

# Episodic specificity induction impacts activity in a core brain network during construction of imagined future experiences

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Recent behavioral work suggests that an episodic specificity induction—brief training in recollecting the details of a past experience—enhances performance on subsequent tasks that rely on episodic retrieval, including imagining future experiences, solving open-ended problems, and thinking creatively. Despite these far-reaching behavioral effects, nothing is known about the neural processes impacted by an episodic specificity induction. Related neuroimaging work has linked episodic retrieval with a core network of brain regions that supports imagining future experiences. We tested the hypothesis that key structures in this network are influenced by the specificity induction. Participants received the specificity induction or one of two control inductions and then generated future events and semantic object comparisons during fMRI scanning. After receiving the specificity induction compared with the control, participants exhibited significantly more activity in several core network regions during the construction of imagined events over object comparisons, including the left anterior hippocampus, right inferior parietal lobule, right posterior cingulate cortex, and right ventral precuneus. Induction-related differences in the episodic detail of imagined events significantly modulated induction-related differences in the construction of imagined events in the left anterior hippocampus and right inferior parietal lobule. Resting-state functional connectivity analyses with hippocampal and inferior parietal lobule seed regions and the rest of the brain also revealed significantly stronger core network coupling following the specificity induction compared with the control. These findings provide evidence that an episodic specificity induction selectively targets episodic processes that are commonly linked to key core network regions, including the hippocampus.

episodic specificity induction | imagination | hippocampus | core network | fMRI

Numerous recent studies have revealed striking overlap in the neural and cognitive processes that support remembering past experiences and imagining future experiences or novel scenes (reviewed in refs. 1, 2). According to the constructive episodic simulation hypothesis (3), similarities between remembering and imagining reflect to a large extent the contributions of episodic memory to both processes (4). However, some evidence indicates that these similarities can also reflect the influence of nonepisodic processes, such as descriptive ability or narrative style, that influence remembering and imagining (5).

We recently developed an experimental approach to distinguishing episodic and nonepisodic influences on remembering and imagining that we refer to as an episodic specificity induction: brief training in recollecting episodic details of recent experiences (reviewed in ref. 6). After receiving an episodic specificity induction (vs. a control induction), participants subsequently remembered past and imagined future experiences with increased episodic but not semantic detail, and the specificity induction had no effect on details generated during tasks that do not draw on episodic memory, such as describing a picture (7) or defining and comparing words (8). We have also shown that the specificity induction boosts performance on such tasks as means-end problem solving (9, 10)

and divergent creative thinking (11) that have also been linked previously to episodic memory. Based on these results, we have proposed that the specificity induction biases participants to adopt a specific retrieval orientation—i.e., to focus on episodic details related to places, people, or actions—and that this heightened focus on episodic details impacts performance on tasks that involve constructing mental events or scenes containing details like those emphasized during the specificity induction (6).

Although our previous work has examined the cognitive processes impacted by the specificity induction, our characterization of those processes, together with previous research concerning the neural underpinnings of remembering and imagining, leads to predictions regarding the neural processes that should be influenced by the induction. Previous studies have indicated that remembering and imagining rely on a common core network of brain regions (12, 13) that overlaps substantially with the default network (14–17). According to a recent meta-analysis (13), this core network includes regions within all of the key segments of the default network, including its medial temporal lobe (MTL) subsystem (hippocampus, parahippocampal and retrosplenial cortex, inferior parietal lobe, ventromedial prefrontal cortex), which has been linked with the construction of imagined events or scenes, and its dorsomedial prefrontal subsystem (dorsomedial prefrontal cortex, dorsolateral prefrontal cortex, lateral temporal cortex), which has been linked with social components of events (15).

## Significance

Recent behavioral studies using an episodic specificity induction—training in recollecting details of past experiences—have suggested a role for episodic memory in imagining future events, solving problems, and thinking creatively. The present fMRI study examines the brain regions impacted by the specificity induction. The experiment shows that receiving a specificity induction led to increased activity in key brain regions previously implicated in detailed event construction, including the hippocampus and inferior parietal lobule, when participants imagined future events. These results provide insights into the influence of episodic memory beyond simple remembering, and may help to guide potential applications for individuals from populations characterized by overgeneralized memory and imagination, such as healthy aging and clinical depression.

