



## Differences in the neural signature of remembering schema-congruent and schema-incongruent events



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### ABSTRACT

New experiences are remembered in relation to one's existing world knowledge or schema. Recent research suggests that the medial prefrontal cortex (mPFC) supports the retrieval of schema-congruent information. However, the neural mechanisms supporting memory for information violating a schema have remained elusive, presumably because incongruity is inherently ambiguous in tasks that rely on world knowledge. We present a novel paradigm that experimentally induces hierarchically structured knowledge to directly contrast neural correlates that contribute to the successful retrieval of schema-congruent versus schema-incongruent information. We hypothesize that remembering incongruent events engages source memory networks including the lateral PFC. In a sample of young adults, we observed enhanced activity in the dorsolateral PFC (DLPFC), in the posterior parietal cortex, and in the striatum when successfully retrieving incongruent events, along with enhanced connectivity between DLPFC and striatum. In addition, we found enhanced mPFC activity for successfully retrieved events that are congruent with the induced schema, presumably reflecting a role of the mPFC in biasing retrieval towards schema-congruent episodes. We conclude that medial and lateral PFC contributions to memory retrieval differ by schema congruency, and highlight the utility of the new experimental paradigm for addressing developmental research questions.

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### Introduction

Our knowledge of the world is represented as schemas in long-term memory (Bartlett, 1932; Piaget, 1929), which guide our behavior and help to form expectations about the surrounding. In everyday life, new information is rarely remembered as an independent instance, but is processed against the backdrop of one's existing schemas. If new information about an event is congruent to one's existing schemas, retrieval of the information may be facilitated because inferential processes help finding the target event with the search frame provided by the schema (Anderson, 1981). At the same time, other studies also showed that incongruent new information can lead to better memory, after biases to falsely retrieve schema-congruent information are taken into account (Brewer and Treyns, 1981; Graesser and Nakamura, 1982; Sakamoto and Love, 2004). Therefore, it is important to understand the commonalities and differences in mechanisms that underlie memory for congruent and incongruent new information. Recent neuroscience studies in rodents (Navawongse and Eichenbaum, 2013; Tse et al., 2007, 2011) and humans (van Kesteren et al., 2010, 2013) suggest that regions in

the medial prefrontal cortex (mPFC) and the medial temporal lobe (MTL) play important roles in the neural networks that underlie memory for schema-congruent information. Based on these findings, van Kesteren and colleagues (2012) proposed that the mPFC serves to detect resonance (or congruency) between new information and an existing schema. If resonance is high, the mPFC dampens hippocampal involvement during memory processing and strengthens direct connections between new information and existing schemas represented in the neocortex.

We recently proposed that – in addition to hippocampus and mPFC – the lateral PFC needed to be included in theorizing about the effects of prior knowledge on learning and memory (Brod et al., 2013). Specifically, we hypothesized that the contributions of lateral vs. medial PFC would differ as a function of task requirements. Similar to van Kesteren and colleagues (2012), we argued that the mPFC evaluates the fit between current information and schema-based expectancies. The lateral PFC should, however, be involved whenever integrating or retrieving new information that is not in line with an existing schema, entailing a higher need for elaboration, context monitoring, and overcoming interference from the schema (Dobbins and Wagner, 2005; Ranganath et al., 2000; Raposo et al., 2009), for example in situations when the to-be-remembered information violates schema-based expectancies (i.e., is incongruent) (Mather et al., 1999; Preston and Eichenbaum, 2013). In sum, retrieving incongruent information

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resembles a source-memory situation and should thus result in strong lateral PFC engagement. In addition, to successfully retrieve schema-incongruent episodes, biases towards schema-congruent outcomes have to be overcome. For this, top-down inhibition during memory retrieval is necessary. Here, the lateral PFC is assumed to interact with the striatum, which has been suggested to direct attention to cues that increase the likelihood of retrieval success (Scimeca and Badre, 2012). Thus, frontostriatal interactions appear key to cognitive control processes during memory retrieval, which are crucial for the successful retrieval of schema-incongruent episodes.

However, the lateral PFC has not been prominent in previous studies on schema-related memory processing. This may reflect the use of memory tasks that tap into common world knowledge. Using rich world knowledge could blur differences between congruent and incongruent events, as incongruity can often be resolved by means of idiosyncratic processing, for example by making up a mediator that ties together two seemingly unrelated objects (e.g., umbrella–bathtub, both are related to water). To overcome this problem, we introduced a novel paradigm in which schemas were experimentally induced, which allowed us to assess differences in neural processing between congruent and incongruent memories. Given that the semantics of the induced knowledge network are well controlled, we can distinguish much clearer between schema-congruent and schema-incongruent events than paradigms relying on word knowledge.

On the first day of our experiment, participants acquired knowledge about novel objects and their ranking in a three-level hierarchy. On the next day, participants encoded episodes (competitions) between pairs of these objects, and were later tested on their memory for the outcome of these competitions, which could be either congruent or incongruent to the hierarchy (schema) learned on the first day, thus resembling everyday memory situations in which an event has to be recalled against the backdrop of a strong schema. This part took place in the MR scanner, which allowed us to examine whether newly acquired prior knowledge affects retrieval of congruent information in ways that are similar to what has been shown for well-consolidated knowledge (van Kesteren et al., 2010) and whether this can be dissociated from retrieving incongruent information that entails a clear schema violation.

We expected that mPFC activation would be greater for congruent than for incongruent information, similar to what was shown for well-consolidated knowledge. Critically, we assumed that successfully retrieving episodes that are related to but inconsistent with the schema would require recollecting the specific context of the encoding situation and overcoming interference from the schema. We predicted that the resulting need for elaboration and controlled processing would be reflected in enhanced activity in the lateral PFC and other areas that are engaged in source memory retrieval, including the parietal cortex and the striatum.

