ORCA – Online Research @ Cardiff

Citation for final published version:

Sommer, Tobias, Hennies, Nora, Lewis, Penelope A. and Alink, Arjen 2022. The assimilation of novel information into schemata and its efficient consolidation. Journal of Neuroscience 42 (30) , pp. 5916-5929. 10.1523/jneurosci.2373-21.2022

Publishers page: https://doi.org/10.1523/jneurosci.2373-21.2022

JNeurosci
THE JOURNAL OF NEUROSCIENCE

Research Articles: Behavioral/Cognitive

The assimilation of novel information into schemata and its efficient consolidation

https://doi.org/10.1523/JNEUROSCI.2373-21.2022

Cite as: J. Neurosci 2022; 10.1523/JNEUROSCI.2373-21.2022

Received: 1 December 2021
Revised: 7 June 2022
Accepted: 11 June 2022

The assimilation of novel information into schemata and its efficient consolidation

Short title: Assimilation and consolidation of schema-related facts

Tobias Sommer[1†], Nora Hennies[1], Penelope A. Lewis[2*], Arjen Alink[1*]

[1] Institute of Systems Neuroscience, University Medical Center Hamburg-Eppendorf, 20246 Hamburg, Germany
[2] CUBRIC, School of Psychology, Cardiff University, Cardiff CF24 4HQ, UK
[†] corresponding author: tsommer@uke.de
* these author contributed equally

No or pages: 29
No of figures: 6
No of table: 1
No of words: abstract 207, introduction 650, discussion 1478
No conflicts of interest.
No acknowledgement

Abstract

Schemata enhance memory formation for related novel information. This is true even when this information is neutral with respect to schema-driven expectations. This assimilation of novel information into schemata has been attributed to more effective organizational processing that leads to more referential connections with the activated associative schema network. Animal data suggest that systems consolidation of novel assimilated information is also accelerated. In the current study, we used both multivariate and univariate fMRI analyses to provide further support for these proposals and to elucidate the neural underpinning of these processes. 28 Participants (5 male) over-learned fictitious schemata for seven weeks and then encoded novel related and control facts in the scanner. These facts were retrieved both immediately and two weeks later, also in the scanner. Our results conceptually replicate previous findings with respect to enhanced vmPFC-hippocampus coupling during encoding of novel related information and point to a prior knowledge-effect that is distinct from situations where novel information is experienced as congruent or incongruent with a schema. Moreover, the combination of both multi- and univariate results further specified the proposed contributions of the vmPFC, precuneus and angular gyrus-network to the more efficient encoding of schema-related information. In addition, our data provide further evidence for more efficient systems consolidation of such novel schema-related and potentially assimilated information.

Significance Statement

Our prior-knowledge in a certain domain, often termed schema, heavily influences whether and how we form memories for novel information that can be related to them. The results of the current study show how a ventromedial prefrontal-precuneal-angular network contributes to the more efficient encoding of novel related information. Furthermore, the observed increase in prefrontal-hippocampal coupling during this process points to a critical distinction from the previously described mechanisms supporting the encoding of information that is experienced as congruent with schema-driven expectations. In addition, we find further support for the proposal based on animal data that prior-knowledge enhances also the consolidation of schema-related information.

Introduction

Whether and how we encode, consolidate and later retrieve novel information is heavily influenced by our prior-knowledge (Alba and Hasher, 1983; Gilboa and Marlatte, 2017). The impact of prior-knowledge on memory has been studied in the framework of schemata (Bartlett, 1932) which are previously acquired and continuously developing associative networks (Ghosh and Gilboa, 2014).

A prominent line of research on the prior-knowledge effect investigates how the congruency of information with schema-driven expectations affects memory, e.g. remembering a palm-tree vs. a polar bear at a beach (van Kesteren et al., 2012; Greve et al., 2019). However, prior-knowledge enhances also memory for novel, previously unknown - and hence expectation-neutral - information that can be related to it, for instance when we learn new facts in our academic field (Brandt et al., 2005; Witherby and Carpenter, 2021). The vmPFC together with the ventral precuneus/retrosplenial cortex (vPC/RSC) are involved also in this effect of prior-knowledge where the contribution of the hippocampus and its coupling with the vmPFC remain so far inconsistent across studies (Tse et al., 2011; van Kesteren et al., 2014; Brod et al., 2016; Liu et al., 2016; Sommer, 2017).

The mnestic advantage for novel schema-related but expectation-neutral information has been attributed to the activation of schema-knowledge. This allows more effective organizational processing leading to assimilation into the associative structure (Ericsson and Kintsch, 1995). In particular, the newly encoded information might be integrated via spreading activations into the existing associative network resulting in referential connections and the association with appropriate retrieval cues (Long and Prat, 2002).

These processes underlying assimilation would not necessarily result in enhanced mean activity in the involved brain areas compared to encoding of schema-unrelated information. The first goal of the current study was therefore to find support for such processes by using multivariate representational similarity analyses (RSA). In particular, after participants had acquired knowledge of experimental schemata (Fig. 1 A) we contrasted the similarity of activity patterns during three encoding rounds of novel schema-related with those of tightly matched control facts. By this means we tested the hypothesis that the rapid integration of schema-related facts into the associative structures results in more consistent representation across encoding rounds (i.e. greater pattern robustness; Xue et al., 2010; Bruett et al., 2020). Moreover, we tested whether the more effective organizational processing would be reflected in more consistent encoding operations across novel schema-related facts. Finally, we tested the hypothesis that assimilation should be evident in higher similarity between encoding of novel schema-related facts and the retrieval of overlearned schema-knowledge.

A second goal of the current study was to provide further evidence with respect to hippocampal-vmPFC coupling during encoding of novel schema-related but expectation-neutral information. In the two studies observing stronger coupling participants encoded arbitrary associations (Liu et al., 2016; Sommer, 2017) whereas in the third students learned real facts, i.e. associations of an already taught with a new term, in their or another discipline (van Kesteren et al., 2014). The diverging results might be caused by the fact that in the other discipline both terms forming a new fact were novel (Carpenter et al., 2018) or that only in the latter study meaningful information was encoded. Both factors were addressed in the current paradigm with the goal to better understand hippocampal-vmPFC coupling during encoding of novel schema-related information.

A series of animal studies showed that prior-knowledge not only influences encoding but also accelerates systems consolidation of novel schema-related expectation-neutral information, i.e. randomly paired flavor-location associations (Tse et al., 2007). In the aforementioned study using a similar design, we showed that also in humans schema-related information might be more rapidly transferred from hippocampal to cortical retrieval (Sommer, 2017). Using meaningful knowledge structures we also showed that nightly replay might underlie this effect (Hennies et al., 2016). A third goal of the current study was therefore to use those meaningful associative structures to conceptually replicate our previous findings and to provide further evidence that novel schema-related expectation-neutral information is transferred more rapidly to neocortical retrieval. To test this hypothesis, participants' memory for novel facts was tested in the MRI scanner immediately after encoding and 2 weeks later.

Methods

Participants

Thirty-two native Germans (mean age: 25.90 years; SD: 3.71 years; 6 males; randomly assigned to one of the two schemata) participated in the study. All had normal or corrected-to-normal vision, and no history of neurological and psychiatric disorders. Participants were required to have no knowledge beyond that of basic schooling at the primary level in the two schema categories (arthropods and cell biology) and no particular interest in biology, medicine, chemistry, and zoology. Informed consent was obtained from all participants before the study, which was approved by the Ethics Committee of the Hamburg Medical Association. The first participant could not be analyzed due to data loss. Two participants dropped out of the study during the schema-knowledge acquisition. For one participant, retrieval results are missing due to technical failure, leaving 28 participants (5 male, 14 for each of the two schemata).

Stimuli

The aim was to experimentally construct two fictitious schemata that fulfilled the four previously identified criteria, i.e. an associative network structure, basis on multiple episodes, lack of unit detail, and adaptability, (Ghosh and Gilboa, 2014) and the neuroscientific definition, i.e. consolidated cortical representation (van Kesteren et al., 2012). At the same time, we aimed to minimize previously described confounds when pre-existing, e.g. academic or other expert, knowledge is used: i) higher curiosity/interest/motivation to learn novel facts in the domain of expertise and ii) the possibility that novel schema-related information had been known before (Witherby and Carpenter, 2021). Moreover, in the area of expertise participants have a higher familiarity with the names of the concepts the novel information has to be associated with, e.g. when “blossom end rot” has to be associated with calcium deficiency the term “blossom end rot” is for experts familiar but novel for control participants (Carpenter et al., 2018). Such greater cue familiarity results in a processing advantage and in differences in (meta-) memory (Chua et al., 2012). Importantly, as the goal of the current study was to characterize the effects of prior-knowledge on memory due to more effective organizational processing and not to in-/congruency, we aimed to minimize the influence of schema driven expectations with respect to the novel facts. However, we also aimed to use not arbitrary associative structures as in our previous and the animal studies (Tse et al., 2007, 2011; Sommer, 2017) but more ecological valid, i.e. meaningful experimental schemata. Novel facts related to such meaningful knowledge structures can be only neutral with respect to specific expectations based on prior experience (as for instance palm-trees and not polar bears are expected at a beach scenery) but are still consistent with more general knowledge. To stay with the above example, even if there is no specific schema-driven expectation for the cause for “blossom end rot” the novel fact “calcium deficiency” is similar to many other possibilities, e.g. sodium deficiency or a fungal attack, that are generally consistent with the student’s knowledge about phytology. The absence of specific schema-driven expectations results at the same time in more detailed, less generalized and gist-like memories (Tse et al., 2007, 2007; Sommer, 2017) which diverges from the more typical schema studies on the effect of schema-congruency where higher false alarm rates are observed (Rojahn and Pettigrew, 1992; van Kesteren et al., 2012).

Schemata

The stimuli from our previous study were translated into German and modified for the purpose of the current study (Hennies et al., 2016). The schemata were constructed with four hierarchical levels (Fig.1 A). The two schemata were parallel in structure and contained facts at each level. In particular, each schema comprised facts about the category (arthropods or cells), its two sub-categories (ant and crabs, cell-types and organelles), their three families each (e.g. symbiotic, hunter and weaver ants) and detailed characteristics of the 12 individual exemplars (two in each family). The detailed facts (approximately 25 facts) about anatomy, habitat, food preferences, and behavioral characteristics for each of the 12 exemplars comprised the main part of the ‘arthropods’-schema. For the ‘cells’-schema a matched number of facts for each of the 12 exemplars existed (see Hennies et al., 2016 for family labels and pictures of the exemplars of the ‘cells’-schema). In addition, each exemplar was presented on 12 different pictures. Novel names were invented for all exemplars in order to avoid large differences in length and complexity of the names. The whole hierarchical associative structure and all facts, i.e. the pictures of the exemplars, related to its nodes and elements were considered as schema - similar to studies employing pre-existing academic or trivial real-world knowledge.

Novel, schema-related facts

For each of the exemplars of both schemata six additional facts were created. Each facts existed in two, equally likely alternatives (e.g. Styga is *2* or *4* cms long, NIV contains *copper* or *nickel*, Fig. 1B). One version, which was randomly chosen for each participant, was encoded as novel schema-related (SR) fact, the other one served as lure for the 2-alterantive forced-choice memory tests. This design ensured that participants could not guess the correct response based on their schema-knowledge and that the novel schema-related facts were indifferent with respect to schema congruency and expectations. The SR facts for the ‘arthropods’-schema served as non-schema related (NS) control facts for the participants who acquired knowledge for the ‘cells’-schema and vice versa. The facts were kept vague to minimize participants guessing about what type of exemplars the control facts were about. The novel facts for both schemata were counterbalanced for the number of words, number of syllables, and numerical values. None of the facts were longer than eight words or 14 syllables so that all facts could easily be read within the presentation time.

Procedure

This experiment was realized with custom-written scripts using Cogent 2000, developed by the Cogent 2000 team at the Functional Imaging Laboratory and the Institute for Cognitive Neuroscience (University College, London).

Acquisition of structured, associative schema-knowledge

In a first session in the institute, participants were randomly assigned to one of the two schemata and performed a test on their prior-knowledge in that category. This pretest involved one picture and 6 statements about each of the 12 category exemplars (using their real not the invented names). When a picture was presented the participant could select the name of the exemplar from 6 response options or select a "?" to indicate not knowing. In response to the statements participants could select "true", "false" or "?". All questions were presented without a time limit. No subjects achieved more than the cut-off of 20% correct responses and therefore all could take part in the experiment.