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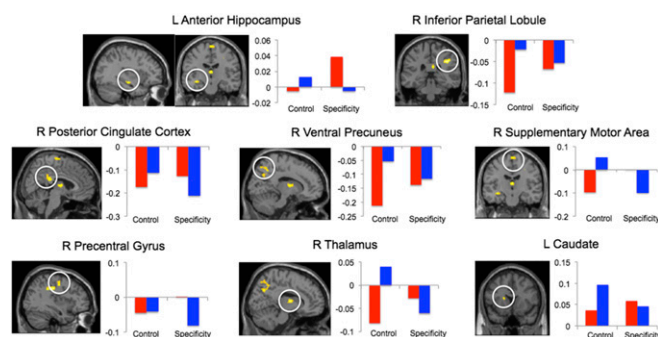
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**Fig. 2.** MTL subsystem regions (and other regions within and outside of the core network) with stronger recruitment for constructing imagined events (relative to the semantic object task) following the specificity induction compared with the control at the threshold of  $P < 0.001$ , uncorrected (with an extent threshold of 65 voxels, yielding a corrected threshold of  $P < 0.05$ ). The y axis of each chart depicts percent signal change (extracted from the region's peak voxel); the red bars depict imagine construction and the blue bars depict object construction. L, left; R, right.

parietal lobe seed served to significantly boost connectivity with the left parahippocampal gyrus, left superior medial frontal gyrus, and left anterior cingulate cortex ( $P < 0.001$ , uncorrected and  $k \geq 38$  voxels, yielding a corrected threshold of  $P < 0.05$ ). These results suggest short-term, functional reorganization in the core network as a function of induction. No activations survived the opposite induction contrast.

## Discussion

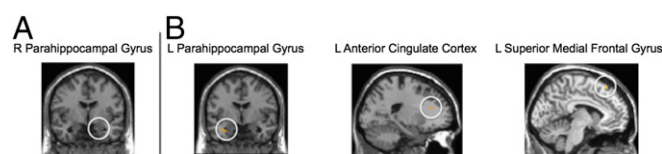
In the present fMRI study, we established the neural signature of an episodic specificity induction for imagining future events. Previous research has suggested that a core network of brain regions comes online when individuals remember past and imagine future events (13), and that this network can be segmented into a MTL subsystem linked to the construction of events or scenes and a dorsomedial prefrontal subsystem linked to the social and self-referential components of these events or scenes (15). We found that participants did indeed activate the core network when generating imagined future events over semantic object comparisons after receiving the specificity and control inductions. Critically, and as hypothesized, receiving the specificity induction compared with either control also led to significantly increased activity in key regions of the MTL subsystem of the core network, including the hippocampus and inferior parietal lobule, when generating future events relative to object comparisons. Postscan responses suggested that the specificity induction was operating as expected in the scanner: significantly more episodic but not semantic details were generated for imagined events following the specificity induction compared with the control, with no differences in any type of detail for object comparisons. This pattern of behavioral results replicates and extends previous work (8), and confirms that differential neural patterns of activity were linked to the experimental manipulation participants received. Further support for a behavior–brain link was established via a parametric modulation analysis, which indicated that induction-related differences in episodic detail in imagined events from the postscan interview significantly modulated induction-related neural activity in the left anterior hippocampus and right inferior parietal lobule (and other regions) during imagine trials in the scanner. This latter finding should be taken as preliminary, however, as it did not emerge with more conservative statistical thresholds (corrected for multiple comparisons; *Materials and Methods*).

The finding that neural induction effects were limited to the construction phase of imagining future events and did not extend

to elaboration is also in line with our hypotheses. We have previously suggested (6) that the specificity induction leads individuals to focus on episodic details related to places, people, and actions of an event or scene and thus targets the process of retrieval orientation—a goal-directed strategy for retrieving an episode in a more or less specific way when presented with a cue (24). The neural induction effects we observed in the MTL subsystem during construction—but not elaboration—suggest that the specificity induction may help participants to adopt a specific retrieval orientation that is used on later tasks that also require participants to construct a mental event or scene that contains details like those emphasized during the induction. This account of the data can also be situated under the theoretical framework of an event model, which is composed, in part, of elements of episodic memory that are bounded in space and sequential time involving physical and figural entities (25). The induction, by facilitating a specific retrieval mode, may help individuals to internally trigger the construction or assembly of a mental event model that is filled with specific details. This notion of construction in an event model also fits with the recent idea that the hippocampus supports the encoding and retrieval of temporal sequences that constitute an event (26–28).

In support of this view, we found increased activity in the left anterior hippocampus during the construction phase of imagination following the specificity induction relative to the control. This finding converges with evidence suggesting that the anterior hippocampus supports the relational processing of elements of an encoded memory at retrieval (29, 30), as well as the flexible recombination of previously learned elements into a novel representation (31). Evidence has also indicated that the anterior hippocampus tracks the content (vs. the temporal ordering) of imagined events (32) and the specificity (vs. abstractness) of imagined events (18, 19) and autobiographical plans (33). The constructive episodic simulation hypothesis (3) posits that imagining future events involves extracting and recombining elements of previous memories into a novel scenario, and that these cognitive processes are in part dependent on the hippocampus. Under this framework, the induction may lead to increased anterior hippocampal activity when participants imagine future events by ramping up processes involved in the extraction and relational recombination of elements of previous memories into a novel scenario.