## Materials and methods

### Participants

26 right-handed and healthy young adults participated in this study (13 females, 13 males, age 20–30, mean age 24.6 years). All participants were healthy and had normal or corrected-to-normal vision. They were recruited from Berlin universities and were paid 37 Euros for their participation. Two participants had to be excluded because they did not acquire the hierarchy on day 1 according to our criterion (see below for details). Three participants were excluded after data acquisition because they did not have enough trials for analysis ( $\leq 10$ ) in at least one condition, due to a misuse of the confidence scale (providing only “unsure” responses). Therefore, the final sample consisted of 21 individuals (11 females, age 20–30, mean age 24.5 years). The Ethics Committee of the German Psychological Society (DGPs) approved the study. All participants gave written, informed consent.

### Stimuli

Participants acquired an artificial, three-level hierarchy that consisted of 36 comic-like figures called fribbles (12 per level; see Fig. 1 for examples). Fribbles have a colored body and 4 appendages (stimulus images courtesy of Michael J. Tarr, Center for the Neural Basis of Cognition and Department of Psychology, Carnegie Mellon University). They are constructed in accordance to a species structure. Within one species (12 in total in the database), all fribbles share the same body, but each of the 4 appendages has 3 possible shapes (81 exemplars in total). We chose the 36 fribbles for our hierarchy to be as distinct as possible by taking the 4 most diverse exemplars out of 9 species. During all phases of the experiment, the fribbles were presented in pairs. All pairs were unique in the sense that two fribbles were only paired once with each other. However, each fribble appeared repeatedly in the course of the experiment. Fribbles that were paired were always drawn from different hierarchy levels.

The 36 exemplars were assigned to the three-level hierarchy in a pseudorandom way, with the constraint that each level contained exemplars of each of the 9 species. To avoid stimulus-specific saliency effects, two versions of hierarchy were created and counterbalanced across participants. Both hierarchies contained the same 36 fribbles, but the assignment of fribble to ranking was flipped, such that the fast fribbles in one hierarchy were the slow ones in the other, and vice versa.

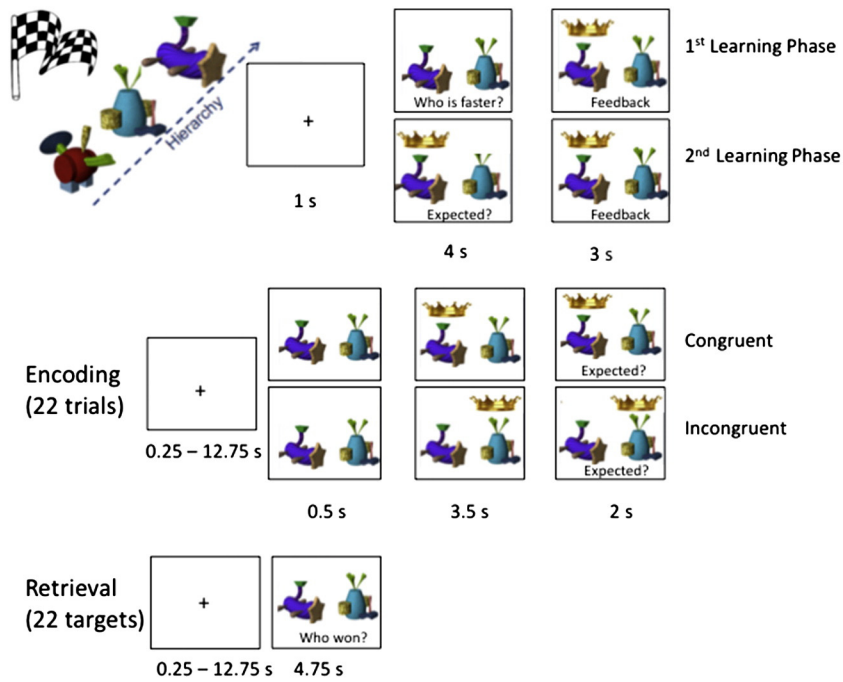
### Task and procedure

#### Day 1: hierarchy learning phase

Participants were tested on two consecutive days. This setting was chosen to allow an initial consolidation of the experimental schema before it had to be applied in the memory task and to avoid overtaxing the participants. Each session took about 90 min. On day 1, they acquired the hierarchy by a two-phase trial-and-error learning task (see Fig. 1).

During the first learning phase, participants were instructed that the fribbles were highly competitive and enjoyed racing against one another. The participants' task was to find out which fribbles were fast, medium fast, or slow. They learned by predicting which of the two presented fribbles (always of different speed levels) was the faster one and received immediate, deterministic feedback on their decision (correct/incorrect). Participants were instructed to give names to the individual fribbles to facilitate learning. Each learning block consisted of 36 trials. The learning blocks were repeated until participants reached a block performance of 90% correct. Learning was subdivided into two subphases: During the first subphase, the participants acquired knowledge of only a subset of exemplars of the whole hierarchy (12 exemplars: 4 fast, 4 medium fast, 4 slow). During the second subphase, participants were asked to assign the 12 learned fribbles to one of the three speed levels and were given corrective feedback. This test ensured that the participants possessed explicit knowledge of the hierarchy. This entire learning phase was repeated for the remaining  $2 \times 12$  exemplars.