The acquisition of schema-knowledge started after the pre-test in the first session and involved seven more sessions in the institute, which were separated by seven days. There were very few exceptions, when participants could not make that day, they came within around 2 days. Sessions were ~1 h long (only session 1 took 2 h), but this could vary as participants completed most tasks in a self-paced way. Between the sessions at the institute, participants deepened their schema-knowledge by working through homework. The first two sessions in the institute and the corresponding homework will be described more in detail in order to give an impression how acquisition of structured schema-knowledge was achieved.

In the first session participants started to learn general background information about their schema (on the category and sub-category level), that was presented self-paced on the computer. Participant's assigned to the 'arthropods'-schema learned for instance that arthropods have an exoskeleton, a segmented body, compound eyes, that the exoskeletons are based on chitin and vary with respect to their stability, that ants have two antenna, two mandibles, live in colonies etc. Participants did at the end of the first session a multiple-choice test on the acquired knowledge with 32 questions with 87.7% (±10%) accuracy (Fig. 1 B). In the following homework the schema facts from session 1 and additional facts were presented as reading material. In addition, the families and exemplars were introduced including the first facts about both hierarchy levels. Moreover, each exemplar was presented on 2 pictures from different perspective. Participants were asked to work through the material and to answer open questions in writing to facilitate and deepen the learning. They were told, that their answers were evaluated in the next session in the institute.

In the second session in the institute, participants were asked to free recall the facts about the exemplars followed by the multiple choice and ten open questions about the schema background. They then repeated learning the background facts followed again by multiple choice and open questions. In the following homework, they repeated the general background facts as well as learning more facts about the families and exemplars by reading and responding to open question. After this homework they had learned all relevant schema-related facts the first time. From there on, this knowledge was repeated and deepened.

In the remaining 6 sessions in the institute and the 5 homework sessions between them participants continued in the same way to recapitulate the facts about all hierarchy levels of their schema, including 12 pictures of each exemplar and their knowledge was tested using various multiple choice and open questions as well as picture naming tests. At the end of each session participants' schema-knowledge was assessed with multiple choice tests for which they did not receive feedback. Based on their performance in these tests the homework sessions were individually adjusted.

Participants showed close to ceiling performance in the multiple-choice and picture naming tests in all session in the institute and participants achieved the cut-off of 85% correct responses after the final session (Fig 1 B). A final test on schema-knowledge (24 questions) about 14 days after the last session in the institute and directly after the delayed retrieval of novel schema-related and control facts in the MR scanner (Fig 1B) showed that participants had successfully acquired schema-knowledge. Participants reached 91.8% (±1.4%) high confidence correct responses and across all confidence levels 96.9% (±0.8%) correct responses (Fig 2B). The response times for high confidence schema-knowledge retrieval was similar to high confidence immediate retrieval of novel schema-related facts and substantially faster than their delayed high confidence retrieval, which occurred in the same session (Fig. 2 D).

Learning exemplar names of the control schema

Differences in familiarity with the names of the schema and control exemplars could affect memory formation independent of the hierarchical, associative knowledge structure that was acquired only for the schema (Chua et al., 2012). The goal was therefore to minimize potential differences in familiarity between the names of schema and control exemplars prior to learning novel facts. Starting in session 2, participant were learning and writing down the names of the control exemplars in random order without any information about the nature of them. Participants expected to be tested on their memory for these 12 words in the next session. Participants were asked to recapitulate the names of the control exemplars in each of the following homework sessions and were tested for them in each of the sessions in the institute. As intended, this procedure resulted in high familiarity and perfect memory for the names of the exemplars of the control schema. However, this tight experimental control also probably established to some degree semanticized and arbitrarily interconnected representations of the control exemplar names, which potentially reduces the observable prior knowledge effect.

Encoding and retrieval of novel schema-related and control facts

Encoding and retrieval of schema-related (SR) and not schema-related (NS) control facts took place in the MR scanner. Three encoding rounds for SR and NS facts were followed by four additional encoding rounds outside of the scanner only for NS facts to reach similar performance in the following immediate memory test in the MR scanner. Similar memory in the immediate retrieval test for novel schema-related and control facts is a critical prerequisite to relate potential differences in forgetting until the delayed memory test to divergent consolidation trajectories. About two weeks later (15.17 ±1.95 days) there was a delayed retrieval test followed by the aforementioned retrieval of schema-knowledge.

The encoding and immediate retrieval rounds took place on the day following the eighth session in the institute. After arrival, participants wrote down the names of the 12 schema and the 12 control exemplars in order to activate their schema-knowledge. Participants were instructed to memorize each novel fact carefully, to focus only on the facts that was presented at the time, and to give each facts equal memorization effort. Participants were also informed about how they would be tested in the retrieval test. In each of the three encoding rounds all novel 72 SR and 72 NS facts (6 for each exemplar) were presented in pseudorandom order (consecutive facts were from different category members). Each encoding round was distributed across two fMRI runs. Each trial started with the presentation of a fact for 4s (Fig. 1 B). Participants were asked in the first round to indicate within this time interval whether they will remember the fact (i.e. judgement of learning; van Buuren et al., 2014; Witherby and Carpenter, 2021) and in the two subsequent rounds whether they remembered the fact (judgement of memory). Therefore, the tasks differed between the first and the later encoding rounds, which we considered acceptable because implicitly there is always an unavoidable difference between the first and subsequent encounters with new information. To foreshadow the results of our across round representational similarity analyses (Figs. 5 and 6), similarity between the first two rounds was rather greater which speaks against a major influence of the different tasks on fMRI results. They had for each hand one button box, pressing the left index finger to indicate 'yes, pressing the right for 'no'. The presentation of the facts was followed by a fixation cross for 500ms, followed by an active baseline task. In this task the fixation cross changed its color from white to either red or blue and participants were instructed to press a corresponding button as quickly as possible. The baseline task was introduced to prevent rehearsal of the previously encoded novel facts and to reduce activity in the default mode network in the implicit baseline (Stark and Squire, 2001). This baseline lasted between 2 - 4 s (jittered) before the next stimulus was presented. After the 3 encoding rounds, participants left the scanner and encoded the NS facts for 4 additional rounds because we aimed for equal performance in the immediate memory test for NR and NS facts. The previous study and further piloting showed that to achieve comparable performance NS items need to be presented twice as many times as SR items (Hennies et al., 2016). The procedure was the same as before.

Participants entered then the scanner again for the immediate retrieval test. All 72 SR and 72 NS facts were tested in a two-alternative forced choice task distributed across two fMRI runs. Each trial started with the presentation of a fixation cross in the middle of the screen between 2-4 sec (jittered). This was followed by the presentation of a fact together with its alternative fact for 6 s. Participants had to choose the correct answer by pressing the corresponding button on one of the two button boxes with the right or left hand within the 6 s interval. Participants had to indicate their confidence by choosing between the options sure, unsure, guess. After each trial the same active baseline task that was employed during the encoding followed. Approximately 2 weeks later participants returned for the delayed retrieval test in the scanner, which was identical to the first test, but the order of facts was re-randomized. After retrieving all 72 SR and 72 NS facts distributed across 2 fMRI runs participants were tested in a final fMRI run on 24 of schema-knowledge facts that were tested in a similar format, i.e. forced choice with confidence ratings.

It should be noted that the lure of a novel fact during retrieval (e.g. ‘4 cm’ when ‘Styga is 2 cm long’ was learned) was not systematically associated as a novel fact with another exemplar (e.g. ‘4 cm’ was not necessarily a novel fact related to another exemplar). This lack of a systematic using each novel fact as both, lure and target might preclude an unambiguous interpretation of the results as noted by a reviewer: The novel schema-related and control facts might have been more familiar than the lures during the recognition tests and the responses could reflect familiarity driven item memory and not assimilation into the schema. However, although we did not systematically used each lure as target in a different recognition trial many lures or at least very similar responses appeared in more than one trial which reduces this potential confound (a list of all retrieval questions and the response alternatives can be found at https://osf.io/aj28h/).

As described participants encoded and retrieved (‘Did you remember?’) the control facts in seven rounds (compared to three rounds for schema-related facts) and immediately retrieved them then. This many rounds was necessary to reach similar performance in the immediate memory test, which was critical for the second goal of the study, i.e. to test prior knowledge effects on consolidation. However, on the other hand the repetitive encoding of object-location associations, respectively word lists has been recently shown to result itself in accelerated system consolidation that is stabilized during sleep (Brodt et al., 2016, 2018; Himmer et al., 2019). In the current study this effect might be even stronger due to the over-learned and consolidated names of the control exemplars. In other words, the tight experimental control might also have resulted in consolidated memory traces for the novel control facts – even if via a different mechanism as hypothesized for the novel schema-related facts.

fMRI data acquisition

Functional magnetic resonance imaging (fMRI) was performed on a 3 T system (Siemens Trio) with a 32-channel head coil. An echo planar imaging T2*-sensitive sequence in 50 contiguous axial slices (3 x 3 x 2.8 mm) with 1 mm gap; TR, 2.96 s; TE, 30 ms; PAT factor 2; flip angle, 80°; matrix 64 x 64) was employed. High resolution (1 x 1 x 1 mm voxel size) T1-weighted structural MRIs were acquired for each subject using a 3D MPRAGE sequence as part of the first scanning session.

fMRI data preprocessing

Functional imaging data were processed using the Statistical Parametric Mapping 12 software (SPM12, Wellcome Department of Cognitive Neurology, London, UK; http://www.fil.ion.ucl.ac.uk/spm). Functional images were realigned and unwarped to correct for susceptibility-by-movement artifacts. The anatomical image were coregistered to the mean functional image of that participant. The anatomical images were then transformed into standard stereotaxic space using DARTEL as implemented in SPM12 and the deformation field applied to the functional images of the same participant. Functional images were smoothed with full-width at half-maximum of 6 mm for the univariate and of 3 mm for the multivariate analyses.

Univariate fMRI analyses

Individual subjects and group level data were analyzed using the general lineal model (GLM) as implemented in SPM 12 in a mass univariate approach. One first level model was set up for encoding and retrieval. The two runs for each of the three encoding rounds as well for the two runs of each immediate and delayed retrieval were concatenated where the run specific constant, the autocorrelation structure and high pass filter were appropriately adjusted. Regressors were created by convolving the onsets with the canonical hrf. For each of the three encoding rounds one regressor for SR and NS facts was created (due to ceiling effects we did not subdivide encoding events into those with a positive and a negative judgment of learning, respectively memory). For immediate and delayed retrieval, regressors were created for the high confidence correct, combined for medium and low confidence correct and for incorrect responses as well as for the final retrieval of the schema facts. In addition, six movement regressors were added as nuisance variables.

On the second level, encoding related activity was analyzed by the main effect of condition in an encoding round × condition (SR vs NS facts) ANOVA. The analysis of retrieval activity was restricted to high confidence hits because for those a behavioral effect of schema-knowledge was observed (Fig. 2 C) which is consistent with previous literature (Long and Prat, 2002; Bein et al., 2020) and it has been argued high confident responses are most informative (e.g., Xiao et al., 2016; Lee et al., 2019). Retrieval activity was analyzed by the main effect of condition and the interaction of condition and delay in a delay (immediate vs. delayed) × condition (SR vs NS facts) ANOVA. To identify areas that might be involved in semantic memory, retrieval activity during high confidence retrieval of the schema facts (after the delayed retrieval of novel facts) was contrasted against high confidence immediate retrieval of novel schema-related facts in a paired t-test.

In addition, two Psycho-Physiological-Interactions (PPI; Friston et al., 1997) were conducted based on previous literature (e.g., Sommer, 2017). The first PPI used as seed the vmPFC cluster (thresholded $p < 0.001$ uncorrected) that was identified by the analysis of encoding activity and contrasted its functional coupling during encoding SR and NS facts for each of the three encoding rounds. On the second level, coupling differences between conditions were analyzed across encoding rounds in an ANOVA with the factor round. The second PPI used as seed the vmPFC cluster identified by the retrieval second level model to be more active during retrieval of SR than control facts immediately and delayed. This PPI contrasted coupling during immediate as well as delayed retrieval of SR with control facts. On the second level, it was analyzed where this coupling increases from immediate to delayed retrieval.

Multivariate fMRI analyses

In order to get parameter estimates for each individual trial as input for the multivariate analyses, for each trial an independent first-level model was created with one regressor containing only the corresponding trial and one for all other trials in that fMRI run (Mumford et al., 2012). In addition, six movement regressors were added as nuisance variables as well a high-pass filter applied and corrected for autocorrelation. The t-maps testing the beta of the trial of interest in each model against the implicit baseline were used for the following RSA to reduce the influence of noisy voxels (Dimsdale-Zucker and Ranganath, 2018). In all RSA we employed a whole brain searchlight approach (radius 3 voxels) and correlated (Pearson's linear rank correlation) the resulting vectors of trial-specific t-values across conditions of interest. The resulting correlation coefficients were averaged within condition after Fisher's Z-transformation and saved as value for the center voxel of the current searchlight.

