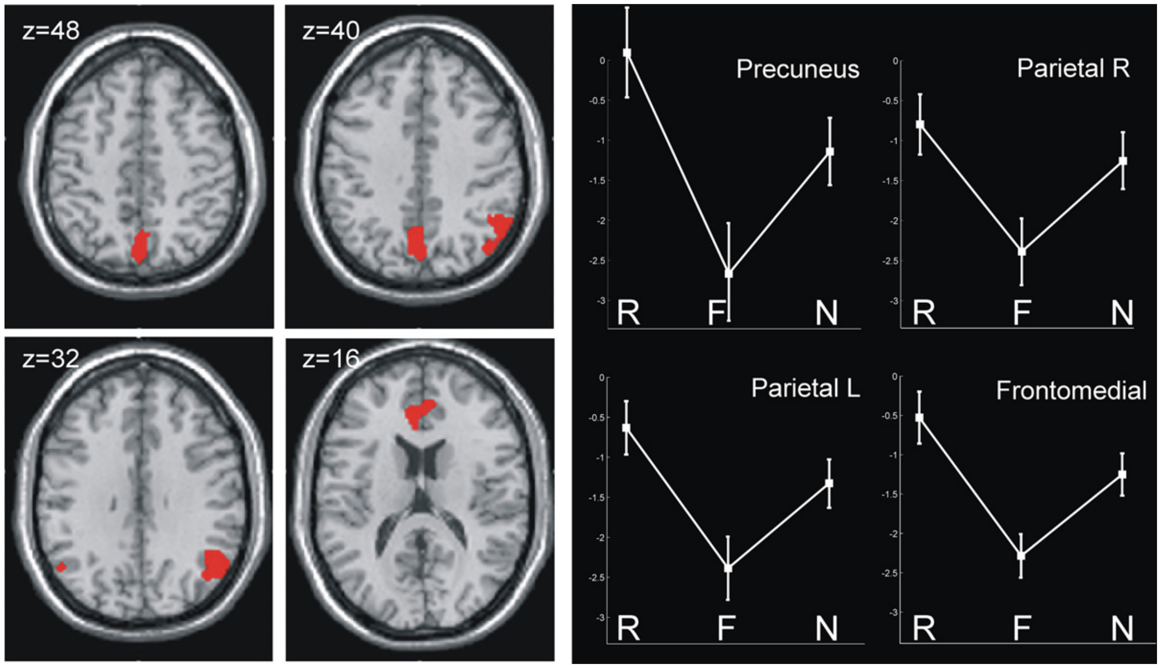

Fig. 1. The clusters showing selectively reduced activation during incidental retrieval failure compared to incidentally retrieved and new items projected on transversal slices. The line graphs depict the parameter estimates (*y*-axis, arbitrary units) corresponding to the experimental conditions in each of the clusters. R – retrieved items, F – failed items, and N – new items.

previous reports of negative relationship between the default mode network and putamen [3], possibly mediated by dopamine [19].

Regarding intentional retrieval, it has been suggested that the brain needs to be in a certain state, or "retrieval mode", in which the retrieval cue can be processed in such way which can lead to recollective experience [10]. The results presented here support the view that retrieval is a state-dependant process, but approach the issue from a novel angle. Majority of studies of state-dependant effects in episodic retrieval have concentrated on identifying brain regions which are active during conscious intention to retrieve, regardless of outcome (cf. [2,4,10]). Complementing these findings, the results presented here suggest that there exists a brain state during which a stimulus that has a matching memory trace in the episodic memory can initiate retrieval, even though there is no top–down bias to do so, while perturbance of this state prevents retrieval from happening despite the presence of the potential retrieval cue.

The finding that the relative deactivation of the brain areas associated with the default mode network suppresses task-irrelevant (incidental) episodic retrieval is in good agreement with the proposed role of task-related deactivations. It has been suggested that suppressing the activation in the default mode network serves to reduce task-irrelevant processing during cognitively demanding tasks [5,12]. Given the relationship between the default mode network and hippocampus [20], a potential mechanism for preventing incidental retrieval from happening could be reducing the receptiveness of hippocampus to signals that the currently processed material has been encountered previously. The concurrent increased activation of putamen suggests a link with the dopamine system [19], which has been suggested previously as an important factor in shifting the hippocampal processing from retrieval to encoding [11] (see also [13]).

With the exception of a single voxel near the parahippocampal gyrus, we did not find any specific brain activation associated to the failure to retrieve memories intentionally. This finding is in good agreement with the suggestion that during intentional retrieval all potential retrieval cues are processed similarly, and this processing is independent of the outcome of the retrieval attempt [10].

The present study does not answer the question whether the disruption of the incidental retrieval was proactive or reactive relative to the processing of the potential retrieval cues. It is possible that the relative deactivation observed here began before the presentation of the potential retrieval cue, perhaps as a result to compensate for perceived decrease in the performance of the main task. Alternatively, the reduction of the activation may reflect a successful attempt to suppress the initiation of the task-irrelevant processing on those occasions when it is relatively weak, whereas in cases where the incidental retrieval did occur the initial trigger signal was so strong that the attempts to disrupt the task-irrelevant processing were abandoned as futile. The small difference observed when examining the effect sizes of the difference between incidentally retrieved and new items, with the new items associated to relatively more deactivation (cf. Fig. 1), offers tentative support for the first alternative. In case the activation level in the default mode network fluctuates due to factors related to the performance of the main task, the brain activation during the new items would be averaged over trials with various activation levels in the default mode network. Incidentally retrieved and failed trials, however, would represent the opposite extremes of the activation values; taking that into account would result in the brain activation patterns observed in this study. Further research is required to understand how and when the brain areas associated with the default mode network perform the gating function in episodic retrieval.

Although we commonly encounter stimuli in our environment which have the potential of acting as retrieval cues, we do not become incapacitated by a constant stream of currently irrelevant episodic memories. Previous research has emphasized the role of "retrieval mode", a specific brain state regulating the intentional retrieval of memories. The present results expand the understanding of the role of wide-spread networks in regulating the access to episodic memories. The finding that deactivation of the brain areas associated with the default mode leads to selective disruption of incidental retrieval is in agreement with the suggested role of such deactivation in suppressing task-irrelevant processing. Further studies are needed to pinpoint at which stage of the cue processing and under which exact circumstances such gating of episodic retrieval operates.

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