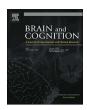
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The impact of perceptual changes to studied items on ERP correlates of familiarity and recollection is subject to hemispheric asymmetries



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ABSTRACT

It is still unclear which role the right hemisphere (RH) preference for perceptually specific and the left hemisphere (LH) bias towards abstract memory representations play at the level of episodic memory retrieval. When stimulus characteristics hampered the retrieval of abstract memory representations, these hemispheric asymmetries have previously only modulated event-related potential (ERP) correlates of recollection (late positive complex, LPC), but not of familiarity (FN400). In the present experiment, we used stimuli which facilitated the retrieval of abstract memory representations. With the divided visual field technique, new items, identical repetitions and color-modified versions of incidentally studied object pictures were presented in either the right (RVF) or the left visual field (LVF). Participants performed a memory inclusion task, in which they had to categorize both identically repeated and color-modified study items as 'old'. Only ERP, but not behavioral data showed hemispheric asymmetries: Compared to identical repetitions, FN400 and LPC old/new effects for color-modified items were equivalent with RVF/LH presentation, but reduced with LVF/RH presentation. By promoting the use of abstract stimulus information for memory retrieval, we were thus able to show that hemispheric asymmetries in accessing abstract or specific memory representations can modulate ERP correlates of familiarity as well as recollection processes.

1. Introduction

According to two-process models, episodic memory access can be achieved via two distinct processes, familiarity and recollection. Familiarity denotes recognizing a stimulus as familiar without being able to retrieve details about the context in which it was previously encountered. Recollection, on the other hand, is defined as the conscious and effortful retrieval of a stimulus and its study episode (for a review, see Yonelinas, 2002). Electrophysiological studies indicate that familiarity processes are associated with the attenuation of an early (~300-500 ms) mid-frontal negativity (FN400). Timing and morphology of the FN400 are similar to the N400, a correlate of semantic priming (Kutas & Federmeier, 2011). Both components can be dissociated from each other on the basis of their topography, however (Bader & Mecklinger, 2017; Bridger, Bader, Kriukova, Unger, & Mecklinger, 2012). Recollection-based retrieval, on the other hand, can be related to an increase in a late (~500-800 ms) parietal positivity (late positive complex, LPC; Mecklinger, 2000; Rugg & Curran, 2007; Rugg & Yonelinas, 2003).

These event-related potential (ERP) indices can be differentially

affected by perceptual manipulations from study to test (Zimmer & Ecker, 2010). Changes to the color, size or orientation of study items as well as exemplar changes from study to test only reduce LPC old/new effects when the changed features are task-relevant either at encoding or retrieval (Curran, 2000; Curran & Cleary, 2003; Ecker, Zimmer, & Groh-Bordin, 2007a; Haese & Czernochowski, 2015; Ranganath & Paller, 1999). Otherwise, equivalent LPC old/new effects emerge for identical repetitions and perceptually modified versions of studied items (Curran & Dien, 2003; Ecker et al., 2007a; Groh-Bordin, Zimmer, & Mecklinger, 2005; Küper, Groh-Bordin, Zimmer, & Ecker, 2012; Tsivilis, Otten, & Rugg, 2001; but see Ecker & Zimmer, 2009).

In contrast, study-test changes to perceptual item features can affect familiarity-related FN400 modulations even when the changed features are task-irrelevant (Ecker et al., 2007a; Groh-Bordin et al., 2005; Schloerscheidt & Rugg, 2004). Yet, perceptually unspecific familiarity-based retrieval can also be induced, for example by promoting verbal-conceptual encoding (Ecker, Arend, Bergström, & Zimmer, 2009) or when the retrieval of abstract-conceptual memory representations is required at test (Ecker & Zimmer, 2009; see also Curran, 2000; Curran & Cleary, 2003; Curran & Dien, 2003).

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Divided visual field experiments have indicated that the two cerebral hemispheres are differentially involved in accessing abstract categorical as opposed to perceptually specific memory representations, at least in the semantic and the implicit memory domains. The divided visual field technique is aimed at limiting initial stimulus processing to only one cerebral hemisphere: Participants are required to hold central fixation while stimuli are presented in either the left visual field (LVF) or the right visual field (RVF) at presentation times that are too short to allow for horizontal eye movements (< 150-180 ms, Bourne, 2006). Under these viewing conditions, the right hemisphere (RH) has shown an advantage not only for general visual object identification (Koivisto & Revonsuo, 2010; McAuliffe & Knowlton, 2001), but also for exemplar-specific object identification (Laeng, Zarrinpar, & Kosslyn, 2003; Studer & Hübner, 2008, Experiment 1). Abstract categorization, on the other hand, can be achieved more quickly by the left hemisphere (LH). Similarly, perceptually specific repetition priming has been observed for items processed by the RH, but not for items processed by the LH (Burgund & Marsolek, 2000; Marsolek, 1995, 2004; Marsolek, Kosslyn, & Squire, 1992; Marsolek, Squire, Kosslyn, and Lulenski, 1994). Neuroimaging, electrophysiology and lesion studies have yielded converging evidence for these hemispheric asymmetries in implicit memory access (Beeri, Vakil, Adonsky, & Levenkron, 2004; Koutstaal et al., 2001; Küper, Liesefeld, & Zimmer, 2015; McMenamin, Deason, Steele, Koutstaal, & Marsolek, 2015; Simons, Koutstaal, Prince, Wagner, & Schacter, 2003).