Encoding-encoding similarity

In a first RSA we aimed to find support for a more rapid integration of novel schema-related facts into the activated associative structure in terms of a greater consistency of the distributed activity pattern across encoding rounds. Therefore we analyzed the robustness of fact-specific activity patterns (e.g. *Texana is 2 cm long* or *NIV contains Copper*) between the succeeding encoding rounds, i.e. between round 1 and 2 as well as between round 2 and 3 (Xue et al., 2010; Bruett et al., 2020). In particular the activity pattern during encoding of a specific fact was correlated with encoding the same fact in the succeeding round (similarity) as well as with encoding of all the other facts in that round (dissimilarity), separately for novel schema-related and control facts. On the second level we contrasted the similarity-dissimilarity difference maps in a 2 (round 1/2 vs. round 2/3) x 2 (SR vs NS) ANOVA.

Encoding-operation similarity analyses

In a second RSA we aimed to find support for more effective organization processing during encoding of novel schema-related facts. Therefore, we aimed to identify brain regions in which prior knowledge affects the encoding operation irrespective of the specific to be encoded fact. To this end we correlated on the one hand activity during encoding each novel schema-related fact with all other schema-related facts in a round, but excluded the 5 other trials with facts related to the same exemplar (e.g. 'Texana') and on the other hand activity during encoding of each novel schema-related fact with all control trials resulting for each round in a SR-SR and a SR-NS correlation per subject. For the latter we excluded also all facts related to one control exemplars to avoid different numbers of correlations contributing to SR-SR and SR-NS similarities. On the second level we contrasted the resulting similarity maps in a 3 (round 1 vs. 2 vs. 3) x 2 (SR-SR vs SR-NS) ANOVA.

To test whether prior knowledge also results in more similar activity patterns related to the encoding operation across rounds, we repeated the above analysis but correlated activity during encoding across succeeding round, e.g. each schema-related trial in round 1 with all other schema-related trials in round 2 except with the 6 trials related to the same exemplar (e.g. 'Texana'). On the second level we ran a 2 (round 1/2 vs. round 2/3) x 2 (SR-SR vs SR-NS) ANOVA.

In addition, with the same goal, we conducted two similar, complementary analyses where we contrasted within and between rounds the correlation of activity during all novel schema-related trials (but again excluded the trials related to the same exemplar) with the correlation of activity during all control trials. This approach resulted at the second level in a 3 (round 1 vs. 2 vs. 3) x 2 (SR-SR vs. NS-NS) and a 2 (rounds 1/2 vs. rounds 2/3) x 2 (SR-SR vs NS-NS) ANOVA.

Encoding–retrieval similarity

As an alternative approach to find support for differences in consolidation due to prior knowledge we computed the similarity of activity patterns between encoding round 1 and immediate as well as delayed retrieval for the novel schema-related and control facts. On the second level we run a 2 (encoding-immediate vs. –delayed retrieval) x 2 (SR-SR vs. NS-NS) ANOVA.

Encoding - schema knowledge retrieval similarity

To more directly test which areas are involved in the assimilation of the novel schema-related facts into the overlearned schemata, we correlated in another RSA activity during encoding novel schema-related facts with activity during retrieval of the schema-knowledge (where we excluded again trials related to the same exemplar) and contrasted it with the correlation of control facts with the retrieval of schema-knowledge. This results at the second level in a 3 (round 1 vs. 2 vs. 3) x 2 (SR-Schema vs NS-Schema) ANOVA. However, it should be noted that this analysis is to some extent confounded by the shortcoming that the schema-knowledge was retrieved only after the delayed retrieval of the novel schema-related and control facts. At this time point, the novel schema-related facts were at least partly already assimilated into the schema-knowledge which may have led to changes in the representation of that initial schema itself, i.e. accommodation.

Multivariate–Univariate Dependence Analysis

Pattern similarity can be caused not only by distributed patterns of activity but also by consistent (de-) activation of voxels in a univariate fashion. Therefore, we conducted a multivariate-univariate dependence analysis (MUD) previously suggested by Aly and Turk-Browne (2015) for significant RSA-peak voxels that were in brain regions which also show univariate effects. In particular, we first multiplied in each voxel of the spheres the normalized values of the corresponding trials, e.g. encoding of a specific fact in round 1 and 2. These products indicate how much a voxel contributes to the correlation, i.e. to pattern similarity. These products and the mean activity of each voxel were averaged across trials and then correlated across voxels. The magnitude of the correlation indicates how much univariate effects contribute to the RSA result.

Importantly however, a MUD correlation does not necessarily imply that the voxels in a sphere show a univariate effect consistently in the same direction but only that voxels activate or deactivate consistently for trials in a condition and that the same voxels contribute to the observed similarity. Therefore, we computed in addition the correlation of the differences in multivariate similarity between conditions in the RSA-peak voxels with the difference in univariate mean activity in the searchlight-sphere around the RSA-peak voxels across participants (Wagner et al., 2016). The differences to the MUD are that the similarity difference in the RSA-peak voxel (i.e. the difference between the correlations across all voxels in the surrounding searchlight sphere) and the difference in mean activity in all voxels of the searchlight sphere are used. This approach is diagnostic of the extent to which the observed similarity difference might be driven by differences in mean activity between conditions.

Correction for multiple comparisons

Results of all fMRI analyses were considered significant at $p < 0.05$, family-wise-error (FWE) corrected for multiple comparisons across the entire scan volume or within the a priori defined anatomical regions of interest (ROIs). ROIs for the bilateral hippocampus, bilateral precuneus/posterior cingulate and angular gyrus were computed from the Harvard-Oxford cortical and subcortical structural atlases. A vmPFC ROI was manually traced on the mean T1 image based on previously published post-mortem data (Mackey and Petrides, 2014) using ITK-SNAP 3.6.0 (Yushkevich et al., 2006). The vlPFC ROI we functionally defined as a sphere with radius 10 mm centered around the previously observed peak voxel (xyz = [-40 4 28]; Sommer, 2017).

Results

Behavioral results

Encoding and retrieval performance was analyzed in mixed effects models using the R base package and the *lme4* as well as the *lmerTest* packages for computing type III ANOVAs with Satterthwaite's method for the approximation to degrees of freedom (Bates et al., 2015; Kuznetsova et al., 2017). Model fit, such as normality of model residuals, was verified using the *check_distribution* function in *R* package *performance* (Lüdecke et al., 2020). Post-hoc Tukey HSD tests were performed using the *lemans* package (Lenth, 2016) if a paired comparison was of relevance for the interpretation of the results.

Encoding

Confirmative (i.e. ‘yes’) responses in the judgement of learning (round 1) and judgment of memory (rounds 2 to 3) for schema-related and control facts were analyzed in mixed effects models with the fixed effects condition (schema vs. control) and encoding round (1 vs. 2 vs. 3) as well as subject as a random factor. This model was compared with a similar one but with a subject specific slope across rounds as additional random factor. Because the model fit was similar ($X^2(5) = 0.6$, $p = .99$) we used the less complex model. The effects of condition and round on judgments of learning, respectively memory (Fig. 2 A) reached significance ($F(1,135.00) = 376.35$, $p < 0.001$; $F(2,135) = 14.67$, $p < 0.001$) but not their interaction (F(2,135.00) = 0.49, p = 0.614). Participant's judgment of memory for the control facts increased outside of the scanner (F(3,78) = 36.48, p < 0.001) where post-hoc Tukey HSD tests show that there was no increase between round 3 and 4 (p = 0.714) but only between round 1 and 2 as well 2 and 3 (p < 0.001; p = 0.007) suggesting participants performance reached an asymptote. A direct comparison with round 3 of learning schema-related facts and round 7 of learning control facts showed less subjective memory (t(26) = 2.48, p < 0.020) for control facts.

The effects of condition and round on reaction times (Fig. 2 B) also reached significance (F(1,81) = 16.813, p < 0.001; F(2,27) = 144.766, p < 0.001) as did their interaction (F(2,81) = 10.005, p < 0.001). Restricting the analyses to confirmatory (i.e. 'yes') responses resulted in a similar pattern, i.e. significant main effects (F(1,81) = 9.532, p = .003; F(2,27) = 186.87, p < .001) but no interaction (F(2,81) = 0.542, p = .584). Reaction times did not further decrease significantly outside of the scanner during learning round 4 to 7 for control facts (F(3,78) = 2.12, p = 0.104). Reaction times in the last round of control facts encoding were faster than in the third and last round of schema-related facts (t(26) = 2.61, p = 0.015).

Immediate and delayed retrieval

Hits during immediate and delayed retrieval were analyzed in mixed models with the fixed effects condition (schema vs. control) and confidence (3 levels) as well as subjects as a random factor with confidence as random slope (Fig. 2 C). This model had a significantly better model fit than a less complex model without the random slope (immediate retrieval $X^2(5) = 174.1$, $p < .001$; delayed retrieval $X^2(5) = 147.8$, $p < .001$). Immediate retrieval showed only a significant effect of confidence level (Fig 2 B; F(2,27) = 264.33, p < 0.001), but not of condition, and no interaction (F(1,108) = 0.0037, p = 0.951; F(2,108) = 0.076, p = 0.923). In other words, the additional 4 encoding rounds outside of the scanner for control facts resulted as intended in a similar immediate hit rate for schema-related and control facts. Therefore, potential difference in delayed memory performance cannot be attributed to differences in the initial memory strength. For delayed retrieval, there was again a significant effect of confidence level (F(2,27) = 24.05, p < 0.001), and also a significant interaction (F(2,81) = 7.13, p = 0.001) which was driven by more high confidence hits for schema-related than control facts (post hoc Tukey HSD p = 0.014), but no effect of condition (F(1,81) = 0.32, p = 0.585). In a mixed model including both retrieval tests with the additional factor and random slope delay (immediate vs.

delayed) the interaction of condition, delay and confidence reached only a trend towards significance (F(2,269.99) = 2.63, p = 0.074) besides the significant effects of delay, confidence and their interaction. (Loftus and Masson, 1994)

The proportion of incorrect responses across the confidence levels was also analyzed in order to test whether prior-knowledge might result in relative higher proportion of high confidence incorrect responses. Neither during immediate nor delayed retrieval was the interaction of schema and confidence significant (immediate retrieval: effect of schema F(1,168) < 0.01, p = .971; effect of confidence F(2,168) = 324.26, p < .001; interaction F(2,168) = < .01, p = .991; delayed retrieval: effect of schema F(1,168) = 0.03. p = .872; effect of confidence F(2,168) = 31.03, p < .001; interaction F(2,168) = 1.28, p = .28).

Reaction times for hits were analyzed in similar mixed models (Fig. 2 D). For immediate retrieval both main effects as well as the interaction reached significance (F(1,101.34) = 55.61, p < 0.001; F(2,38.19) = 40.30, p < 0.001; F(2,101.04) = 31.68, p < 0.001) indicating overall slower retrieval of schema-related facts, where there was no difference for high confidence but for lower confidence hits. Also, for delayed retrieval both main effects and the interaction reached significance (F(1,100.96) = 8.49, p = 0.0041; F(2,47.95) = 47.95, p<0.001; F(2,100.90) = 3.68, p = 0.029) suggesting a similar pattern, i.e. no difference for high confidence hits. In a mixed model including both retrieval tests with the additional factor and random slope delay, the effects of condition (F(1,225.86) = 43.13, p < 0.001), confidence (F(2,37.08) = 50.45, p < 0.001), and delay (F(1,28.02) = 59.27, p < 0.001), as well as the condition × delay (F(2,226.13) = 20.17, p < 0.001) and the confidence × delay interaction (F(2,225.33) = 4.35,p = 0.014) reached significance indicating overall slower retrieval and a smaller difference between conditions after the delay.

Univariate fMRI results

Encoding

At first, we present activity related to retrieval of the overlearned schema-knowledge although it was assessed last (i.e. after delayed retrieval of novel schema-related and control facts) because its consolidation is the basis for the assimilation of novel schema-related facts. We contrasted retrieval of schema-knowledge with immediate retrieval of novel schema-related facts because both refer to schema-exemplars and were similarly fast. Activity during retrieval of the over-learned schema-knowledge was greater in the vlPFC and other areas (Fig. 3 A, Table 1). Activity in the other three conditions, i.e. immediate retrieval of control facts as well as delayed retrieval of schema-related and control facts, is plotted in transparent bars because these conditions did not contribute to the statistical test that identified this area. We present it to show that activity did not differ between the immediate and delayed retrieval of novel-schema-related and control facts. This plot shows that activity during retrieval of the schema-knowledge was also greater than during immediate retrieval of control facts and delayed retrieval of novel schema-related and control facts.

