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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.

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 Treyens, 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 (≤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 2×12 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.