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Review article

From fluency to recognition decisions: A broader view of familiarity-based remembering

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ABSTRACT

The goal of this article is to critically examine current claims and assumptions about the FN400, an event-related potential (ERP) component which has been related to familiarity memory though some uncertainty exists regarding the cognitive processes captured by the FN400. It is proposed that familiarity can be multiply determined and that an important distinction has to be made between a recent-exposure, relative familiarity mechanism indexed by the FN400 and an absolute/baseline familiarity mechanism being reflected by a coincidental but topographically distinct ERP effect. We suggest a broader conceptualization of the memory processes reflected by the FN400 and propose an unexpected fluency-attribution account of familiarity according to which familiarity results from a fast assessment of ongoing processing fluency relative to previous events or current expectations. The computations underlying fluency attribution may be closely related to those characterizing the relative familiarity mechanism underlying the FN400. We also argue that concerted activation of the perirhinal cortex (PrC) and the lateral prefrontal cortex (PFC) plays a pivotal role for fluency attributions and the generation of the FN400.

1. Introduction

Familiarity is a global measure of memory strength that supports recognition memory judgments. Familiarity is usually described as a feeling of recency or oldness that is qualitatively distinct from recollection, the retrieval of details of a prior study episode, i.e. where and when a particular event took place (Yonelinas et al., 2010). Neuropsychological studies, neuroimaging research as well as experimental animal studies have been conducted to explore the functional characteristics and the neural underpinnings of familiarity and recollection. These studies have provided strong support for the dual-process view of recognition memory according to which familiarity and recollection make independent contributions to recognition memory and can be dissociated on the functional and the neural level (Bastin et al., 2019; Mandler, 2008; Rugg and Curran, 2007; Rotello et al., 2004; Yonelinas, 1997).

One way to examine the functional characteristics of familiarity and recollection and how they contribute to recognition memory judgments is to explore event-related potential (ERP) old/new effects. ERPs reflect time-locked changes in scalp-recorded electrophysiological brain activity. Due to their high temporal resolution in the millisecond domain they allow to online monitor memory processes across electrode montages and to dissociate neurocognitive processes on the basis of temporal or topographical differences with high temporal resolution. ERP old/new effects are differences between correctly classified old (studied) and new (unstudied) items in a recognition task, which provide measures of successful retrieval. ERPs elicited by correctly classified old items are more positive-going than those elicited by correctly classified new items. Of note for the present report, in a large number of studies, ERP old/new effects have been shown to differ according to whether recognition is based on familiarity or recollection.

ERP studies on recognition memory revealed that recollection has a unique ERP signature, i.e. the parietal old/new effect (see Rugg and Curran, 2007, or Friedman and Johnson, 2000, for a review). It takes the form of more positive going waveforms for hits than correct rejections between 400 and 600 ms which are most pronounced at (left) parietal recording sites. Its topography shows a left parietal maximum for words but is more widespread for pictures (Gutchess et al., 2007) or actions (Leynes and Bink, 2002). Serval studies employed the remember/know procedure, a well-established method to estimate familiarity and recollection, to explore the ERP correlate of recollection. With this procedure, people are asked to evaluate their memory judgements and

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to respond "remember" when recognition is accompanied by the retrieval of specific details of the study event, and to respond "know" when recognition is based on a feeling of familiarity (Gardiner, 1988). As would be expected from an ERP measure indicative of recollection, the parietal old/new effect is larger for remembered items which are given a remember-response than a know-response (Curran, 2004; Leynes and Bink, 2002). It is also sensitive to common operational definitions of recollection, e.g., it is larger for items associated with correct than incorrect source judgments (Senkfor and Van Petten, 1998). To complete this evidence, the parietal old/new effect is larger when more details from a prior study episode are remembered (Voss and Paller, 2009) and absent in patients who lack the capacity for recollection (Addante et al., 2012; Düzel et al., 2001; Mecklinger et al., 1998).

Another of these old/new effects is the mid-frontal old/new effect, also called FN400 or FN400 old/new effect. It is this ERP old/new effect that is the main topic of this article. It takes the form of more positive going ERP waveforms for hits than correct rejections and is most pronounced between 300 and 500 ms at frontal recording sites. In the literature, the term FN400 is sometimes used interchangeable to refer to a negativity elicited with maximal amplitude between 300 and 500 ms or to the attenuation of this negativity in an experimental condition. Unless specified otherwise, we will use this latter denotation throughout this article. Supporting the view that the FN400 is associated with familiarity memory, the magnitude of the FN400 co-varies with familiarity strength, operationalized as confidence with which recognition decisions are given (Woodruff et al., 2006; Yu and Rugg, 2010). Consistent with the view that familiarity is available earlier than recollection, the FN400 is also present with speeded response requirements whereas the parietal old/new effect is absent when recognition decisions have to be given under speeded conditions (Mecklinger et al., 2011). The FN400 has also been reported for false alarms to words which were semantically similar to studied words (Curran, 2000; Nessler et al., 2001), as would be expected if the effect reflects an acontextual form of memory strength. The profound evidence that familiarity and recollection can be dissociated on the functional and neuronal dimension with ERP measures is complemented by reports showing that the FN400 and the parietal old/new effect can be doubly dissociated (Jäger et al., 2006; Stenberg et al., 2009; Woodruff et al., 2006). However, some fundamental issues related to this topic are still unsettled. More specifically, whereas recollection and its ERP correlate are well-described, there is more ambiguity regarding the electrophysiological characterization of familiarity.