During encoding the main effect of SR > NS across rounds was significant in the vmPFC, in a cluster comprising the ventral precuneus/retrosplenial cortex (vPC/RSC) as well as in the superior parietal cortex (Fig. 3B) implicating greater activity during encoding of novel schema-related facts. The interaction of condition and round showed that in the vmPFC and vPC/RSC the difference was greater in the first than the last round (Table 1 for full list of results). Moreover, the vmPFC was more strongly coupled with the hippocampus, fusiform, supramarginal and inferior frontal gyri, dorsal precuneus and superior parietal cortex during encoding of schema-related than control facts (Fig. 3 C). The interaction with round showed that this difference in coupling in the hippocampus and dorsal precuneus was largest in round 1.

Retrieval

The vmPFC and the vPC/RSC were also more active during retrieval of novel schema-related than control facts irrespective of delay (Fig. 4 A). The PPI using the vmPFC cluster as seed revealed stronger coupling differences with the precuneus/posterior cingulate between retrieval of SR and NS facts after the delay (Fig. 4 B). A region of the vmPFC, in particular the subgenual ACC, showed an increase in activity only during delayed retrieval of schema-related facts whereas the hippocampus revealed a decrease in activity from early to delayed retrieval only of control facts (Fig. 4 C). There was no such interaction effect in the vlPFC ROI (largest Z = 1.43, p = 0.661 at [-42 0 18]) contrary to our previous study (Sommer, 2017).

Multivariate fMRI results

Encoding-encoding similarity

In Fig 5 A right panel we present the results of the encoding-encoding similarity analysis irrespective of prior knowledge (i.e. the main effect similar greater dissimilar) in order to visualize its sensitivity because contrasting schema-related and control facts using this measure revealed only relatively subtle differences. In particular, pattern robustness in terms of encoding-encoding similarity between rounds was greater for novel schema-related than control facts in the right inferior frontal gyrus (IFG, [48 12 21], Z = 3.90, Fig. 5 A left panel). Importantly though, as the IFG was not an a priori defined ROI the peak would not survive correction for multiple comparisons. We decided to still report and visualize it for exploratory reasons because the IFG has been observed before to be more active and stronger coupled with the hippocampus during schema retrieval (Bein et al., 2014; van Buuren et al., 2014; Wagner et al., 2015).

The interaction of similarity and encoding round showed that encoding-encoding similarity between the first two rounds was greater for schema related items in early visual cortex ([0 -90 3] Z = 3.93, Fig. 5 B left panel) and the amygdala ([27 -3 -18], Z = 4.10) and between round 2 and 3 in the precuneus ([9 -72 39] Z = 4.78, Fig 5B right panel) where only the latter peak reached significance corrected for multiple comparisons. Because the precuneus also showed univariate effects (Fig 3 A) we conducted a multivariate-univariate dependence analysis (MUD; see methods; Aly and Turk-Browne, 2015) which revealed no correlation between the observed multivariate effect and the univariate effect (r = -.098, p = .122).

Encoding operation similarity analysis

The RSA analysis comparing correlations between encoding of schema related facts with schema related facts (SR-SR) and the correlation between encoding schema related facts and novel facts (SR-NS) within each round revealed the vmPFC ([3 51 -9], Z = 5.66) and vPC/RSC ([-15 60 21], Z = 6.72) as well as the midcingulate gyrus ([0 -15 48], Z = 5.23), left middle frontal gyrus ([-21 15 42], Z = 4.82) and the right central operculum ([48 -18 21], Z = 4,57) as a main effect across the three rounds. Notably, when multiple facts related to the same exemplar they were excluded. Because the first two areas also showed univariate effects we conducted MUD analyses for the peak voxels which revealed no correlation for the vmPFC (r = .028, p = .694) but did show a weak correlation for the vPV/RSC (r = .254, p = .006). Therefore, we correlated in addition the differences in multivariate similarity in the RSA-peak voxels and the differences in univariate mean activity in the searchlight-spheres around the RSA-peak voxels between conditions across participants which revealed no relationship (r = .301, p = .115; r = .189, p = .337) suggesting no major contribution of univariate activity differences between conditions to the multivariate results.

The interaction between the within-round similarity and round (Fig. 6 A) showed greater similarity in the vmPFC ([-3 48 -6], 6.37), vPC/RSC ([-9 -60 30], Z = 5.45), bilateral angular gyrus ([-48 -60 24], Z = 4.56; [51 -51 27], Z = 4.07), OFC ([-27 36 -12], Z = 7.52) and left hippocampus ([-33 -24 -12], Z = 3.75) in the first compared to the third round. For the first two peaks we again computed a MUD analysis to disentangle uni- and multivariate contributions. This showed subtle but significant correlations between uni- and multivariate effects (vmPFC: r = .113, p = .038; vPC/RSC: r = .249, p < .001). Therefore, we correlated again in addition the multivariate difference in the peak-voxels and the mean univariate differences in the corresponding searchlight sphere across participants which revealed only a trend towards significance for the vPC/RSC (r = -.225, p = .202; r = .323, p = .094).

The across round encoding operation similarity analysis (Fig. 6 B) revealed as main effect (i.e. across rounds) the vmPFC (-9 51 0], Z = 3.50) and the vPC/RSC ([-12 -57 15], Z = 4.87; [15 -54 18], Z = 4.28) but no interaction with round. The MUD analyses showed a subtle but significant correlation only in the vmPFC (r = .244, p < .001; r = -.056, p = .495; r = .028, p = .686) where the additional follow-up correlation of RSA-peak differences in similarity and mean activity in the corresponding searchlight-spheres suggested that the univariate contributed r = -197, p = .316; r = .280, p = .150; r = .442, p = .019) only to the second peak in the vPC/RSC.

In addition we computed a complementary within-round encoding operation similarity analysis in which we contrasted the correlation between the novel schema-related facts (SR-SR) with the correlation of the control facts (NS-NS), excluding the trials related to the same exemplar. This also revealed greater similarity across rounds in the vmPFC ([-12 57 -3], Z = 5.79) and precuneus/RSC ([-15 -60 21], Z = 4.59; [-6 -48 12], Z = 6.13). Because both areas also showed univariate effects we conducted a multivariate-univariate dependence analyses (Aly and Turk-Browne, 2015) for the three peak voxels. The univariate contribution to the observed similarity differences correlated towards a trend in the vmPFC (r = .105, p = .085), and in the first peak in the vPC/RSC (r = .003, p = .096; r = -.037, p = .574). Thus, in the vmPFC and parts of the vPC/RSC univariate effects might have contributed modestly to the similarity.

The interaction of round and schema-related vs. control showed that the difference in similarity was greater in the first round in vmPFC (Fig. 6 A; [-9 57 0], Z = 5.98), OFC ([-

27 36 -12], Z = 7.25), bilateral angular gyrus (Fig 6 A; [-48 -66 21], Z = 4.18; [51 -51 27], Z = 4.13), and the vPC/RSC ([-3 -54 18], Z = 4.10). The multi-univariate dependence analyses for these peaks revealed a marginal trend towards a correlation only for the precuneus (r = .092, p = .089). Therefore, pattern similarity in the precuneus appears to be, a least to some degree, related to unidirectional changes in voxel activity. Across rounds similarity of encoding operation was also greater for schema than control trials in the vmPFC (Fig. 6 B; [-9 54 0], Z = 4.37) and vPC/RSC ([-6 -48 12], Z = 6.30; [6 -45 15], Z = 5.20). The univariate-multivariate dependence analyses revealed no significant correlation (r = .083, p = .130; r = .050; p = 380, r = .008, p = .859).

Encoding–retrieval similarity

The contrast of encoding-retrieval similarities showed higher similarity during encoding and retrieval of novel schema-related facts at both delays in the middle temporal ([54 -57 3], Z = 5.31) and left angular gyrus ([-45 -57 42], Z = 4.23). The interaction revealed an increase in the parahippocampus ([27 -36 -15], Z = 4.08).

Encoding - schema knowledge retrieval similarity

We observed a main effect of greater similarity between encoding novel schema-related than control facts with the retrieval of schema-knowledge in the vmPFC ([-9 51 0], Z = 5.36, Fig. 6 C), the vPC/RSC(-3 -54 18], Z = 4.51; [-15 -60 21], Z = 3.78) and the posterior cingulate ([0 .30 36], Z = 5.34). The MUD analyses for the regions where we observed univariate effects showed subtle but significant correlations for the vmPFC and one peak in the vPC/RSC (r = .215, p = .001; r = .150; p = .008; r = .053 p = .400). However, the individual differences in multivariate similarity and univariate mean activity did not correlate across participants (r = -.103, p = .602; r = .065, p = .743; r = .046, p = .815) suggesting that the similarity difference was not caused by a consistently greater activity in the voxel of the sphere.

Finally, an interaction with round in terms of greater difference in round 1 than round 3 was observed in the posterior cingulate ([-3 -30 36], Z = 4.64), the left middle frontal gyrus ([-27 24 45], Z = 5.52), right middle temporal gyrus ([57 -21 -18], Z = 5.09), as well as trends towards significance in the bilateral angular gyrus ([-42 -60 21], Z = 4.55; [51 -33 33], Z = 4.46).

Discussion

The over-learning procedure in the current study likely resulted in semanticized, cortical representations of the schema-knowledge. Learning of novel schema-related but expectation-neutral facts strongly benefited from this prior knowledge. On the neural level, we observed enhanced vmPFC-hippocampal coupling when information can be assimilated in prior-knowledge. Not only was mean activity greater in vmPFC and the vPC/RSC but also the distributed activity patterns in these areas showed greater similarity, i.e. consistency for schema-based encoding operations with the angular gyrus within and between rounds. Consolidation of the assimilated facts was also enhanced, as reflected by slightly higher confidence retrieval and an increase in vmPFC activity and vmPFC-precuneus coupling.

Acquisition of schema-knowledge

The repetitive reactivation of the hierarchical schema-knowledge in various contexts (in the institute, at home, on computer screens, as written handouts) and retrieval formats (essay-like texts, free recall, multiple-choice questions, pictures) across 7 weeks was expected to result in semanticized and consolidated associative knowledge structures (Sekeres et al., 2018; Ferreira et al., 2019). The close to ceiling performance already early in learning (Fig 1 B) and, even more so, in the schema-knowledge memory test 14 days after the last training session (Fig. 2 C) where response times were very fast (Fig. 2 D) show that the knowledge was highly overlearned and likely semanticized. The strong involvement of the vlPFC in retrieval of schema-knowledge further supports its proposed semanticization because this area has been implicated in semantic memory and in retrieval of semanticized memory (Binder and Desai, 2011; Sommer, 2017). Taken together, the acquired schema-knowledge very likely fulfilled the previously schema-defining criteria of being an associative network structure, based on multiple episodes, lacking unit detail, being adaptable as well as being cortical, i.e. semantic, representations (van Kesteren et al., 2012; Ghosh and Gilboa, 2014).

Encoding of novel schema-related facts

The substantially higher judgments of memory for novel schema-related facts together with the more learning rounds for control facts that were necessary to reach similar performance in the immediate memory test illustrate the power of the prior-knowledge effect in the current paradigm (Fig. 2 A). Due to the invented schemata we can rule out the possibility that congruency with schema-driven expectations or differences in interest/motivation to learn the novel facts had a systematic effect on this mnestic advantage (Chua et al., 2012; Witherby and Carpenter, 2021). The possibility that the much more rapid learning of novel schema-related facts was not driven by their assimilation but rather based on better item-level memory, i.e. familiarity based recognition, cannot be ruled out. However, the only difference between retrieval of novel schema-related and control facts was observed in terms of more high confidence responses which are unlikely driven by familiarity and schema-knowledge is known to impact predominantly recollection-based recognition (Long and Prat, 2002; Brandt et al., 2005). Taken together, the observed effect is likely driven by more effective organizational processing which results in assimilation of the novel facts into the pre-activated associative network (Ericsson and Kintsch, 1995) but schema effects on item-memory cannot be ruled out.