During the second learning phase, 36 pairs of fribbles, drawing from all 36 exemplars, were presented consecutively within one block. This time, however, participants were directly presented with the outcome of the race (by a crown shown above the winner) and were asked whether they had expected this result based on the learned hierarchy. In half of the cases, the supposedly faster fribble won (congruent condition), in the other half the supposedly slower fribble won (incongruent condition). Participants stated their answer on a 6-point confidence scale: sure yes, rather sure yes, unsure yes, unsure no, rather sure no, sure no. Subsequently, corrective feedback (correct/incorrect) was provided. As with the first learning phase, blocks of 36 trials were presented until the performance criterion of 90% of correctly classified congruent/incongruent episodes was reached. This setting already accustomed the participants to the memory task that would be done on day 2.



**Fig. 1.** Experimental design. On day 1, participants acquired a hierarchy via a trial-and-error learning task in which they had to predict outcomes of a race between two fribbles. During the first learning phase, they learn the hierarchy with 12 exemplars per block until performance  $\geq 90\%$  (procedure repeated three times for all 36 exemplars). During the second phase, pairs of all 36 exemplars were presented within one block and participants were directly presented with the outcome of the race (via a crown) and were asked whether they expected this result based on the hierarchy. On day 2, after a short recapitulation of the hierarchy via the second learning phase, participants performed a memory task in which they had to remember episodes that were either congruent or incongruent with the hierarchy learned on day 1.

#### Day 2: fMRI memory task

On day 2, participants started with a short recapitulation of the hierarchy knowledge by performing the task of the previous day's second learning phase. Performance criterion was again 90% of correct answers. After successful completion, participants were presented with all 36 exemplars and had to assign each to its speed level. Before entering the scanner, participants were given instructions about the upcoming memory task and requested to move as little as possible in the scanner. In addition, they were instructed to use a visual encoding strategy, such that they would form a mental image of each fribble pair incorporating the race outcome. Afterwards, the participants were placed in the MRI scanner. A structural scan was performed followed by the functional scans.

The memory task (see Fig. 1), which was performed afterwards, consisted of 8 encoding and 8 retrieval blocks (176 unique pairs in total, 88 schema-congruent episodes, 88 schema-incongruent episodes), which were presented alternately. Each block consisted of 22 pairs, of which 11 were congruent. The encoding blocks were similar to the second learning phase, during which participants were shown pairs of fribbles drawn from differing speed levels and were informed which one of the fribbles had won the race (with a crown shown above the winner). Again, in half of the trials, the supposedly faster fribble won (congruent condition), in the other half the slower fribble won (incongruent condition). However, different from the second learning phase, participants were now instructed to additionally memorize the pairs as well as the race outcome and no immediate corrective feedback was provided. They were also informed that 50% of the outcomes were incongruent to the hierarchy. In addition to trying to memorize the pair–outcome association, the participants were asked to indicate whether they had expected the outcome of the race based on the fribbles' positions in the hierarchy. This reminded them again of the hierarchy and ensured that the schema was being processed during encoding. As during the second learning phase, they were asked to state their confidence on a 6-point confidence scale. A feedback on the participants' average performance (percent correct) was provided after the last trial of each encoding block.

The retrieval block always started 8 s after the preceding encoding block. Here, participants were presented with the same pairs from the previous encoding block again in a pseudo-randomized order, with the constraint that fribble pairs that were among the last five pairs during the encoding block did not appear as one of the first five pairs during retrieval. This ensured that the related encoding episode was cleared from short-term memory. Participants had to decide whether they remembered the left or the right fribble as being the winner during the encoding phase. Again, a 6-point confidence scale was used (left/right: sure, rather sure, unsure). They were explicitly reminded that only the outcome of the immediately preceding encoding block was relevant for their decision in the retrieval phase. After each retrieval block, the participants were given feedback (percent correct) on their memory performance, followed by a break of 15 s before the next encoding block started. The 8 cycles of encoding and retrieval were divided into two runs that were separated by a longer break of about 5 min.

Finally, to check whether participants had modified their hierarchy knowledge in the course of the memory task, they were again asked to assign the 36 exemplars to their corresponding speed levels. This was done after they had left the scanner.

#### fMRI data acquisition

Whole-brain MRI data was collected with a Siemens 3 T Trio Magnetom. Structural data was acquired using a T1-weighted 3D magnetization-prepared rapid gradient echo sequence (TR 2500 ms, TE 2500 ms, sagittal orientation, spatial resolution  $1 \times 1 \times 1$  mm). Functional data was acquired using a single shot echo-planar imaging (EPI) gradient echo sequence that is sensitive to BOLD contrast (direction = interleaved, FOV = 216 mm, TR = 2500 ms, TE = 30 ms, number of slices = 45, slice thickness = 2.5 mm, matrix =  $72 \times 72$ , voxel size =  $3 \times 3 \times 2.5$ , distance factor = 20%). The scanning window, after being aligned to the genu and splenium of the corpus callosum, was tilted vertically by  $15^\circ$  to help attenuate signal dropout

in orbitofrontal regions (Deichmann et al., 2003; Weiskopf et al., 2006). To ensure reaching a steady-state condition, the first three scans of each run were discarded. To optimize statistical efficiency of our rapid event-related design, jittered fixation periods were used, which were optimized with Optseq 2 (Dale, 1999). To estimate and correct for geometric distortion and signal loss in the EPI, a 53-seconds fieldmap sequence was also measured.