For example, it has been proposed that the FN400 is functionally and electrophysiologically not distinct from the N400 (Voss and Federmeier, 2011), an ERP measure of semantic memory that can be observed in semantic priming studies (Kutas and Federmeier, 2000). A related controversy regarding the functional significance of the FN400 was initiated by the claim that the FN400 is indicative of enhanced implicit conceptual fluency and can be taken as an index of familiarity only under restricted circumstances, i.e. when conceptual implicit memory closely co-varies with familiarity (Paller et al., 2007). The initial view that the FN400 signifies the familiarity of a prior episode or elements of an episode has also been disputed by reports arguing that the FN400 rather reflects the attribution of fluency to prior experience (Lucas and Paller, 2013; Leynes et al., 2017).

In this article, we will first discuss studies that explore commonalities and differences between the N400 and the FN400 and we will argue that the FN400 as a measure of episodic familiarity is qualitatively distinct from the N400 and that it is crucial that adequate operational definitions for ERP contrasts are used when inferences on the functional significance of ERP effects are made from their scalp topography. In this section, we will also critically explore the conceptual implicit memory view of the FN400 and show that there is an increasing number of experimental effects that cannot be accounted for by a pure implicit conceptual priming account and by this challenge such a narrow conceptualization of the FN400. We will argue that familiarity and conceptual implicit priming in most cases cannot be fully dissociated because they rely on common fluency processes and that it is crucial to understand the factors that govern when fluency is experienced as familiarity. Second, studies will be reviewed that indicate that familiarity is multiply determined. In this subsection, we will argue that an important distinction has to be made between a relative familiarity mechanism indexed by the FN400 and the absolute (baseline) familiarity of events being reflected by a simultaneous but topographically distinct ERP effect. It will be shown that reports that compare judgments of lifetime familiarity with judgments of the frequency of recent experimental exposures support this distinction between two interrelated familiarity mechanisms. Third, we will introduce the unexpected fluency attribution account of familiarity according to which familiarity results from a fast and automatic assessment of surprising processing fluency. Fourth, a review of recent studies addressing the relationship between fluency and familiarity will explore the validity of the unexpected fluency attribution account. Fifth, top-down influences on the FN400 will be discussed, a point which is of high relevance under the assumption that familiarity results from an attributional process and which is often neglected when familiarity is considered to be an integral part of a memory representation. Finally, a comprehensive neurocognitive account of the FN400 and the processes it reflects will be introduced. It will be discussed that this account not only serves to solve controversies on what the FN400 reflects but also allows to identify the factors that give rise to the feeling of familiarity and govern the transition of fluency to familiarity. The boundary conditions under which fluency is attributed to familiarity will be identified and the neural underpinnings of fluency and familiarity signals will be outlined.

2. The FN400 can be functionally dissociated from the N400

The view that the FN400 is a neural correlate of familiarity was questioned by the claim that the FN400 cannot functionally and electrophysiologically be dissociated from the N400 (Voss and Federmeier, 2011). By this view, the FN400 old/new effect is produced by an attenuation of the N400, a negative going ERP component related to semantic processing (Kutas and Hillyard, 1980). It is a monophasic negativity that is present at around 400 ms with a maximum at centro-parietal recordings that systematically co-varies with the processing of semantic information. The N400 is elicited by a large range of linguistic and non-linguistic stimulus types (see Kutas and Federmeier, 2011, for a review). Evidence relevant for the claim that the FN400 and the N400 cannot be dissociated comes from a study that compared both components by combining a semantic priming manipulation with a continuous recognition memory task (Voss and Federmeier, 2011). In this study, test words were repeated once in a continuous recognition memory task and were occasionally primed by a semantically related word preceding the target word. Old/new effects were examined by contrasting unprimed words on their first and second presentation and semantic priming was operationalized as the ERP difference between primed target words and the preceding prime. As the N400 attenuation effect in the semantic priming contrast was topographically indistinguishable from the old/new effect in the memory contrast, the authors conclude that the FN400 is functionally identical with an attenuation of the N400 to old items and reflects enhanced conceptual fluency that typically occurs for repeated items in recognition tests that employ meaningful stimuli (Voss and Federmeier, 2011).