On the neural level, the much more efficient encoding of novel schema-related facts was paralleled by higher coupling of the vmPFC and hippocampus in addition to higher mean activity in the vmPFC and the vPC/RSC where in the hippocampus no activity difference was observed (Fig. 3 B/C). These results conceptually replicate our previous findings using very different but also experimental schemata, i.e. associative structures of random object-location associations, that also did not result in expectations about the nature of novel facts, and also another study employing arbitrary expectation-neutral information (Liu et al., 2016; Sommer, 2017). Together, these studies therefore support a model that predicts stronger vmPFC-hippocampal coupling when novel expectation-neutral information can be related to prior-knowledge (Gilboa and Marlatte, 2017). On the first sight this interpretation stands in contrast to the prominent SLIMM model that proposes that the vmPFC inhibits hippocampal encoding when it detects information congruent to our expectations, i.e. reduced vmPFC-hippocampus coupling and less hippocampal activity when schema-congruent information is encoded (van Kesteren et al., 2012; Greve et al., 2019).

However, two distinct prior-knowledge effects might exist that are mediated by qualitatively different encoding operations: When schemata allow specific expectations based on previous encounters with the to be encoded information (i.e. palm-trees at a beach) there is reduced vmPFC-hippocampus coupling when congruent information is encoded (van Kesteren et al., 2012). This type of prior-knowledge effects results in enhanced gist memory prone to schema-based distortions. However, when expectation-neutral novel information can be assimilated into a schema, e.g. a novel fact in our academic discipline, that is further developed by this (i.e. accommodation) vmPFC-hippocampal coupling is increased which results in enhanced and more accurate memory formation (Long and Prat, 2002; Brandt et al., 2005; Tse et al., 2007).

The multivariate analyses show that more efficient encoding of novel schema-related facts seems not to be predominantly reflected in less encoding variability perhaps due to the rapidity of integration (Fig. 5).The greater item-specific similarity in the IFG for novel schema-related facts – although not predicted and hence not significant after correction for multiple comparisons – would be consistent with this structure's previously described role in representing dissimilarities during knowledge integration (Schlichting et al., 2015). However, prior-knowledge substantially enhanced the consistency of the encoding operations in the vmPFC, vPC/RSC and angular gyrus suggesting more effective organizational processing (Fig. 6). In the first two areas we observed higher mean activity replicating earlier findings with expectation-neutral (Maguire et al., 1999; Tse et al., 2011; van Kesteren et al., 2014; Liu et al., 2016; Sommer, 2017) but also schema-congruent facts (van Kesteren et al., 2013; Bonasia et al., 2018). The multivariate-univariate dependence analyses suggested that the two effects might reflect different processes or distinct aspects of the same process. Activity in the vPC/RSC has been associated with retrieval, in particular with retrieval during encoding of novel information (Huijbers et al., 2012; Sestieri et al., 2017; van Kesteren et al., 2020) - consistent with activation of schema-knowledge during encoding. The greater consistency of the distributed activity patterns across all schema-trials suggest that irrespective of the current to be encoded fact (e.g. 'Texana is 2 cm long') the superordinate schema-knowledge is activated.

The greater similarity of activity patterns during encoding of novel schema-related than control facts with the retrieval of the overlearned schema-knowledge supports this interpretation. However, because the schema-knowledge was only retrieved after the potential assimilation of the novel information might have been already complete, this similarity might reflect both, effects of assimilation and accommodation. This interpretation would also apply to the greater consistency of encoding operations in the angular gyrus. Interestingly, the angular gyrus has been - also by using multivariate analyses of activity patterns - implicated in combining different schema components when it is applied to novel related information (Wagner et al., 2015). The vmPFC has been suggested to bind together co-activated vPC/RSC and angular gyrus representations to form a superordinate knowledge template and to maintain the active schema when novel information is processed (Gilboa and Marlatte, 2017). This interpretation of our multi- and univariate results would be consistent with the more effective organizational processing of the novel related information proposed by cognitive psychologists (Ericsson and Kintsch, 1995), i.e. the integration in the associative network which leads to referential connections and the association with appropriate retrieval cues.

The difference between encoding of schema-related and control facts was larger early in learning in several analyses. It is possible that overlearning the names of the control exemplars resulted in an arbitrary associative structure of these meaningless terms. After participants associated facts with the elements of this structure in the first round, it became to some extent schema-like. Alternatively, after the first round the novel schema-related facts may have already been assimilated to a large degree, which would also reduce the difference to encoding of the control facts.

Consolidation

The phenomenon that prior-knowledge leads also to more efficient consolidation has been described only relatively recently (compared to the long history of schema-effects in memory) in the aforementioned animal studies using novel expectation-neutral schema-related information (Tse et al., 2007, 2011). We confirmed this effects in humans in our previous study where we translated the animal experiment to an fMRI design (Sommer, 2017). In the current study, using very different experimental schemata, we conceptually replicated this effect. The impact on consolidation was rather subtle and was specific to high confidence responses which is however consistent with previous reports on prior-knowledge effects in recognition memory (Long and Prat, 2002; Brandt et al., 2005). The subtly of the prior-knowledge effect on consolidation might be also a side effect of the seven learning rounds needed for the control information to reach similar immediate memory performance because repetitive encoding and retrieval might result itself in faster systems consolidation – although via different mechanisms (Brodt et al., 2016, 2018; Himmer et al., 2019). In the current study this effect might be even stronger due to the over-learned and consolidated names of the control exemplars. Using the same paradigm, we previously showed that sleep spindle density as a proxy for nightly replay and systems consolidation predicted the individual benefit of prior-knowledge on novel related facts (Hennies et al., 2016). This finding supports the interpretation that the reduced forgetting we observed in the current study is caused by more efficient systems consolidation.

Prior-knowledge resulted in an increase in vmPFC-precuneus coupling and of vmPFC and hippocampus activity from immediate to retrieval of schema-related facts two weeks later. In our previous study we did not observe the vmPFC but vlPFC, i.e. a semantic memory area, to contribute more strongly to the retrieval of assimilated information after two weeks (Sommer, 2017). This difference might be caused by differences in the experimental designs, for instance that the schemata in our previous study were much simpler, no meaningful hierarchical associative structures and probably semanticized to a larger degree by even more intense over-learning. However, the vmPFC (and RSC) has been implicated before in the retrieval of assimilated schema-related facts (Tse et al., 2011) and the parallel relative increase in hippocampal activity would be consistent with the incidental retrieval of associated schema knowledge during high confidence recognition (Schultz et al., 2022). This parallel involvement of cortical, i.e. vmPFC and RSC, and hippocampal retrieval would be consistent with the Trace Transformation theory that proposes that both episodic and cortical traces can exist in parallel (Sekeres et al., 2018).

Conclusions

The increased vmPFC-hippocampal coupling during the highly efficient encoding – likely due to their assimilation - of novel schema-related expectation-neutral facts suggests a prior-knowledge effect which is distinct from situations where the prior-knowledge allows expectations. Together, our uni- and multivariate results support cognitive and neuroscientific models about the processes underlying the putative assimilation, i.e. that a vmPFC, vPC/RSC, angular-network results in the activation of schema knowledge enabling more effective organizational processing of novel related facts. Moreover, the results confirm that assimilation of novel related information also results in more effective consolidation which is reflected, for not fully semanticized information, in vmPFC activity.

References

Alba JW, Hasher L (1983) Is Memory Schematic? Psychol Bull 93:203–231.

Aly M, Turk-Browne NB (2015) Attention Stabilizes Representations in the Human Hippocampus. Cereb Cortex:bhv041.

Bartlett FC (1932) Remembering: An experimental and social study. Cambridge, UK: Cambridge University.

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. J Stat Softw 67:1–48.

Bein O, Reggev N, Maril A (2014) Prior knowledge influences on hippocampus and medial prefrontal cortex interactions in subsequent memory. Neuropsychologia 64:320–330.

Bein O, Reggev N, Maril A (2020) Prior knowledge promotes hippocampal separation but cortical assimilation in the left inferior frontal gyrus. Nat Commun 11:4590.

Binder JR, Desai RH (2011) The neurobiology of semantic memory. Trends Cogn Sci 15:527–536.

Bonasia K, Sekeres MJ, Gilboa A, Grady CL, Winocur G, Moscovitch M (2018) Prior knowledge modulates the neural substrates of encoding and retrieving naturalistic events at short and long delays. Neurobiol Learn Mem 153:26–39.

Brandt KR, Cooper LM, Dewhurst SA (2005) Expertise and recollective experience: recognition memory for familiar and unfamiliar academic subjects. Appl Cogn Psychol 19:1113–1125.

Brod G, Lindenberger U, Wagner AD, Shing YL (2016) Knowledge Acquisition during Exam Preparation Improves Memory and Modulates Memory Formation. J Neurosci 36:8103–8111.

Brodt S, Gais S, Beck J, Erb M, Scheffler K, Schönauer M (2018) Fast track to the neocortex: A memory engram in the posterior parietal cortex. Science 362:1045–1048.

Brodt S, Pöhlchen D, Flanagin VL, Glasauer S, Gais S, Schönauer M (2016) Rapid and independent memory formation in the parietal cortex. Proc Natl Acad Sci 113:13251–13256.

Bruett H, Calloway RC, Tokowicz N, Coutanche MN (2020) Neural pattern similarity across concept exemplars predicts memory after a long delay. NeuroImage 219:117030.

Carpenter SK, Haynes CL, Corral D, Yeung KL (2018) Hypercorrection of high-confidence errors in the classroom. Memory 26:1379–1384.

Chua EF, Hannula DE, Ranganath C (2012) Distinguishing highly confident accurate and inaccurate memory: Insights about relevant and irrelevant influences on memory confidence. Memory 20:48–62.

Dimsdale-Zucker HR, Ranganath C (2018) Representational Similarity Analyses. In: Handbook of Behavioral Neuroscience, pp 509–525. Elsevier. Available at: https://linkinghub.elsevier.com/retrieve/pii/B9780128120286000276 [Accessed September 8, 2021].

Ericsson KA, Kintsch W (1995) Long-term working memory. Psychol Rev 102:211–245.

Ferreira CS, Charest I, Wimber M (2019) Retrieval aids the creation of a generalised memory trace and strengthens episode-unique information. NeuroImage 201:115996.

Friston KJ, Buechel C, Fink GR, Morris J, Rolls E, Dolan RJ (1997) Psychophysiological and modulatory interactions in neuroimaging. NeuroImage 6:218–229.

Ghosh VE, Gilboa A (2014) What is a memory schema? A historical perspective on current neuroscience literature. Neuropsychologia 53:104–114.

Gilboa A, Marlatte H (2017) Neurobiology of Schemas and Schema-Mediated Memory. Trends Cogn Sci 21:618–631.

Greve A, Cooper E, Tibon R, Henson RN (2019) Knowledge is power: Prior knowledge aids memory for both congruent and incongruent events, but in different ways. J Exp Psychol Gen 148:325–341.

Hennies N, Lambon Ralph MA, Kempkes M, Cousins JN, Lewis PA (2016) Sleep Spindle Density Predicts the Effect of Prior Knowledge on Memory Consolidation. J Neurosci 36:3799–3810.

Himmer L, Schönauer M, Heib DPJ, Schabus M, Gais S (2019) Rehearsal initiates systems memory consolidation, sleep makes it last. Sci Adv 5:eaav1695.

Huijbers W, Vannini P, Sperling RA, C.M. P, Cabeza R, Daselaar SM (2012) Explaining the encoding/retrieval flip: Memory-related deactivations and activations in the posteromedial cortex. Neuropsychologia 50:3764–3774.

Kuznetsova A, Brockhoff PB, Christensen RHB (2017) **lmerTest** Package: Tests in Linear Mixed Effects Models. J Stat Softw 82 Available at: http://www.jstatsoft.org/v82/i13/ [Accessed March 2, 2021].

Lee H, Samide R, Richter FR, Kuhl BA (2019) Decomposing Parietal Memory Reactivation to Predict Consequences of Remembering. Cereb Cortex 29:3305–3318.

Lenth RV (2016) Least-Squares Means: The *R* Package **lsmeans**. J Stat Softw 69 Available at: http://www.jstatsoft.org/v69/i01/ [Accessed March 2, 2021].

Liu Z-X, Grady C, Moscovitch M (2016) Effects of Prior-Knowledge on Brain Activation and Connectivity During Associative Memory Encoding. Cereb Cortex:bhw047.

Loftus GR, Masson MEJ (1994) Using confidence intervals in within-subject designs. Psychon Bull Rev 1:476–490.

Long DL, Prat CS (2002) Memory for Star Trek: the role of prior knowledge in recognition revisited. J Exp Psychol Learn Mem Cogn 28:1073–1082.

Lüdecke D, Makowski D, Indrajeet Patil, Waggoner P (2020) easystats/performance: performance 0.4.7. Zenodo. Available at: https://zenodo.org/record/3952174 [Accessed March 2, 2021].

Mackey S, Petrides M (2014) Architecture and morphology of the human ventromedial prefrontal cortex. Eur J Neurosci 40:2777–2796.