#### *Statistical analysis: behavioral data*

Behavioral learning and memory scores were analyzed using R (Version 3.0.2; R Core Team, 2014). Given that the learning phases terminated when participants reached criterion ( $\geq 90\%$  correct), we calculated the number of learning blocks needed to reach criterion for the first and second learning phase separately, averaging across the 3 groups of 12 exemplars in the first learning phase. For the encoding phase of the memory test, mean classification performance was calculated. For the retrieval phase, percentage of hits (correctly remembered winner) was calculated separately for schema-congruent and schema-incongruent episodes. Student's *t*-tests were performed to determine differences from chance level (50%, one-sample *t*-test) and differences between the congruent and incongruent conditions (paired-sample *t*-test). In addition, reaction time differences between the within-subject factors memory and congruency were assessed using an *F*-test. Finally, to test whether participants had modified their hierarchy knowledge in the course of the fMRI-memory task, results of the explicit hierarchy tests administered before and immediately after the MRI part were compared using a paired-sample *t*-test. In addition, potential differences in memory performance due to the use of two different hierarchies that were counterbalanced across participants were tested using a two-sample *t*-test.

#### *Statistical analysis: fMRI data*

Data was preprocessed and analyzed using FEAT in FSL (FMRIB's Software Library, <http://www.fmrib.ox.ac.uk/fsl>, Smith et al., 2004). First, non-brain tissue was removed from the analysis. Second, slice time (interleaved) and motion correction (using MCFLIRT) were applied. Third, data was spatially smoothed using a 5-mm full-width half-maximum Gaussian filter. The FILM prewhitening technique was used to account for the intrinsic temporal autocorrelation of BOLD imaging. Using FUGUE in FSL, distortions in the EPI sequences due to magnetic field inhomogeneities, which were measured with a fieldmap image, were compensated by geometrically unwarping the EPI images and ignoring areas with signal loss greater than 10%. Low-frequency artifacts were removed by applying a high-pass temporal filter (Gaussian-weighted straight-line fitting,  $\sigma = 80$  s). Registration to subject-specific high-resolution T1 image and subsequently to standard image (Montreal Neurological Institute, MNI, 2 mm isotropic voxels) was carried out using FLIRT (Jenkinson and Smith, 2001).

After preprocessing, individual time series were modeled separately for the two runs with separate regressors for each of the 4 events (congruent successful, congruent unsuccessful, incongruent successful, incongruent unsuccessful), and separately for the encoding and retrieval phases. For this study we focused on the effects of schema congruency on memory retrieval. Therefore, our paradigm, with its rapidly alternating encoding and retrieval blocks, is suboptimal for the identification of subsequent memory effects, which are typically examined in experimental designs with more trials and substantially longer study-test delays (see the Discussion section). Event length for retrieval was 4.75 s, with the onset being linked to the presentation of the fribbles, trials with unsure response were modeled as regressors of no interest. The regressors were generated by convolving the impulse function related to the onsets and lengths of events of interest with a Gamma hemodynamic response function (HRF). Contrast images were computed for each run per subject. In a second step, the two runs were spatially

normalized, transformed into MNI standard space, and combined into one model using a higher-level within-subjects fixed effects analysis. In a third step, an across-subjects analysis was carried out using a mixed-effects model (FLAME, Woolrich et al., 2004).

Because of our a priori predictions about differential contributions of medial and lateral prefrontal areas to schema-related memory retrieval, we conducted our main analyses using a priori defined anatomical regions of interest (ROIs). Anatomical ROIs of the lateral and medial prefrontal cortices were defined based on FSL's Harvard Oxford Cortical Structural Atlas. The lateral PFC ROI consists of the bilateral superior, middle, and inferior frontal gyri areas. The mPFC ROI consists of the bilateral frontal medial cortex area. To identify which other brain regions contribute to schema-related memory retrieval, we additionally conducted corresponding whole-brain analyses of the fMRI data. Across all whole-brain and ROI analyses, *z* statistic images were thresholded voxel wise at a threshold of  $z > 2.3$ . To correct for multiple comparisons within the ROIs and across the whole brain, we applied a cluster-extent threshold technique. We used the 3DClustSim program of the AFNI software package ([http://afni.nimh.nih.gov/pub/dist/doc/program\\_help/3dClustSim.html](http://afni.nimh.nih.gov/pub/dist/doc/program_help/3dClustSim.html)) to conduct a Monte Carlo simulation analysis using our ROIs as masks. Smoothness of our group-level data was estimated on the residual time series image using AFNI's 3dFWHMx ([http://afni.nimh.nih.gov/pub/dist/doc/program\\_help/3dFWHMx.html](http://afni.nimh.nih.gov/pub/dist/doc/program_help/3dFWHMx.html)). The IPFC mask contained 37,663 voxels, the mPFC mask contained 4160 voxels ( $2 \times 2 \times 2$  mm). A simulation with 10,000 runs yielded minimum cluster extents of 76 (IPFC) and 43 (mPFC) voxels to maintain a family-wise error rate of  $p < .05$ . Accordingly, for the whole-brain mask, a simulation with 10,000 repetitions determined a minimum cluster extent of 113 to maintain a family-wise error rate of  $p < .05$ .

Three sets of analyses were conducted: first, to examine brain areas generally important for successful memory retrieval, a successful retrieval (SR) > unsuccessful retrieval (UR) contrast was computed, regardless of congruency. Second, to characterize effects of successful memory retrieval specifically in congruent and incongruent conditions, the SR > UR contrasts were computed for congruent and incongruent trials separately. Finally, to examine the interaction between memory and congruency, we report brain regions where differences between SR and UR trials were larger in the congruent than in the incongruent condition and vice versa ( $[\text{congruent SR} > \text{congruent UR}] > [\text{incongruent SR} > \text{incongruent UR}]$ , and vice versa).

