

# 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 experienceenhances 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. Inductionrelated 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  $\mid$  imagination  $\mid$  hippocampus  $\mid$  core network  $\mid$  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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In light of our behavioral characterization of the specificity induction, we hypothesize and test here that (i) this induction should impact primarily structures within the MTL subsystem, in particular those regions—the hippocampus and inferior parietal lobule—that have been linked previously to detailed episodic retrieval and to imagining of specific (vs. general) future events (18-20). Moreover, our behavioral characterization of the specificity induction as affecting primarily participants' retrieval orientation when they construct mental events or scenes leads us to predict that (ii) these effects will be observed mainly during the initial construction of an event. We adopted a constructionelaboration paradigm used in previous studies of remembering and imagining (21) to test this hypothesis, whereby an initial phase of event construction is distinguished from later event elaboration. To maximize our power to detect possibly subtle effects of the specificity induction, we replaced the remembering condition with additional imagining trials. We also hypothesized that (iii) induction-related differences in the episodic detail of imagined events from a postscan interview would modulate induction-related differences in neural activity in the construction of imagined events during scanning in the hippocampus and inferior parietal lobule. Resting-state functional connectivity analyses with hippocampal and inferior parietal lobule seed regions and the rest of the brain were also performed to test whether (iv) stronger coupling between these regions and other core network areas would be observed following the specificity relative to control induction.

To address our predictions, participants completed a withinsubjects fMRI paradigm in one session (Fig. S1). In each segment in the scanner, participants (i) viewed one of two short videos, completed a short filler task, and then received the episodic specificity induction or one of two control inductions; (ii) viewed 36 object cues after receiving an induction and, for each cue, generated an imagined event or an object size sentence and definitions (i.e., the main tasks); and (iii) completed a resting-state scan. Different stimuli were used in each segment for the induction and main tasks (counterbalanced across participants). For each of the main task scanning trials, we collected reaction time to construct, and detail and engagement ratings. Following scanning, participants verbally generated their thoughts for each main task cue and completed additional ratings. A similar approach was tested in a behavioral pilot in which induction effects were observed (8).

# Results

### Main Task Results.

Imagining future events. Behavioral variables collected in the scanner (reaction time and subjective ratings for detail and engagement; Table S1) did not vary as a function of induction ( $F_{1,31} \le$ 1.82; P values  $\geq$  0.19). Critically, generative responses (Table S2) collected in the postscan interview indicated that participants generated significantly more total details for imagined events but not object comparisons—that followed the specificity induction compared with the control ( $F_{1,31} = 8.87$ ; P = 0.006;  $\eta_p^2 =$ 0.22); critically, this increase in total details for imagined events was driven by a selective and significant boost in the production of episodic details—but not semantic details—following the specificity induction relative to the control ( $F_{1,31} = 24.12$ ; P <0.001;  $\eta_p^2 = 0.44$ ). No induction-related differences were exhibited for any type of detail generated on object comparisons  $(F_{1,31} \le 1.05; P \text{ values } \ge 0.31)$ . Results of the postscan ratings appear in Table S3.

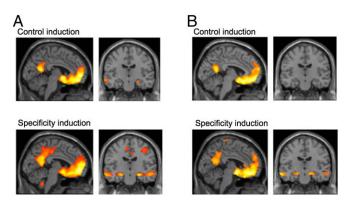
Following both inductions, participants exhibited significant and broad core network activation for imagining events over object comparisons during the construction phase and elaboration phase (P < 0.001, uncorrected and  $k \ge 65$  voxels, yielding a corrected threshold of P < 0.05; Fig. 1 and Table S4). These findings replicate previous work (13, 19, 21) and indicate that participants were completing the main tasks in the scanner as expected.

Critically, participants exhibited significantly greater activation in several core network regions following the specificity induction compared with the control for constructing imagined events over object comparisons (P < 0.001, uncorrected and  $k \ge 65$  voxels, yielding a corrected threshold of P < 0.05; Fig. 2 and Table S5). These included several core network regions (13): the left anterior hippocampus, right inferior parietal lobule, right posterior cingulate cortex, and right ventral precuneus. To further characterize the results, descriptive plots for percent signal change in these regions and the others that emerged are presented in Fig. 2. Note that error bars are not plotted as a result of potential noise, and significance tests were not run on these data (22, 23).