Maguire EA, Frith CD, Morris RG (1999) The functional neuroanatomy of comprehension and memory: the importance of prior knowledge. Brain 122 (Pt 10):1839–1850.

Mumford JA, Turner BO, Ashby FG, Poldrack RA (2012) Deconvolving BOLD activation in event-related designs for multivoxel pattern classification analyses. NeuroImage 59:2636–2643.

Rojahn K, Pettigrew TF (1992) Memory for schema-relevant information: A meta-analytic resolution. Br J Soc Psychol 31:81–109.

Schlichting ML, Mumford JA, Preston AR (2015) Learning-related representational changes reveal dissociable integration and separation signatures in the hippocampus and prefrontal cortex. Nat Commun 6:8151.

Schultz H, Sommer T, Peters J (2022) Category-sensitive incidental reinstatement in medial temporal lobe subregions during word recognition. Learn Mem 29:126–135.

Sekeres MJ, Winocur G, Moscovitch M (2018) The hippocampus and related neocortical structures in memory transformation. Neurosci Lett 680:39–53.

Sestieri C, Shulman GL, Corbetta M (2017) The contribution of the human posterior parietal cortex to episodic memory. Nat Rev Neurosci 18:183–192.

Sommer T (2017) The Emergence of Knowledge and How it Supports the Memory for Novel Related Information. Cereb Cortex N Y N 1991 27:1906–1921.

Stark CE, Squire LR (2001) When zero is not zero: the problem of ambiguous baseline conditions in fMRI. Proc Natl Acad Sci U A 98:12760–12766.

Tse D, Langston RF, Kakeyama M, Bethus I, Spooner PA, Wood ER, Witter MP, Morris RG (2007) Schemas and memory consolidation. Science 316:76–82.

Tse D, Takeuchi T, Kakeyama M, Kajii Y, Okuno H, Tohyama C, Bito H, Morris RG (2011) Schema-dependent gene activation and memory encoding in neocortex. Science 333:891–895.

van Buuren M, Kroes MCW, Wagner IC, Genzel L, Morris RGM, Fernandez G (2014) Initial Investigation of the Effects of an Experimentally Learned Schema on Spatial Associative Memory in Humans. J Neurosci 34:16662–16670.

van Kesteren MT, Ruiter DJ, Fernandez G, Henson RN (2012) How schema and novelty augment memory formation. Trends Neurosci 35:211–219.

van Kesteren MTR, Beul SF, Takashima A, Henson RN, Ruiter DJ, Fernández G (2013) Differential roles for medial prefrontal and medial temporal cortices in schema-dependent encoding: From congruent to incongruent. Neuropsychologia 51:2352–2359.

van Kesteren MTR, Rignanese P, Gianferrara PG, Krabbendam L, Meeter M (2020) Congruency and reactivation aid memory integration through reinstatement of prior knowledge. Sci Rep 10:4776.

van Kesteren MTR, Rijpkema M, Ruiter DJ, Morris RGM, Fernández G (2014) Building on prior knowledge: schema-dependent encoding processes relate to academic performance. J Cogn Neurosci 26:2250–2261.

Wagner IC, van Buuren M, Bovy L, Fernández G (2016) Parallel Engagement of Regions Associated with Encoding and Later Retrieval Forms Durable Memories. J Neurosci 36:7985–7995.

Wagner IC, van Buuren M, Kroes MC, Gutteling TP, van der Linden M, Morris RG, Fernández G (2015) Schematic memory components converge within angular gyrus during retrieval. eLife 4:e09668.

Witherby AE, Carpenter SK (2021) The rich-get-richer effect: Prior knowledge predicts new learning of domain-relevant information. J Exp Psychol Learn Mem Cogn Available at: http://doi.apa.org/getdoi.cfm?doi=10.1037/xlm0000996 [Accessed March 19, 2021].

Xiao X, Dong Q, Chen C, Xue G (2016) Neural pattern similarity underlies the mnemonic advantages for living words. Cortex 79:99–111.

Xue G, Dong Q, Chen C, Lu Z, Mumford JA, Poldrack RA (2010) Greater neural pattern similarity across repetitions is associated with better memory. Science 330:97–101.

Yushkevich PA, Piven J, Hazlett HC, Smith RG, Ho S, Gee JC, Gerig G (2006) User-guided 3D active contour segmentation of anatomical structures: significantly improved efficiency and reliability. NeuroImage 31:1116–1128.

Table 1: univariate fMRI results

contrast	area	xyz coordinate peak voxel	Z-value peak voxel
encoding			
SR > NS main effect	vmPFC	0 54 -15	4.34
	ventral precuneus/RSC	-9 -57 15	6.36
		12 -57 18	4.67
	superior parietal cortex	-36 -78 39	5.34
		48 -72 33	4.79*
	post cingulate cortex	-3 -36 33	4,81
NS > SR main effect	frontal pole	-30 51 21	5.00
		36 54 18	5.32
	anterior cingulate cortex	6 36 18	5.69
	occipital pole	9 -81 -3	6.94
	lateral occipital cortex	-45 -78 0	4.85
		33 -90 -9	4.78
SR > NS increase across rounds	supramarginal gyrus	57 -39 24	4.95
	inferior frontal gyrus/insula	-51 -6 0	4.82
		54 12 -3	4.88
	anterior cingulate cortex	-3 33 15	4.93
SR > NS decrease across rounds	vmPFC	-3 51 -32	4.70
	ventral precuneus/RSC	-12 -57 15	4.09
	dorsal medial PFC	-3 36 39	6.07
	inferior frontal gyrus	-45 39 -12	5.92
	dorsolateral PFC	-42 15 42	4.88
PPI SR > NS seed vmPFC main effect	hippocampus	-21 -24 -15	3.99
	fusiform gyrus	-30 -57 -15	5.33
		33 -54 -12	6.00
	inferior frontal gyrus	48 36 3	5.63
	superior parietal cortex	15 -66 51	5.04
		33 -42 42	4.91
	dorsal precuneus	-9 -39 57	5.03
		-9 -69 51	4.89
	supramarginal gyrus	-57 -45 27	4.98
PPI SR > NS seed vmPFC decrease across rounds	hippocampus	-27 -21 -21	3.63
		15 -12 -21	5.09
	dorsal precuneus	9 -63 51	6.69
retrieval			
SR > NS	vmPFC	3 30 -21	4.57
	ventral precuneus/RSC	-9 -57 15	6.49
		9 -54 15	5.68
NS > SR	anterior cingulate cortex	-6 33 21	5.06
	insula	-39 15 -9	4.97
		33 18 -15	4.46*
	frontal pole	24 57 -3	4.66
increase SR > NS	vmPFC	-6 18 -9	3.76

	hippocampus	27 -24 -15	3.74
PPI increase SR > NR seed vmPFC	ventral precuneus	15 -48 33	4.23
schema-knowledge			
schema retrieval > immediate novel SR retrieval	ventro-lateral PFC	-42 9 30	3.99
	anterior cingulate cortex	9 18 39	5.31
	ventral precuneus	21 -66 3	5.04
	insula	30 24 -9	5.09
		-30 24 -6	4.96
	ventral striatum	-18 9 -6	4.84
		18 25 -6	5.58

Peal coordinates in MNI space. Correction for multiple comparisons was done on the whole-brain level or within pre-defined anatomical regions of interest, specifically the hippocampus, precuneus/retrosplenial cortex (RSC) and ventromedial prefrontal cortex (vmPFC). * trend towards significance

Figure 1. Schema and timeline of the experiment. A) Hierarchical structure of one of the two schemata (arthropods) and exemplar names of the other schema (cells) which served as control in this example. Schema and control were randomized across participants. See Hennies et al., 2016 for a figure with the hierarchical structure of the 'cell'-schema. B) Acquisition of schema knowledge and familiarization with the control names over 7 weeks with 1 learning session per week in the institute and homework in-between. Participants achieved high performance in the multiple-choice questions (mc questions) and the picture naming task of their schema. In the scanner, participants encoded 3 times (encoding round 1 to 3) 72 novel facts related to the exemplars of their schema and 72 facts related to their control exemplars. In encoding round 4 to 7 outside of the scanner, they only repeated the control facts to ensure equal immediate memory for schema-related and control facts In the first encoding round, participants judged whether they will remember the novel facts in rounds 2 to 7 whether they did remember it. Encoding was followed by immediate retrieval of all learned novel facts in the scanner. 2 weeks later all facts were retrieved again in the scanner followed by retrieval of 24 of the overlearned schema-knowledge facts During retrieval two equally plausible response alternatives were presented (targets and lures were randomized across participants) and participants indicated their confidence on a 3-point scale (hc – high, mc – medium, lc - low confidence).

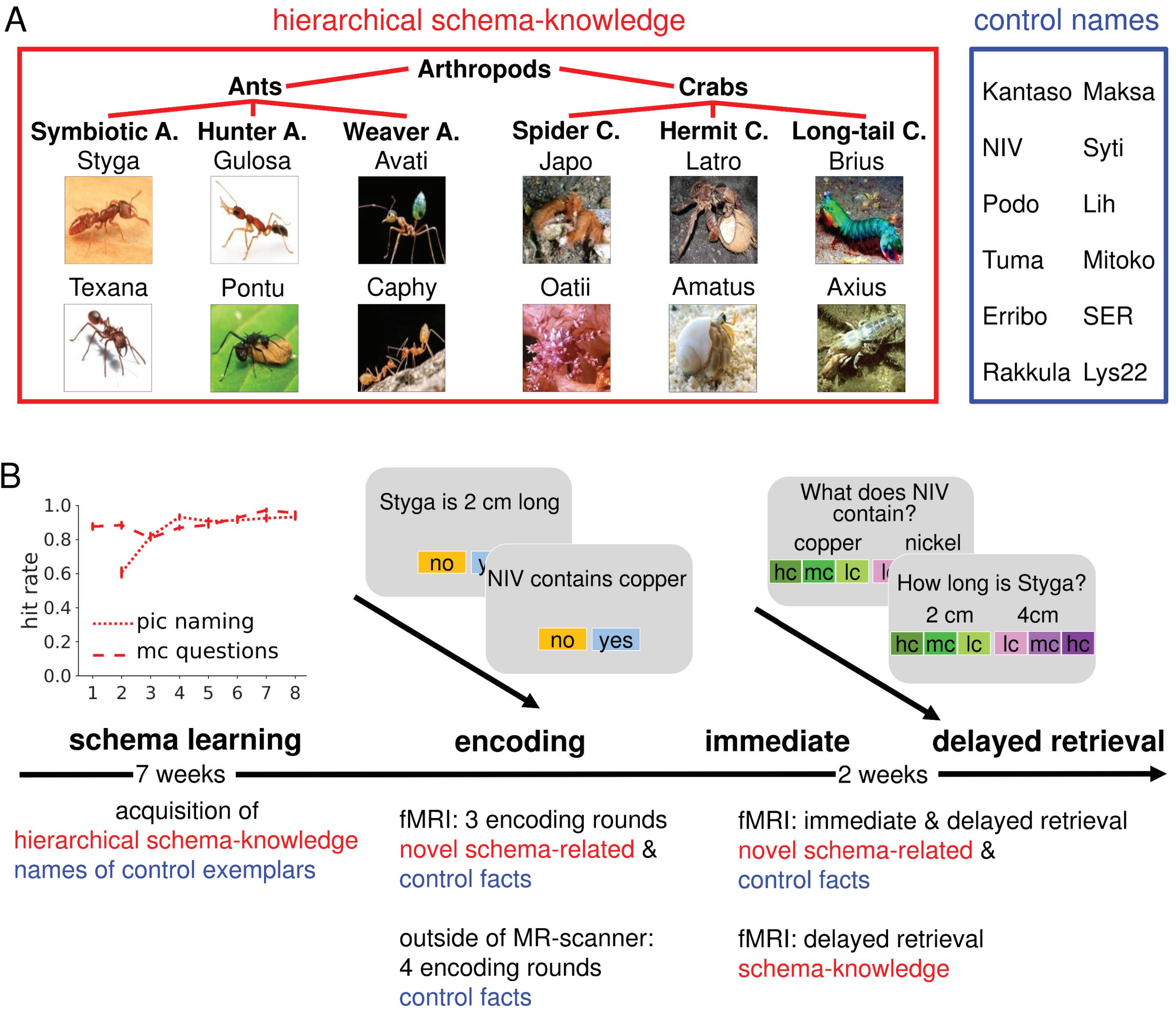
Figure 2. Behavioral results. A) Encoding rounds 1 to 3 for novel schema-related and control facts took place in the MR scanner, rounds 4 to 7 only for control facts outside of the scanner. In the first round participants rated whether they will remember the fact (judgment of learning) and in round 2 to 7 whether they did remember the fact (judgement of memory). B) Response times for the judgment of learning (round 1), respectively judgment of memory (round 2 to 7) during encoding. C) Proportion of high (hc), medium (mc) and low confident (lc) hits (relative to all responses in that delay x schema condition) during immediate and delayed retrieval for the schema-related and control facts as well as for the a subset of facts of the schema knowledge only during delayed retrieval. D) Retrieval times for high, medium and low confident hits during retrieval. Error bars are standard errors of the mean around the mean, corrected for interindividual differences (Loftus and Mason 1994).