In addition, psychophysiological interaction (PPI) analyses were performed using FSL to assess connectivity between subcortical and PFC regions. Two seeds (left HC and left striatum, particularly the putamen) with a radius of 5 mm were chosen based on peak activation in the SR > UR contrasts. In addition to the functional relevance of both the striatum and the hippocampus in the retrieval of source information (Han et al., 2012; Hayes et al., 2011; Scimeca and Badre, 2012; Spaniol et al., 2009), a further advantage of choosing these subcortical regions as seeds is their comparably well-defined spatial location and small size. We examined differences in coactivation of the two seeds with our two PFC ROIs that were used for the analyses above. A first-level general linear model (GLM) was constructed for the two runs with three regressors: a physiological regressor (the deconvolved time course from the seed region), a psychological regressor that represented the contrast of the two experimental conditions (congruent SR > incongruent SR and vice versa), and an interaction regressor that represented the interaction of psychological and physiological regressors. Again, the two runs were combined using a higher-level within-subjects fixed effects analysis and, subsequently, a between-subjects mixed-effects model.

## **Results**

### *Learning and memory performance*

For the first learning phase, participants needed on average 2.6 blocks (range: 2–5) to acquire the hierarchy within a group of 12

exemplars (performance criterion  $\geq .90$ ). For the second learning phase, during which pairs of all 36 exemplars were presented together within one block, participants needed on average 1.4 blocks (range: 1–3) to perform at 90%. During the repetition of the second learning phase on day 2, participants needed on average 1.3 blocks (range: 1–3).

During encoding, participants classified 93% (SD = 4.6) of the outcomes correctly as congruent/incongruent. During retrieval, memory performance (see Table 1) was significantly better for schema-congruent than for schema-incongruent episodes ( $t(20) = 4.07$ ,  $p < 0.001$ ,  $d = .89$ ), with memory being significantly above chance level for both schema-congruent (mean = 71%, SD = 0.08,  $t(20) = 12.46$ ,  $p < .001$ ,  $d = 2.58$ ) and schema-incongruent episodes (mean = 62%, SD = 0.08,  $t(20) = 6.56$ ,  $p < .001$ ,  $d = 1.43$ ). Concerning the reaction times (see Table 1), the F-test revealed a main effect of memory ( $F(1,20) = 22.99$ ,  $p < .001$ ,  $\eta_p^2 = .535$ ), indicating longer reaction times for UR as compared to SR episodes, but neither a main effect of congruency ( $F(1,20) = .02$ ,  $p = .89$ ) nor an interaction between retrieval success and congruency ( $F(1,20) = .55$ ,  $p = .47$ ). The comparison of the explicit hierarchy tasks tested before (mean = 34.48 out of 36 exemplars correctly classified) and after the fMRI-memory phase (mean = 35.19 out of 36 exemplars correctly classified) revealed no indication that the participants modified their schema during the fMRI-memory phase ( $t(20) = -1.85$ ,  $p = .08$ ). There was no difference in memory performance between the two hierarchies used for counterbalancing ( $t(19) = .07$ ,  $p = .94$ ).

### fMRI results

#### Differences in activity based on memory, congruency, and their interaction

At the whole brain level, the analysis of successful memory retrieval (i.e., SR > UR; see Fig. 2), independent of congruency, revealed stronger activation for SR than UR trials in areas involving the left hippocampus, medial PFC, striatum, superior parietal lobule, inferior frontal gyrus, cingulate gyrus, and visual areas in lateral and medial occipital cortex.

The subsequent analyses examined differences in the neural correlates of successful memory retrieval between congruent (SR > UR) and incongruent (SR > UR) events in the predefined lateral and medial PFC ROI's. While successfully retrieved congruent events were associated with stronger activation in the mPFC, successfully retrieved incongruent events were associated with stronger activity in the lateral PFC, in particular in its dorsal parts (DLPFC, see Fig. 3). To formally probe the interaction between memory and congruency within our ROI's, we examined whether successful memory retrieval was differentially expressed in the congruent and incongruent conditions ([congruent SR > UR] > [incongruent SR > UR], and vice versa), respectively (Fig. 3). Larger differences between SR and UR trials for incongruent as compared to congruent events were found in the DLPFC (see Fig. 3, right panel). The opposite contrast, which determined regions that exhibit larger differences for the congruent as compared to the incongruent condition, revealed activation in the ventral mPFC (see Fig. 3, left panel).

We also explored differences in successful memory retrieval between congruent and incongruent conditions across the whole brain. As can be seen in Table 2, additional activity for successfully retrieved congruent events was found in the left middle temporal

gyrus, the superior frontal gyrus, and the bilateral cingulate gyrus. Incongruent events yielded activation in areas including the superior parietal lobe, the bilateral striatum, the inferior temporal gyrus, and precuneus. For the interaction of congruency  $\times$  retrieval success, no additional activation was found for the congruent > incongruent contrast, whereas additional activation for the incongruent > congruent contrast was revealed in the bilateral superior parietal lobe, extending into the supramarginal gyrus, the occipital cortex, and the inferior temporal gyrus.

#### Congruency differentially modulated connectivity in remembered trials

PPI analyses were performed using seed regions in the left HC and in the left putamen that were defined based on activation in the SR > UR contrasts. Based on theoretical conceptions and results from the retrieval success  $\times$  congruency interaction, we focused our search on two anatomical PFC regions, namely the middle and the medial frontal gyri. The putamen revealed significant coactivation with the right DLPFC (Brodmann area 9, middle frontal gyrus), which was stronger during incongruent SR than congruent SR trials (see Fig. 4). No differences in interaction due to congruency were observed between left striatum and ventral mPFC. The left HC also revealed no differences in coactivation based on congruency with the ventral mPFC or DLPFC.

### Discussion

New information is remembered differently depending on its congruency with already existing world knowledge. However, the neural signature of the differences between successfully retrieved schema-congruent and schema-incongruent events has remained elusive, presumably because real-life schemas are often inherently fuzzy and vary across people. In this study, we experimentally induced artificial task-relevant knowledge. This allowed identification of characteristic activation differences between schema-congruent and schema-incongruent episodes during memory retrieval.