In contrast, relatively little is known about the role that these hemispheric asymmetries play at the level of episodic memory retrieval. Behavioral research on the subject has been sparse and has yielded inconclusive results: An RH advantage for perceptually specific cued word recall was found in one experiment (Marsolek et al., 1994) but not in another (Marsolek et al., 1992). The single electrophysiological study on this topic has shown that at least recollection-based memory access can be more exemplar-specific when it is governed by the RH compared to the LH (Küper & Zimmer, 2015). In an incidental study phase, participants performed a size estimation task on visual objects presented at fixation. In a subsequent test phase, new items, identical repetitions of study items and different exemplars from the same category as studied items were presented to the LVF/RH or the RVF/LH using the divided visual field procedure. Participants performed a direct memory inclusion task in which they had to categorize both identical repetitions and different exemplars as "old". Exemplar-specific perceptual information was thus task-irrelevant. Nevertheless, behavioral and FN400 old/new effects were larger for identical repetitions compared to different exemplars, irrespective of the cerebral hemisphere items were presented to. In contrast, indices of recollection-based memory showed hemispheric asymmetries: LPC old/new effects were more pronounced for identical repetitions compared to different exemplars with LVF/RH presentation, but equivalent for both types of old items with RVF/LH

It would be premature, however, to deduce from this result pattern that the hemispheric asymmetries described above come to bear only in recollection-based episodic memory, but have no impact on familiarity processes. The stimuli used in Küper and Zimmer's (2015) experiment were distinct exemplars from the same object category. These can differ substantially from each other with respect to a variety of perceptual features, such as size, color, orientation, global outline and local detail. The memory inclusion task required participants to categorize both identical repetitions and different exemplars of studied items as "old". This is much more difficult to achieve, however, when both types of "old" items differ across several dimensions and may thus appear visually very dissimilar (see McMenamin et al., 2016). Previous research in the implicit memory domain has already shown that such task and/ or stimulus characteristics can promote the retrieval of perceptually specific instead of abstract memory representations in the LH (e.g. Marsolek, 1999, Experiment 3; Studer & Hübner, 2008, Experiment 2). This may have been the case in Küper and Zimmer's (2015) study and

could have obscured the impact of hemispheric asymmetries on familiarity as indexed by FN400 old/new effects.

In the present study, we thus examined hemispheric asymmetries in episodic memory access using stimuli which benefitted the retrieval of abstract memory representations: In a divided visual field experiment similar to the one of Küper and Zimmer (2015), we had participants perform a memory inclusion task on identical or color-modified versions of study items. In contrast to the previous experiment, identical and perceptually modified versions of studied items were thus always identical as to their shape and, irrespective of their surface color, easily identifiable as one and the same object.

Given the high degree of similarity between identically repeated and color-modified study items, we expected to find comparable behavioral old/new effects for both types of "old" items (cf. Ecker et al., 2009; Groh-Bordin et al., 2005; Tsivilis et al., 2001). Hemispheric asymmetries in behavioral old/new effects have previously only been observed with a short study-test interval, a low number of test items and blocked testing of identically repeated and modified study items (Marsolek et al., 1994). As the present study did not feature any of these, we expected to find the above result pattern, for both LVF/RH and RVF/LH presentation (cf. Küper & Zimmer, 2015; Marsolek et al., 1992).

In ERP measures, the experimental conditions should nevertheless bring a potential LH advantage for accessing abstract, perceptually unspecific memory representations to the foreground. For RVF/LH presentation, we thus expected to find not only equivalent LPC old new effects, but also comparable FN400 effects for identical and color-modified versions of study items.

At the same time, the present study allows us to examine whether LVF/RH presentation results in the retrieval of perceptually specific memory representations, even when identically repeated and modified study items are visually very similar and thus difficult to distinguish (see McMenamin et al., 2016). Given the robustness of the RH advantage for perceptually specific memory access in the implicit memory domain, we hypothesized that this would be the case. For LVF/RH presentation, we thus expected to find increased FN400 and LPC old/new effects for identically repeated study items compared to color-modified versions.

2. Methods

2.1. Participants

20 students of Saarland University participated in the present study. Data from one participant had to be discarded because it did not yield a minimum of 15 EEG artifact-free trials in each cell of the experimental design. The remaining 19 participants (18 female, 20–37 years old, mean age 25.2 years) reported being right-handed and having normal or corrected-to-normal vision. All participants gave informed consent after the nature of the experiment had been explained to them.

2.2. Stimuli

The stimulus set comprised 240 colored photographs and 240 black-and-white photographs of 240 familiar objects. Each object was thus depicted in a colored and in a black-and-white version. Black-and-white pictures were generated by converting the original color versions (see Küper et al., 2015, for examples) of object photographs to grayscale versions with the aid of Corel Draw Graphics Suite. One half of the picture stimuli showed objects larger than a shoebox while the other half showed objects smaller than a shoebox. Assignment of stimuli to experimental conditions (see Section 2.3) was counterbalanced across participants.

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