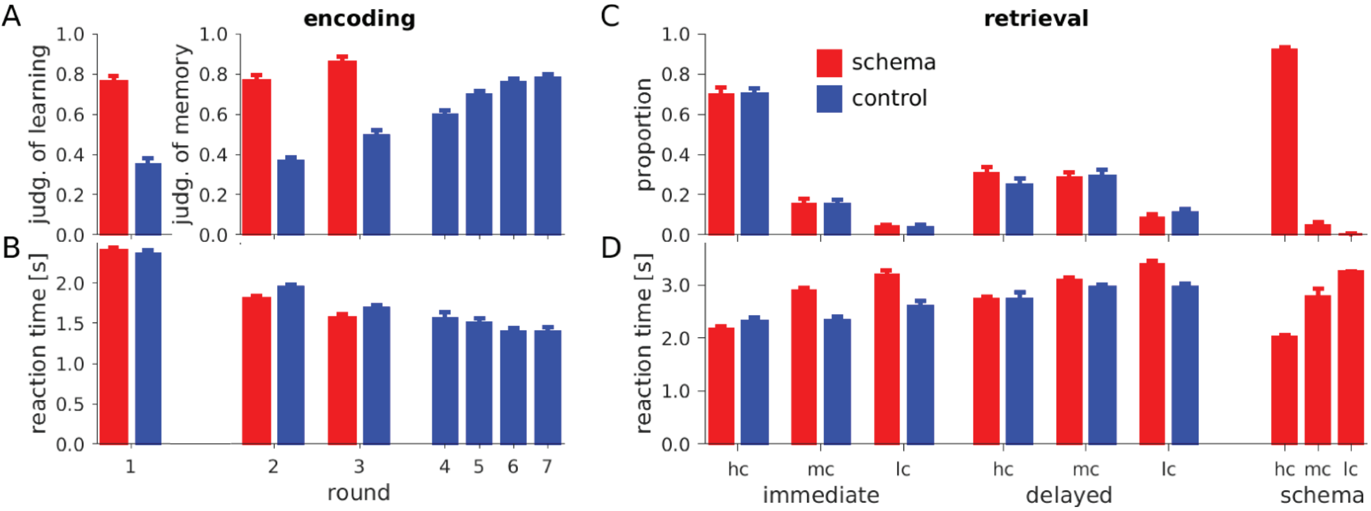
Figure 3. Activity related to retrieval of the over-learned schema knowledge and to the encoding of novel schema-related and control facts. A) Activity during retrieval of the overlearned schema–knowledge (after the delayed retrieval of the novel schema-related and control facts) was greater in the ventrolateral PFC (and other areas) compared with immediate retrieval of novel schema-related facts (red bar). Activity during retrieval of schema-knowledge was statistically contrasted against immediate retrieval of schema-related facts because response times were similar in both conditions (Fig. 2 D). Activity in the other three conditions (immediate retrieval of control facts as well as delayed retrieval of schema-related and control facts) in this voxel is plotted in transparent bars because it was not statistically tested against retrieval of schema-knowledge. B) During encoding of novel schema-related (SR, red bars) than control (NS, blue bars) facts activity was greater in the vmPFC and the vPC/RSC. C) Coupling differences between encoding schema-related and control facts. The vmPFC was more strongly coupled with the hippocampus and fusiform gyrus during encoding of schema-related (SR) than control (NS) facts .in the three rounds. Error bars are standard errors of the mean around the mean, corrected for interindividual differences (Loftus and Mason 1994). Visualization threshold $p < 0.001$,uncorrected.

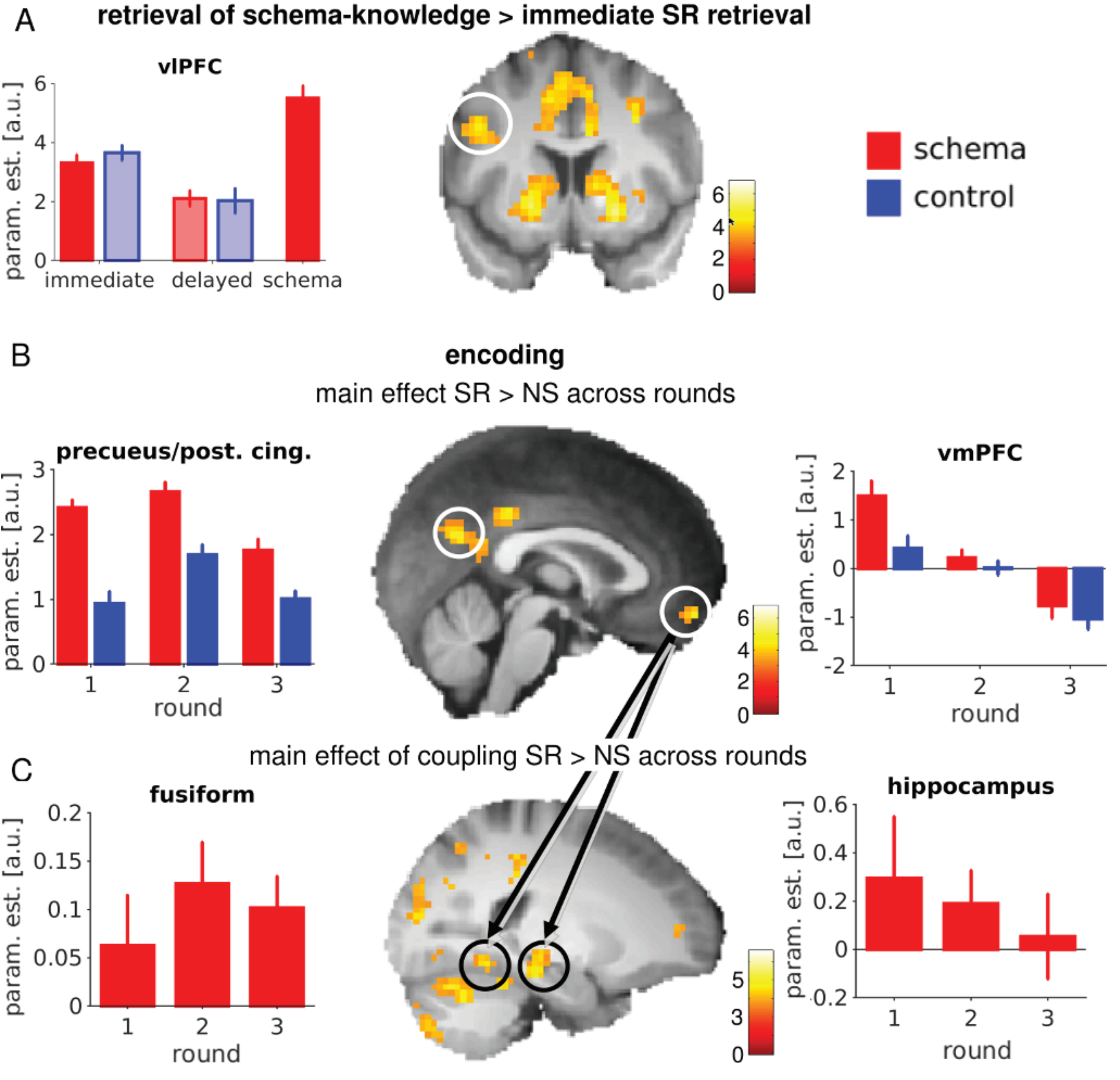
Figure 4. Activity differences during retrieval. A) During immediate and delayed retrieval of schema-related (SR, red bars) facts activity was greater in the vmPFC and the vPC/RSC. B) The Difference in coupling of the vmPFC with the precuneus during retrieval of schema-related (SR) and control (NS) facts increased from immediate to delayed retrieval. C) The vmPFC (subgenual ACC) and the hippocampus showed a larger activity increase from immediate to delayed retrieval of schema-related (SR, red bars) than control (NS, blue bars) facts. Error bars are standard errors of the mean around the mean, corrected for interindividual differences (Loftus and Mason 1994).Visualization threshold $p < 0.001$,uncorrected.

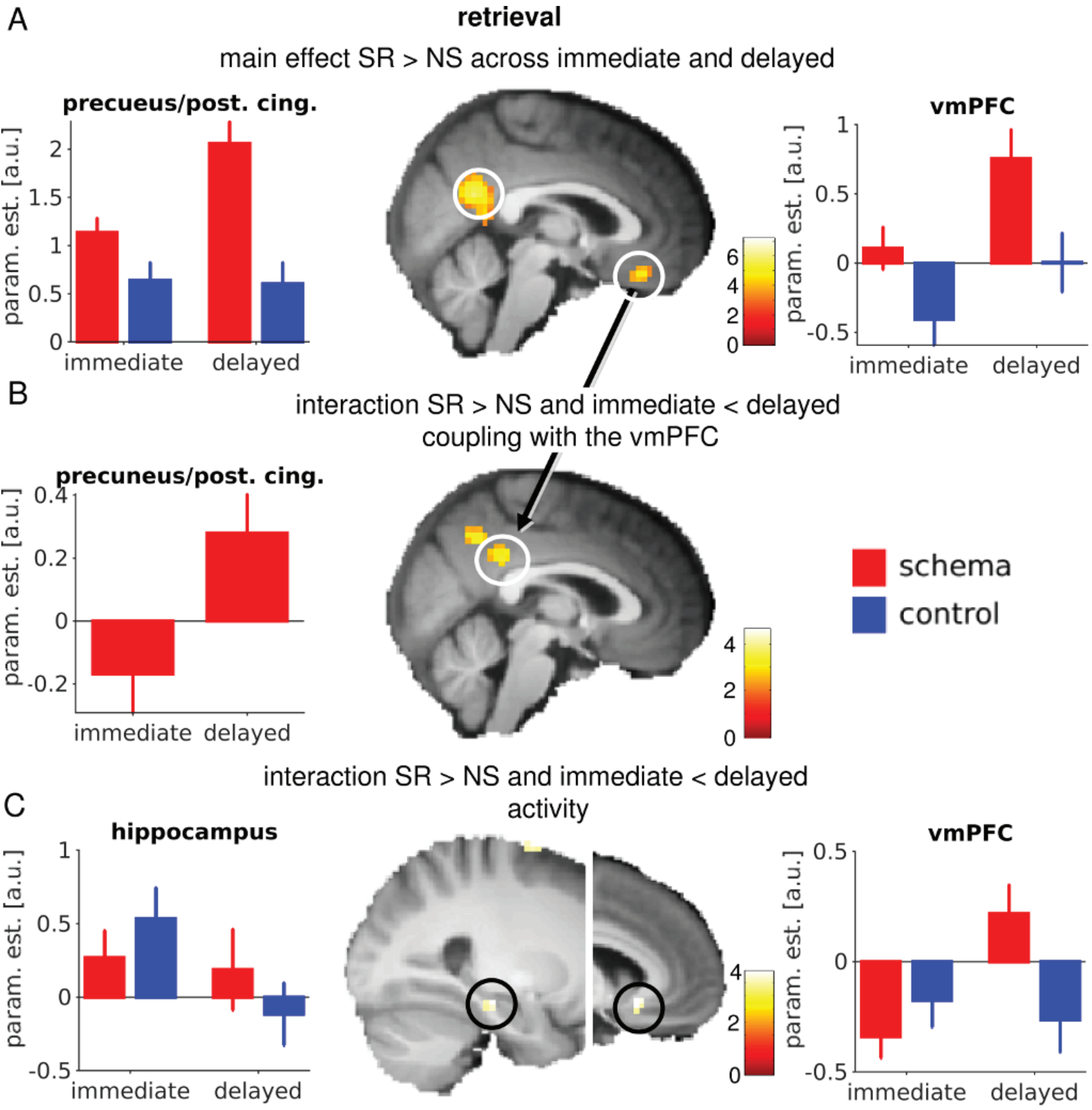
Figure 5. Encoding-encoding similarity (pattern robustness). A) Encoding-encoding similarity between succeeding rounds was greater for novel schema-related (SR, red bars) than control facts (NS, blue bars) in the right IFG (left panel). The overall sensitivity of this approach is visualized in the right panel of A in terms of the main effect. B) Encoding-encoding similarity between the first two rounds was greater in early visual cortex (left panel) and between round 2 and 3 in the precuneus (left panel) for novel schema-related (SR) than control facts (NS). Note that the IFG and cuneus cluster are not significant corrected for multiple comparisons and are reported for exploratory reasons. Error bars are standard errors of the mean around the mean, corrected for interindividual differences (Loftus and Mason 1994). Visualization threshold $p <$ 0.001, uncorrected.