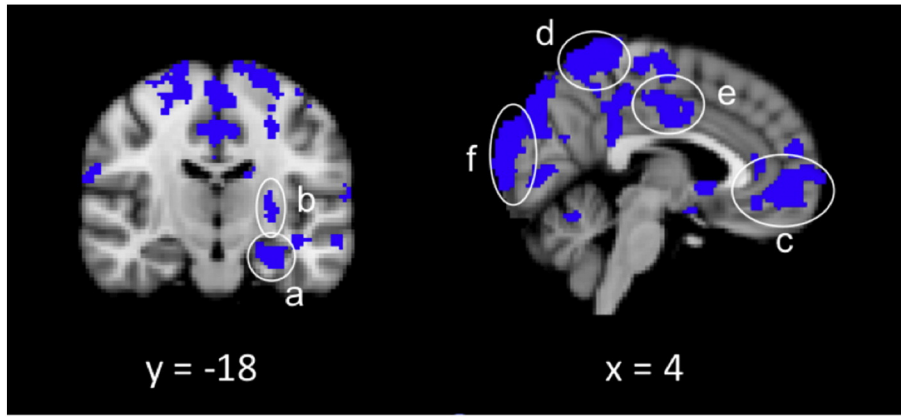
In line with studies using world knowledge, we observed enhanced mPFC activity for the successful retrieval of schema-congruent relative to schema-incongruent episodes (cf. van Kesteren et al., 2010, 2013). Importantly, for successfully retrieved schema-incongruent episodes, we found enhanced activation in DLPFC, PPC, and striatum. In addition, the striatum and the DLPFC showed increased connectivity for successfully retrieved schema-incongruent episodes relative to schema-congruent episodes.

The involvement of the DLPFC and its crosstalk with the striatum for successfully retrieved incongruent episodes is in accordance with our assumption that retrieving the specific situational context of the encoding situation helps overriding schematic knowledge (cf. Mather et al., 1999). Both regions have repeatedly been found in source or context memory tasks (Han et al., 2012; Hayes et al., 2011; Ranganath et al., 2000; Raposo et al., 2009; Spaniol et al., 2009). Frontostriatal circuits are considered to be particularly important for declarative memory retrieval when control demands are high, for example in situations in which one has to overcome interference (Scimeca and Badre, 2012). Scimeca and Badre (2012) suggested that the striatum directs attention to cues that increase the likelihood of retrieval success, and that these cues are maintained in working memory and semantically elaborated by the lateral PFC. This suggestion is consistent with claims that lateral PFC activation in retrieval situations in which distinctive properties of a memory trace have to be isolated reflects an active construction of the context of the encoding situation (Han et al., 2012; Preston and Eichenbaum, 2013; Raposo et al., 2009). The striatum thus takes on a "gate keeper" role that determines which cues are goal-relevant and should thus be elaborated by the lateral PFC (Scimeca and Badre, 2012). Our findings of enhanced activity in striatum and DLPFC as well as of a stronger connectivity between the two for successfully retrieved schema-incongruent episodes provide support for this hypothesis. Remembering episodes that do not fit the schema resembles a source

**Table 1**

Mean and standard deviations of behavioral results from each condition at retrieval. Accuracy refers to mean percentage remembered trials in congruent and incongruent conditions. Reaction times (in ms) are presented separately for SR and UR episodes.

Trial type	Congruent		Incongruent	
	Accuracy	RT	Accuracy	RT
SR	.71 (.08)	2409 (365)	.62 (.08)	2426 (354)
UR	–	2576 (419)	–	2553 (364)



**Fig. 2.** Main effect of memory. Regions showing enhanced activation for successfully retrieved vs. for unsuccessfully retrieved trials encompassed left hippocampus (a) and striatum (b, peak = [−26 −18 −18]), medial PFC (c, peak = [−8 52 −2]), precuneus and superior parietal lobule (d, peak = [18 −42 70]), cingulate gyrus (e, peak = [−18 −4 32]), and visual areas in lateral and medial occipital cortex (f, peak [4 −96 16]).

memory situation in which retrieval must be directed towards the recovery of task-relevant detail, which is in our case the episode of the “slower” exemplar winning the race. In addition, interference from knowing that the outcome of this episode runs against the schema has to be overcome.

In addition to striatum and DLPFC, we also found stronger activity for successfully retrieved schema-incongruent episodes in the bilateral superior PPC. Consistent with the above argument of a source memory-like situation for schema-incongruent remembered episodes, the PPC has been implicated to signal “retrieval success” for hits versus correct rejections and to be particularly active in source memory tasks in which details have to be recovered (Henson et al., 1999; Konishi et al., 2000; Wagner et al., 2005; Yonelinas et al., 2005). Cabeza et al. (2008) provided an integrative perspective on PPC activation during memory retrieval and suggested that the superior PPC supports a voluntary (top-down) engagement in memory search. Interestingly, a lateral PPC regions that overlaps with the one found in this study has also been shown to be sensitive to expectancy violations in a memory retrieval situation in which targets were preceded by invalid cues (O'Connor et al., 2010). In line with previous research, our findings of stronger PPC activity for successfully retrieved schema-incongruent episodes fit the hypothesis that remembering such episodes entails source-memory-like processes that pose high demands on control and search processes.