Nonetheless, we are cautious in interpreting too heavily the precise location of increased induction-related activity within the hippocampus. Several factors can influence the location of hippocampal activity (reviewed in ref. 34), and work from the spatial cognition domain on the anterior–posterior hippocampal axis suggests that the anterior hippocampus supports coarse-grained (vs. fine-grained) representations, at least those that are spatial (refs. 35, 36; reviewed in ref. 37). The anterior hippocampus has also been associated with the encoding of novel simulations into memory (38). However, if the induction simply helped participants to encode novel representations into memory, we would have



**Fig. 3.** Resting-state functional connectivity results following the specificity compared with the control induction for (A) a left anterior hippocampal seed region (extracted from a peak voxel xyz of  $-34, -16, -12$ ) and (B) a right inferior parietal lobule seed region (extracted from a peak voxel xyz of  $38, -32, 36$ ) and the rest of the brain at a threshold of  $P < 0.001$ , uncorrected (with an extent threshold of 38 voxels, yielding a corrected threshold of  $P < 0.05$ ).





until the trial was over. At the end of each trial, the screen changed and participants rated (*i*) how detailed the mental image of their imagination was (from 1 to 5, with 1 indicating no/few details and least vivid to 5 indicating many details and most vivid) and (*ii*) whether they stayed engaged on task (either 1 indicating yes or 2 indicating no). Eighteen total object comparison trials were also included per segment and matched with imagined events for task structure and response mode (*SI Materials and Methods*). Although both main tasks required generative search and retrieval (55), only the imagine task required generating episodic content.

**Resting State.** In each of the two segments following the main task runs, participants completed a resting-state scan for 7 m, 13 s in which they viewed a black background with a white fixation cross.

**Postscan Interview.** Immediately after scanning, participants completed a postscan interview (19, 21). Participants viewed each object cue from the scanner (in the same order to reduce cognitive load) and verbally reported whatever they had thought about (without adding new details). Each trial was completed in a self-paced manner without input or probing from the experimenter, and, following each trial, participants completed four ratings for imagined events and two for object comparisons (*SI Materials and Methods*) provides information on additional ratings). Pilot testing before the study commenced ( $n = 2$ ) showed that participants could describe what they had silently generated.

Participants' actual verbal reports for imagined events and object comparisons were audio-recorded for later transcription and scoring with the autobiographical interview procedure (56). For imagined events, bits of information contained in these verbal reports were segmented. Each detail was classified as either episodic or semantic to the main event described. Episodic details included the who, what, where, and when elements of the central event specific in time and place; semantic details included factual information, off-topic and repetitive information, and commentary. For object comparisons, bits of information were also segmented and scored into detail subcategories (as in ref. 8). The main measure of interest was elements of the central object definitions that were on-task and meaningful; extraneous details included elements of the reports that were off-topic, repetitive, not meaningful, or commentary. Two independent raters blind to all experimental hypotheses and the induction conditions scored the verbal reports after completing an interrater reliability assessment of 20 trials of imagined events and object comparisons from the pilot subjects not included in the main study. Reliability was high across scored measures (Cronbach's standardized  $\alpha \geq 0.90$ ). Additional information on scoring is provided in *SI Materials and Methods*.

#### fMRI Acquisition, Preprocessing, and Analysis Parameters.

**Main task approach.** Scanning and preprocessing parameters for the main tasks are provided in *SI Materials and Methods*. Preprocessed data were statistically analyzed by using the general linear model (examples of this approach are provided in refs. 19, 21). Each participant's blood oxygen level-dependent (BOLD) response for (*i*) construction and (*ii*) elaboration were modeled separately for each imagined event trial and each object comparison trial by using SPM12's canonical hemodynamic response function (hrf) with first-level fixed-effects models. One first-level model was created for the control induction runs and one for the specificity induction runs. The hrf for construction (i.e., regressors for imagine and object construction) was applied 2 s after cue onset, and the hrf for elaboration (i.e., regressors for imagine and object elaboration) was applied 2 s after the participant made a button press [mean elaboration (jittered) = 8.65 s across tasks]. The entire 20-s duration of each trial was not modeled to reduce contamination effects. The BOLD response for the rating phase of each trial was also modeled at the rating onset (i.e., regressors for imagine and object rating), and subject-specific movement parameters for each run were added as covariates of no interest.