To further link the key induction-related behavioral and brain results, the detail scores obtained from the postscan interview were entered as a modulator of interest during the construction phase of imagined events and object comparisons in the scanner. For the detail index, episodic details on the imagine task and ontopic, factual information on the objects task were used. Critically, induction-related differences in detail were significantly related to induction-related differences in neural activity during the construction of imagined events over object comparisons following the specificity induction compared with the control; these parametric modulation effects were evident in the left anterior hippocampus, right inferior parietal lobule, and right ventral precuneus, as well as the right anterior hippocampus and other regions (P <0.005, uncorrected and  $k \ge 10$  voxels; further details regarding thresholding are provided in Materials and Methods). This analysis (Fig. S2 and Table S6) indicates that the key induction-related behavioral effect (i.e., greater episodic details for imagined events following specificity vs. control) modulated the key induction-related neural effect (i.e., greater activation in the left anterior hippocampus and right inferior parietal lobule for imagined events following the specificity vs. control).

The induction-related results were selective to the construction phase; no significant activations in any direction were evident for elaboration. There were also no significant activations for the opposite contrasts of task and induction.

Resting-state analyses. To more fully characterize the influence of the induction manipulation, we examined its effects on subsequent resting-state connectivity of key core network regions that emerged from the main task analyses: the left anterior hippocampus (xyz, -34, -16, -12) and right inferior parietal lobule (xyz, 38, -32, 36). Following the specificity induction relative to the control (Fig. 3 and Table S7), the left anterior hippocampal seed served to significantly boost connectivity with the right parahippocampal gyrus, and the right inferior



**Fig. 1.** Main task results for (*A*) constructing and (*B*) elaborating on imagined events (relative to the semantic object task) following the control induction and following the specificity induction at the threshold of P < 0.001, uncorrected (with an extent threshold of 65 voxels, yielding a corrected threshold of P < 0.05). This pattern of findings closely parallels that of the core network, which overlaps with the default network (13–17).

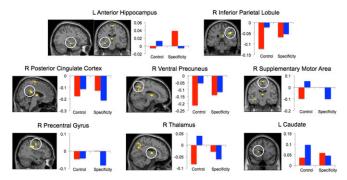


Fig. 2. MTL subsystem regions (and other regions within and outside of the core network) with stronger recruitment for constructing imagined events (relative to the semantic object task) following the specificity induction compared with the control at the threshold of P < 0.001, uncorrected (with an 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 lobule 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  $k \ge 38$ 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

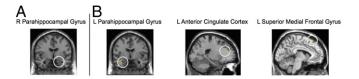


Fig. 3. Resting-state functional connectivity results following the specificity compared with the control induction for (A) a left anterior hippocampal seed region (extracted from a peak voxel xyz of -34, -16, -12) and (B) a right inferior parietal lobule seed region (extracted from a peak voxel xyz 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).

expected to observe increases in details generated in the postscan for cues involving imagined events and object definitions following the specificity induction, but we found effects only for imagined events. Future work should continue to identify subregions of the hippocampus that map onto subcomponents of imagining events or scenes by using high-resolution fMRI (discussed in ref. 39), as well as the role of lateralization in the hippocampus and other brain regions during simulation (40).

We also found increased induction-related neural activity in the right inferior parietal lobule when participants constructed imagined future events. Like the anterior hippocampus, the inferior parietal lobule has been implicated in studies in which participants imagine events in more specific (vs. more general) detail (19), particularly during the construction phase (21). The inferior parietal lobule is also part of the MTL subsystem that is thought to track with episodic memory, event imagination, and scene content (15), and activity in this region has been associated with the successful retrieval and integration of perceptual details from memory (20). In a related topic, we found evidence that activity in the right ventral precuneus increased following the specificity induction relative to the control for imagined events. The inferior parietal lobule and ventral precuneus have recently been linked to mental orientation in space, time, and person (41). We have also previously found that the right ventral precuneus exhibits increased activity during repeated future simulations (e.g., ref. 42), but it is unclear whether these changes are specifically related to changes in event detail.

In addition, we found preliminary evidence suggesting that the specificity induction may impact the processing of contextual scene details and more self-relevant, social details into a novel simulation. Following the specificity induction compared with the control, resting-state functional connectivity analyses showed stronger coupling between the left anterior hippocampal seed and a key region linked with scene processing (i.e., right parahippocampal gyrus; refs. 42–44) and between the right inferior parietal lobule seed and scene (i.e., left parahippocampal gyrus) and social regions (i.e., left superior medial frontal gyrus; refs. 15, 42), as well as the left anterior cingulate cortex. The anterior cingulate cortex is part of the frontoparietal control network (45) that has been associated with emotional processing and executive functions including cognitive control. However, because resting-state analyses involve measuring neural activity in the absence of task demands, we are cautious about interpreting these induction-related findings too heavily. Because the induction affected neural functioning during task performance that immediately preceded the resting-state scans, it is unclear whether the short-term reorganization of functional networks in the absence of task demands is a result of (i) the induction manipulation or (ii) the specific neural processing that emerged as a result of the induction during the main tasks. Although the specific processing that emerged as a result of the induction could plausibly have the same effect as the induction itself, future work should investigate this issue more systematically by having participants perform the restingstate scans immediately after receiving an induction.