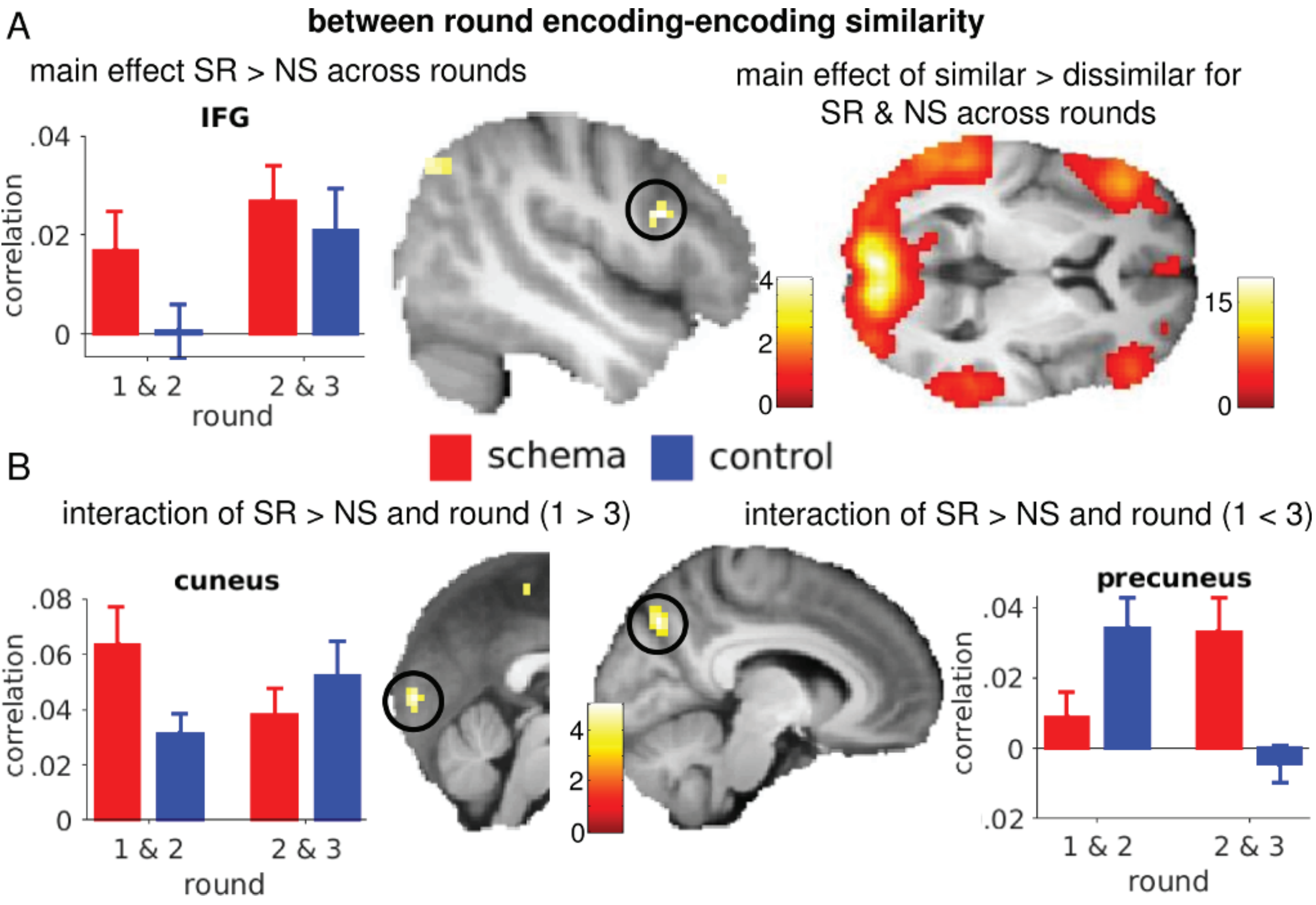
Figure 6. Encoding operation similarity. A) Encoding-operation similarity within rounds was early in learning greater between encoding of novel schema-related (SR-SR, red bars) than between schema-related and control (SR-NS, blue bars) facts in the vPC/RSC, vmPFC, and the bilateral angular gyrus. B) Encoding-operation similarity between rounds during encoding of novel-related (SR-SR) facts was also grater compared to SR-NS facts in the vPC/RSC and vmPFC. C) Operation similarity between encoding of schema-related facts and retrieval of schema knowledge was also greater compared to the encoding of control facts in the vPC/RSC and vmPFC. Error bars are standard errors of the mean around the mean, corrected for interindividual differences (Loftus and Mason 1994). Visualization threshold $p < 0.001$, uncorrected.

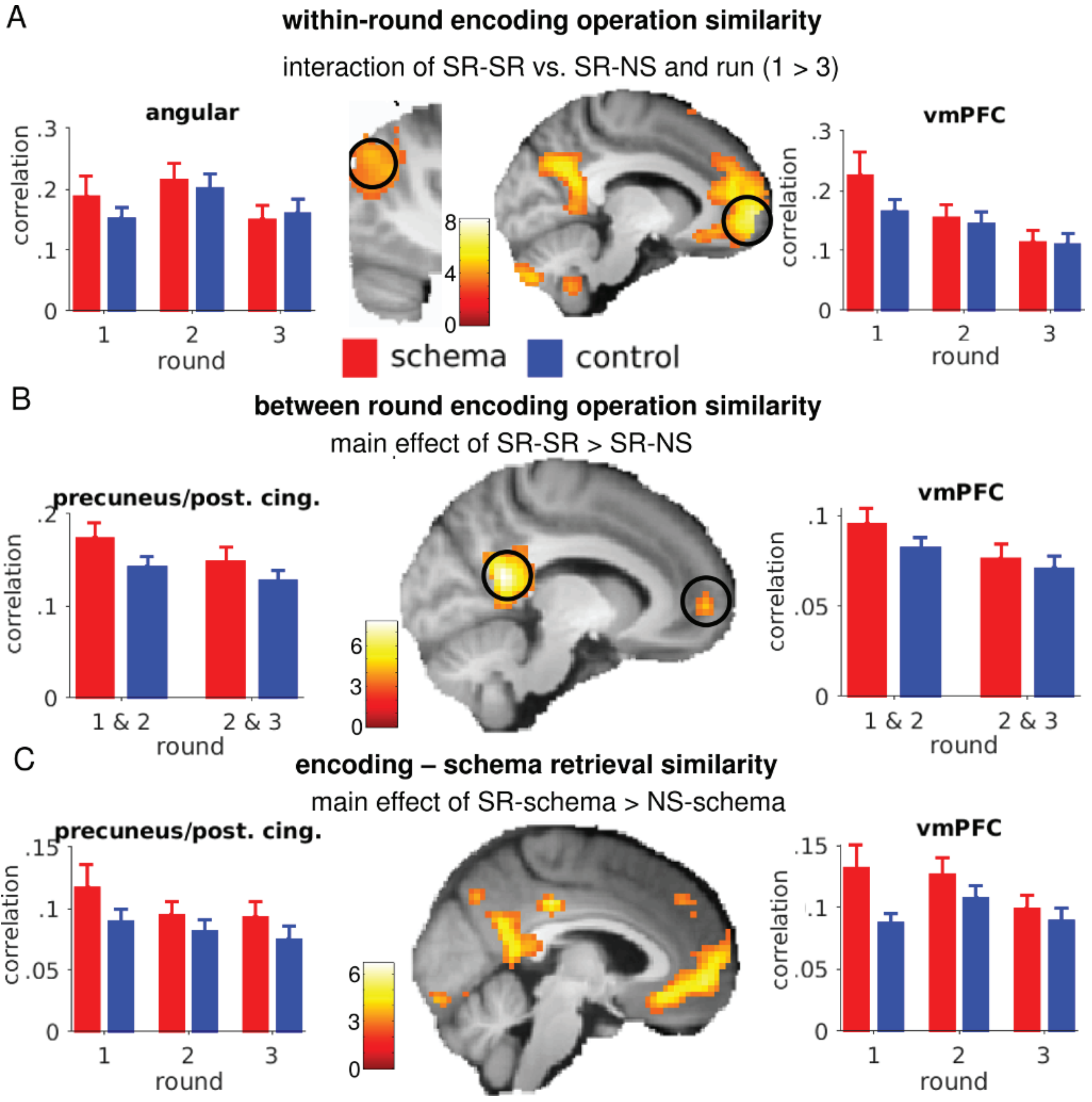

A
hierarchical schema-knowledge
Arthropods
Ants
Crabs
Symbiotic A.
Hunter A.
Weaver A.
Spider C.
Hermit C.
Long-tail C.
Styga
Gulosa
Avati
Japo
Latro
Brius
Texana
Pontu
Caphy
Oatii
Amatus
Axius
control names
Kantaso
Maksa
NIV
Syti
Podo
Lih
Tuma
Mitoko
Erribo
SER
Rakkula
Lys22
B
hit rate
1.0
0.8
0.6
0.4
0.2
0.0
1 2 3 4 5 6 7 8
pic naming
mc questions
Styga is 2 cm long
no
NIV contains copper
no
yes
What does NIV contain?
copper
nickel
hc mc lc
How long is Styga?
2 cm
4cm
hc mc lc lc mc hc
schema learning
encoding
immediate
delayed retrieval
7 weeks
2 weeks
acquisition of
hierarchical schema-knowledge
names of control exemplars
fMRI: 3 encoding rounds
novel schema-related &
control facts
outside of MR-scanner:
4 encoding rounds
control facts
fMRI: immediate & delayed retrieval
novel schema-related &
control facts
fMRI: delayed retrieval
schema-knowledge


A
encoding
judg. of learning
judg. of memory
1.0
0.8
0.6
0.4
0.2
0.0
B
reaction time [s]
2.0
1.5
1.0
0.5
0.0
1
2
3
4
5
6
7
round
C
retrieval
proportion
🟥 schema
🟦 control
D
reaction time [s]
3.0
2.0
1.0
0.0
hc
mc
lc
immediate
delayed
schema


A
retrieval of schema-knowledge > immediate SR retrieval
vlPFC
param. est. [a.u.]
0
2
4
6
immediate
delayed
schema
0
2
4
6
schema
control
B
encoding
main effect SR > NS across rounds
precueus/post. cing.
param. est. [a.u.]
0
1
2
3
1
2
3
round
0
2
4
6
vmPFC
param. est. [a.u.]
-2
-1
0
1
2
1
2
3
round
C
main effect of coupling SR > NS across rounds
fusiform
param. est. [a.u.]
0
0.05
0.1
0.15
0.2
1
2
3
round
0
3
5
hippocampus
param. est. [a.u.]
-0.2
0
0.2
0.4
0.6
1
2
3
round


A
retrieval
main effect SR > NS across immediate and delayed
precueus/post. cing.
param. est. [a.u.]
2
1.5
1
0.5
0
immediate
delayed
6
4
2
0
vmPFC
param. est. [a.u.]
1
0.5
0
-0.5
immediate
delayed
B
interaction SR > NS and immediate < delayed
coupling with the vmPFC
precuneus/post. cing.
param. est. [a.u.]
0.4
0.2
0
-0.2
immediate
delayed
4
2
0
schema
control
C
interaction SR > NS and immediate < delayed
activity
hippocampus
param. est. [a.u.]
1
0.5
0
-0.5
immediate
delayed
4
2
0
vmPFC
param. est. [a.u.]
0.5
0
-0.5
immediate
delayed


A
between round encoding-encoding similarity
main effect SR > NS across rounds
IFG
.04
.02
0
correlation
1 & 2
2 & 3
round
4
2
0
main effect of similar > dissimilar for SR & NS across rounds
15
0
schema
control
B
interaction of SR > NS and round (1 > 3)
cuneus
.08
.06
.04
.02
0
correlation
1 & 2
2 & 3
round
4
2
0
interaction of SR > NS and round (1 < 3)
precuneus
.04
.02
0
.02
correlation
1 & 2
2 & 3
round



A within-round encoding operation similarity

interaction of SR-SR vs. SR-NS and run (1 > 3)

B between round encoding operation similarity

main effect of SR-SR > SR-NS

C encoding – schema retrieval similarity

main effect of SR-schema > NS-schema