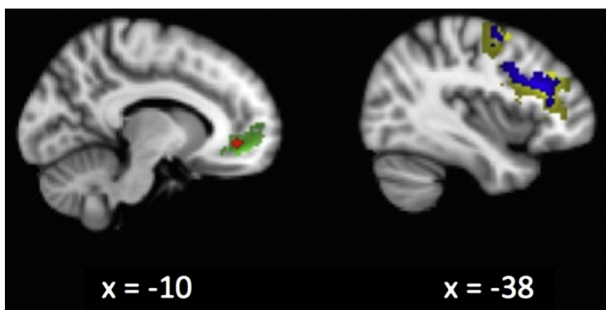
In keeping with previous work (van Kesteren et al., 2010), we found that the mPFC played a key role in retrieving information that is

congruent with an experimentally established schema. In addition, we showed that the mPFC is involved in memory retrieval even when the lag between encoding and retrieval is very short, which provides evidence for the notion that the mPFC is involved in schema-related memory retrieval at all periods (Preston and Eichenbaum, 2013). Existing work postulates that the mPFC evaluates the fit between new

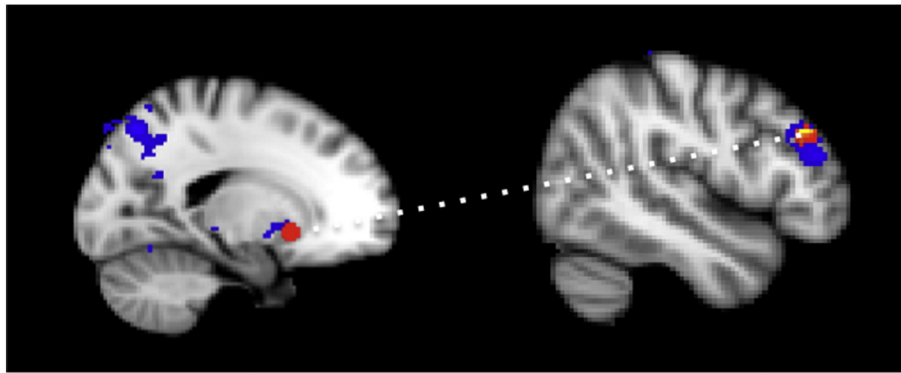
**Table 2**

Regions exhibiting stronger activation for SR than for UR trials in the whole-brain contrast, separately for congruent and incongruent events and for the congruency × memory interaction. For better characterizing the local maxima of the clusters, clusters presented in this table were thresholded at the voxel threshold of 2.6.

Region	x	y	z	#voxels	z-Max
<i>Congruent SR–UR</i>					
Bilateral mPFC	−10	44	−6	1887	3.92
Bilateral cingulate gyrus	0	−20	44	276	3.18
Right postcentral gyrus	8	−36	68	262	3.05
Left cerebellum	−48	−70	40	229	3.25
Left middle temporal gyrus	−58	−4	−24	207	3.47
Left superior frontal gyrus	−10	30	60	154	3.25
Left hippocampus	−26	−18	−18	100	3.39
<i>Incongruent SR–UR</i>					
Left precuneus/superior parietal lobule	−6	−76	52	6643	3.8
Left middle frontal gyrus	−34	28	20	1255	4.12
Right cuneal cortex	4	−88	32	500	3.76
Left inferior temporal gyrus	−52	−58	−16	448	3.7
Right cerebellum	18	−60	−16	425	3.18
Right middle frontal gyrus	46	40	18	331	3.49
Bilateral cingulate gyrus	0	0	36	306	3.37
Right caudate	12	14	−2	291	3.81
Left postcentral gyrus	−60	−4	10	235	3.31
Left putamen	−16	12	−4	235	3.76
Left precuneus	−4	−36	48	255	3.71
Left postcentral gyrus	−60	−4	8	228	3.28
Right central opercular cortex	56	−6	6	189	3.52
Bilateral supplementary motor cortex	−4	−8	62	173	3.27
Left frontal pole	−16	46	44	117	3.13
Bilateral cingulate gyrus	0	−38	26	117	3.45
Left postcentral gyrus	−56	−8	24	115	3.33
<i>Congruent SR–UR &gt; incongruent SR–UR</i>					
–					
<i>Incongruent SR–UR &gt; congruent SR–UR</i>					
Bilateral lateral occipital cortex/left superior parietal lobule	−10	−72	58	2467	3.67
Left middle frontal gyrus	−34	30	22	1054	3.76
Right superior parietal lobule	38	−48	52	440	3.17
Left precentral gyrus	−26	−8	52	283	3.23
Right frontal pole/middle frontal gyrus	46	38	20	202	3.11
Right middle frontal gyrus	32	4	56	145	3.02
Left inferior temporal gyrus	−46	−52	−10	116	2.9



**Fig. 3.** Congruency × memory interaction in the prefrontal cortex. Left (x = −10): Differences between SR and UR events that are larger in the congruent than in the incongruent condition were revealed in the ventral mPFC (peaks [−4 32 −16], depicted in red). Right (x = −38): The opposite contrast, in which differences are larger for the incongruent than for the congruent condition, revealed two clusters (depicted in blue) in the DLPFC (peaks [−34 30 22] and [46 38 20]). Interactions are overlaid on the SR > UR contrast for congruent (green) and incongruent (yellow) events.