To examine whether participants displayed typical neural patterns of performance on the imagined event and object comparison tasks and to test for any induction-related effects, we computed contrasts for (*i*) imagine construction > object construction and (*ii*) imagine elaboration > object elaboration. At the second level, we entered the contrast images into random-effects one-sample *t* tests for each induction separately for (*i*) construction and (*ii*) elaboration to ensure that typical neural patterns of core network recruitment were observed after each induction and phase (13, 19, 21). Critically, at the second level, we also entered contrast images into random-effects paired *t* tests whereby each pair of scans included the respective control induction contrast image and specificity induction contrast image for each participant separately for (*i*) construction and (*ii*) elaboration. An interaction effect was also computed (*SI Materials and Methods*).

The significance threshold and minimum cluster size ( $P < 0.001$ , uncorrected and  $k \geq 65$  voxels), equivalent to  $P < 0.05$  corrected for multiple comparisons, was determined via Analysis of Functional NeuroImages' (AFNI)

3dClustSim program (in June 2015) by using a Monte Carlo simulation (10,000 iterations) within the 3D whole-brain search volume (179,380 2-mm<sup>3</sup> voxels) to estimate the overall probability of false positives (as in refs. 39, 57). To minimize the possibility of false positives with cluster thresholding in functional neuroimaging analyses (58), we used a version of the 3dClustSim program that is free from technical problems uncovered in previous versions, and that incorporated the correct smoothing value (i.e., derived from the group residual mean-square images) with a conservative cluster-defining threshold (i.e.,  $P < 0.001$  vs.  $P < 0.01$ ).

Next, we performed a parametric modulation analysis in SPM by including regressors in the first-level models outlined earlier for control and specificity runs separately (as in ref. 18). Although we used a cognitive experimental manipulation—a feature of the methodological design that should pinpoint in a systematic way the impact of the behavioral induction on neural performance—we took this additional step to relate behavioral and neural data. We entered, trial-by-trial, a detail score for each imagined event and object comparison obtained in the postscan interview as a covariate of interest for each respective imagine construction and object construction trial (i.e., regressors for imagine detail and object detail). We focused on the behavioral detail index and the construction phase fMRI data because results indicated induction-related effects on these key outputs. The detail score covariate was modeled linearly, represented the orthogonal contribution of detail in the absence of any other covariates, and was mean-centered according to SPM algorithms. We contrasted the modulatory effects of imagine detail covariate > object detail covariate during the construction phase at the first level. At the second level, we entered these first-level contrast images into a random-effects paired *t* test whereby each pair of scans included the respective control induction contrast image and specificity induction contrast image for each participant. This analysis allowed us to identify which regions during construction showed differential activity following the specificity induction compared with the control as modulated by an index of detail for imagined events over object comparisons.

A significance threshold of  $P < 0.005$ , uncorrected with an extent threshold of 10 contiguously activated voxels (2 mm<sup>3</sup>) was applied for whole-brain testing of the parametric modulation (the same or similar thresholds were used for parametric modulation analyses in refs. 18, 59, 60). Although the results of this particular analysis did not survive more stringent corrected thresholds, we included it as preliminary induction-related evidence of a behavior–brain link (a theoretical and quantitative justification of the threshold is provided in ref. 61).

**Resting-state approach.** For the resting-state scans, we performed a series of preprocessing steps (including global signal regression) on the raw data followed by a series of functional connectivity-specific preprocessing steps (*SI Materials and Methods*). For the analyses (based on refs. 62, 63), seed regions in the hippocampus and inferior parietal lobule (i.e., a 6-mm sphere centered on the region's peak voxel) were selected on the basis of results from the main task analyses and in line with a priori hypotheses. To create whole-brain correlation images, the averaged time series across all voxels comprising a seed region of interest (ROI) was used as the variable of interest with the time series corresponding to each voxel across the brain via Pearson's product moment correlation. Comparisons of connectivity strength with seed regions across specificity and control inductions were made by using a pairwise *t* test in AFNI. All statistical analyses of correlation data were performed on Fisher *z*-transformations (64), which are approximately normally distributed. Results involve those voxels that survived a statistical threshold of  $P < 0.001$ , uncorrected with an extent threshold of 38 contiguously activated voxels applied for whole-brain testing (search volume of 266,816 2-mm<sup>3</sup> voxels) using 3dClustSim and equivalent to a significance threshold of  $P < 0.05$ , corrected for multiple comparisons. Note that the cluster extent required to achieve a corrected  $\alpha$  of 0.05 with a voxelwise threshold of  $P < 0.001$  here was smaller than the extent required in the main task analysis as a result of differences in EPI acquisition and the smoothness of the data.

Visualization and localization steps for the main tasks and resting-state analyses are provided in *SI Materials and Methods*. All data and materials are available upon request.

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