Another caveat of the present study is that we did not obtain differences in detail ratings in the scanner as a function of induction. Participants could have plausibly rated their simulations as more detailed in the scanner following the specificity induction compared with the control. Nonetheless, previous work has suggested that subjective rating scales may not be the most sensitive measure of episodic detail. Studies have found that subjective ratings of detail and vividness for episodic simulations are higher in older adults than in young adults or are similarly rated (46–49), yet objective scoring measures routinely show that older adults produce fewer episodic details in their narratives compared with young adults (46, 47). Despite the complexities associated with measuring event detail, this outcome allows us to interpret the data patterns knowing that the imagined events after both inductions were, at least subjectively, matched on features that can contribute to the behavioral and neural expressions of simulation.

Taken together, the results suggest that the cognitive processes that are isolated and enhanced via the episodic specificity induction behaviorally are linked to key neural regions in the core network implicated in remembering and imagining events, including the hippocampus. Future work should continue to investigate the contributions of episodic memory, from behavioral and neural perspectives, to cognitive tasks that could involve episodic elements of past experiences, such as imagination, problem-solving, and creativity. These findings may also help to guide interventions for individuals from populations characterized by overgeneralized memory and imagination, such as healthy aging (49) and clinical depression (50–52), that have been shown to benefit from specificity inductions in previous behavioral research (7, 9, 53).

## **Materials and Methods**

Participants. Thirty-two young adults (mean age, 21.0 y, SD, 2.38; 20 female) participated in the study, recruited via advertisements at universities in Boston, MA. All participants were right-handed and fluent in English and had normal or corrected-to-normal vision and no history of neurological or psychological impairment. They all gave written informed consent and were treated in a manner approved by Harvard University's ethics committee. An additional seven participants were excluded for excessive movement or task noncompliance.

Induction Materials and Procedure. An overview of the scanning and postscan design is provided in Fig. S1. To begin each of the two main segments in the scanner, participants received an induction after viewing a ~2-min video of a man and woman performing kitchen activities and completing a 2-min number judgment filler task on a computer screen. Participants viewed the computer screen via a mirror attached to the scanner head coil and scanner-compatible headphones. All participants received the episodic specificity induction in one of the two segments; for the other segment, half of the participants were randomly assigned to receive the impressions control induction and half received the math control induction. Participants were randomly assigned to receive the specificity induction first or one of the two control inductions first, and induction order was counterbalanced across participants. Participants were in the scanner for this portion of the study but were not scanned, heard induction questions over a loud speaker, and responded out loud. Inductions with interviews were audio-recorded (ref. 7 includes full scripts); all inductions took an average of 5 min and did not differ significantly in length.

The episodic specificity induction consisted of a question set based on the cognitive interview (54), a forensic protocol that boosts accurate details associated with eyewitness events. Participants were told that they were the chief expert about the video, and then responded to three mental imagery probes to report everything about the video's setting, people, and actions as specifically and in as much detail as possible. Open-ended follow-up questions were used to probe generated details. Information on the control inductions is provided in *Si Materials and Methods*.

**fMRI Materials and Procedure.** In each of the two segments following the induction, participants completed four runs of functional neuroimaging: three task runs during which they viewed 36 total object cues of the main tasks in an event-related design and one resting-state run. Three practice trials of each main task were completed to ensure understanding.

Main Tasks. Each main task run was 7 m, 34 s in duration and began and ended with 16 s of fixation. Within each run, six imagined event trials and six object comparison trials were randomly presented with the construction-elaboration paradigm for 20 s each (19, 21). Following each trial, two ratings appeared (4 s each), and then a rest period during which a basic odd/even number judgment task was performed (mean, 6 s; jittered at 4 s, 6 s, or 8 s). Participants made responses during the main tasks via an MR-compatible five-button response box in their right hand.

Eighteen total imagined event trials were included per segment. For each trial, the word "imagine" appeared on one line of the screen, followed by the instruction "near future event" on the next line, followed by the cue in capital letters on the third line. As in previous work (8, 19, 21), participants were instructed to silently generate a novel future event or scenario that could happen to them within the next few years in as much detail as possible that was somehow related to the cue, plausible, new, viewed from a field perspective, and specific to one time and place. By using the construction-elaboration paradigm, participants were instructed that they should press their thumb when they had constructed each imagined event, and, after pressing their thumb, should elaborate or fill in all of the details of the event

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  $\alpha \ge 0.90$ ). 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 fixedeffects 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  $k \ge 65$  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 (S/ 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 wholebrain 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  $\boldsymbol{\alpha}$  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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