**Fig. 4.** PPI between striatum and DLPFC. A psychophysiological interaction (PPI) analysis with a seed in the left putamen revealed connectivity with a right DLPFC cluster (red), which was stronger for SR schema-incongruent outcomes than for SR schema-congruent episodes. Activations are overlaid on the congruency  $\times$  memory interaction results (blue).

information and a schema and weighs the influence of the schema during memory retrieval (Brod et al., 2013; Preston and Eichenbaum, 2013; van Kesteren et al., 2012). The mPFC is suggested to achieve this via influencing memory processing in the limbic system, especially in the HC, supposedly through inhibitory connections (Bein et al., 2014; Navawongse and Eichenbaum, 2013; Nieuwenhuis and Takashima, 2011; Schlichting and Preston, 2015; Wang and Morris, 2010). Evidence for this claim comes from recent studies with patients suffering from lesions in the ventral mPFC (Ghosh et al., 2014; Warren et al., 2014). Compared to control patients, patient with ventral mPFC lesions displayed less schema-reinstatement (Ghosh et al., 2014) and less schema-related memory intrusions in the Deese–Roediger–McDermott (DRM) paradigm (Warren et al., 2014), which suggests that an intact mPFC would increase the weight of schema-congruent memories. Further support is provided by animal models, in which inhibition of the mPFC has been found to impair memory retrieval (Tse et al., 2011). The present study adds to this literature by showing that the mPFC is important for biasing retrieval towards schema-congruent episodes at all stages of memory consolidation, in addition to being involved in retrieving consolidated memories (Gilboa, 2004; Takashima et al., 2006).

Again consistent with van Kesteren et al. (2010), we neither found less HC activity nor enhanced connectivity between mPFC and HC for the retrieval of congruent compared to incongruent information. The left hippocampus contributed to successful memory retrieval for both schema-congruent and schema-incongruent episodes, without significant difference between the two. One likely explanation for this result is that reductions in hippocampal contributions to memory retrieval, which have been suggested for the retrieval of congruent information (van Kesteren et al., 2012), have been only reported for long-term retention of information over days or weeks after encoding (Takashima et al., 2006), and not after shorter delays as the one used in this experiment.

To the best of our knowledge, this study is the first to clearly distinguish brain regions that support the successful retrieval of schema-congruent and schema-incongruent episodes. The study by van Kesteren and colleagues (2010) found dorso- and ventrolateral PFC regions to be more active for remembered vs. for forgotten associations, but did not find additional differences in lateral PFC due to congruency. We speculate that the object-fabric combinations used in that study, which were classified as congruent/incongruent based on world knowledge in a pilot study, attenuated the differences between congruent and incongruent information. The present approach of using experimentally induced schemas is better suited to assess differences in memory for schema-congruent and schema-incongruent episodes because its hierarchically organized and semantically restricted task space introduces a clear and well-controlled distinction between episodes that match and episodes that run counter to previously established schemas. Furthermore, the present paradigm also allows

close monitoring of the strength of the schema. By this, differences in schema strength between participants are minimized and unlikely to affect our results.

Our study has several limitations. First, while our current design has the advantage that congruent and incongruent events are clearly separable and incongruent events entail a clear schema violation, we did not fully disentangle semantic and episodic memory processes during the retrieval of schema-congruent episodes. Although participants were informed that only relying on their hierarchy knowledge would not help them master this task, responses in some congruent trials during the retrieval phase might still have been made based only on schema expectation and not with memory of the observed episode. Along this line, recognition studies typically report higher false alarm rates for schema-congruent as compared to schema-incongruent lures (Brewer and Treyns, 1981; Graesser and Nakamura, 1982; Sakamoto and Love, 2004, for a meta-analysis see Stangor and McMillan, 1992), which suggests that taking into account false alarm rates attenuates the memory advantage typically found for schema-congruent episodes. Since the focus of our experiment was on comparing successful and unsuccessful cued-recall of an event, we do not have a measure of false alarms. However, we addressed these issues by leaving out trials associated with an unsure response in the analyses, with the rationale that these trials are more likely to reflect guessing based on the schema and not memory of the episode. In addition, one might assume that answering purely based on the schema would be faster and less effortful than revisiting the encoding episode (presumably the case for incongruent trials), which in turn would be associated with slower RTs. However, the pattern of reaction times, which are known to be highly sensitive to differences in strategies and effort during memory retrieval (cf. Buckner et al., 1998; Henson et al., 2000; Tyler et al., 1979), speaks against this view. We found no main effects of congruency or congruency by memory interactions for reaction times, but only a main effect of memory, with slower reaction times for forgotten than for remembered episodes. Finally, we report the effects of an experimentally established schema only on memory retrieval, but not on encoding. We do this because the present paradigm, with its rapidly alternating encoding and retrieval blocks, is insufficient for the identification of subsequent memory effects. Such effects are typically observed in experimental designs with more trials and substantially longer study-test delays (cf. Stark and Squire, 2000; Uncapher and Rugg, 2005). We tested for main effects of subsequent memory, both across conditions and separately for congruent and incongruent events. None of the contrasts yielded significant activations in any brain area. In future studies, the present paradigm could be extended by a delayed test phase to also assess subsequent memory effects.

## Conclusion

This study indicates that the successful retrieval of schema-related but incongruent episodes is facilitated by retrieving the specific situational context of the encoding situation and by overcoming biases from the schema. This is reflected by an enhanced activation in DLPFC, PPC, and striatum for successfully retrieved incongruent episodes, and enhanced connectivity between striatum and DLPFC. Furthermore, this study suggests that the mPFC plays a role in biasing retrieval towards schema-congruent episodes already for recently acquired schemas and even when the lag between encoding and retrieval is very short. Using experimentally established schemas allows assessing the effects of pre-existing knowledge on learning and memory under well-controlled experimental conditions (Brod et al., 2013; Kumaran et al., 2012; van Buuren et al., 2014). This is especially important when comparing groups of individuals with large differences in world knowledge. For instance, quasi-experimental work on age differences in associations among prior knowledge, learning, and memory is inherently confounded by age-graded differences in pre-existing knowledge structures (Brod et al., 2013). Hence, we recommend the experimental induction of knowledge structures for studying the effects of prior knowledge on learning and memory, especially when pre-existing individual differences in world knowledge are likely to be large.

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