As we have argued previously (Bridger et al., 2012), there are at least two critical points in the design of the Voss and Federmeier (2011) study that may have compromised finding reliable ERP old/new effects and that raise doubts regarding the conclusion drawn by the authors. First, even though the old items in the old/new contrast were not primed when the memory contrast was assessed, these old items were primed at their initial presentation and this history of previous priming may have been present in the ERPs elicited by their second presentation. It is likely that this has obscured the old/new contrast (see Strózak et al., 2016a, for a similar problem of finding old/new effects for primed words). As a second problematic point, Voss and Federmeier (2011) used a double response procedure in which memory judgments followed pleasantness judgments. This unusual combination of semantic and episodic response requirements for one and the same test cue led to rather long inter stimulus intervals and may have eliminated any behavioral priming effects. Also, the additional semantic processing demands imposed by the pleasantness judgments may have obscured memory-related processes. A related argument has been put forward by Leynes and Addante (2016), who did not find any FN400 effects in a recognition memory study in which old/new decisions were combined with liking judgements. Finally, the high proportion of primed words could have additionally enhanced semantic processing, as for example the built-up of expectancies regarding prime-target relationships, and this may have further obscured finding ERP old/new effects. These lines of reasoning underscore the high relevance of controlling for confounding factors when exploring ERP responses related to episodic memory judgments. See also Voss and Paller (2009) who highlight the importance of controlling for guess responses when analyzing memory-related ERP effects as another example.

In an effort to overcome the limitations inherent in the design of the Voss and Federmeier (2011) study and to employ more common operational definitions of recognition memory and semantic priming, we conducted a study in which a semantic priming manipulation was embedded in the study phase of a standard recognition memory task (Bridger et al., 2012). To unconfound priming and recognition memory, old/new effects in the ensuing test phase were examined for words from the study phase which were not preceded by a semantic prime. Using this standard study-test paradigm with a semantic priming manipulation in the study phase and an exploration of old/new effects in the test phase, we were able to find a robust behavioral effect of semantic priming accompanied by a smaller N400 for semantically primed words than words preceded by unrelated primes. In addition, there was a robust old/new effect in the test phase with the expected frontal scalp topography in the FN400 time window (300–500 ms). Of note, as illustrated in Fig. 1, the scalp topography of the FN400 differed in anteriority from the central maximum distribution of the N400. These findings show that with a simple study-test paradigm in which episodic recognition is not confounded by semantic priming, the FN400 in the old/new contrast was functionally distinct from the N400 indexing semantic priming. This underscores the high relevance of using appropriate operational definitions when making inferences from topographic differences of ERP effects on distinct cognitive mechanisms (see Bader and Mecklinger, 2017, as an illustrative example).

Similar conclusions on the separability of the FN400 and the N400 were drawn by Strózak et al. (2016a). Combining a semantic priming manipulation with recognition memory judgments, the authors found no topographic differences between the FN400 in the old/new contrast and the N400 in the priming contrast when the priming manipulation was part of the test phase. In this situation, both effects showed a maximum at midline central electrodes. Notably, however, when priming was measured in the study phase as in the Bridger et al. (2012) study, the N400 still showed a midline central maximum but the recognition (FN400) effect to unrelated words in the test phase was additionally present at frontal recording sites as one would expect if the N400 and the FN400 are topographically distinct. Of note, Strózak et al. (2016a) also used a single response procedure with episodic memory judgments. This further underscores the high relevance of avoiding confounds between episodic and semantic processing when exploring commonalities and differences between the N400 and the FN400 and supports the view that both components show distinct topographic distributions when these confounds are avoided.

A number of contemporary ERP studies explored the interplay between processing fluency and recognition memory (to be reviewed in section 4) by means of a masked repetition priming manipulation (Woollams et al., 2008; Lucas et al., 2012; Li et al., 2017; Wang et al., 2015). Even though it is unclear which form of fluency was induced by the masked priming manipulation (perceptual or conceptual fluency or a combination of both), in all four reports the priming contrast did not modulate the FN400 but rather elicited an N400 effect with a posterior distribution. This effect was topographically distinct from the anterior FN400 effect (measured in a contrast between know-hits and misses), which provides further support for the view that the N400 and the FN400 and the processes they reflect can be functionally dissociated. Completing this pattern of results, another functional dissociation between the FN400 and the N400 was revealed in a study that directly contrasted semantic priming and recognition memory (Greve et al., 2007). In the test phase of an associative memory task, an FN400 with old word pairs exhibiting more positive-going waveforms than new word pairs was obtained only for word pairs that were preceded by a semantic prime. This effect was functionally and topographically dissociable from a central maximum N400, which was attenuated for old word pairs as compared to new pairs. In contrast to the FN400, this latter N400 effect was present in both conditions, i.e. with and without

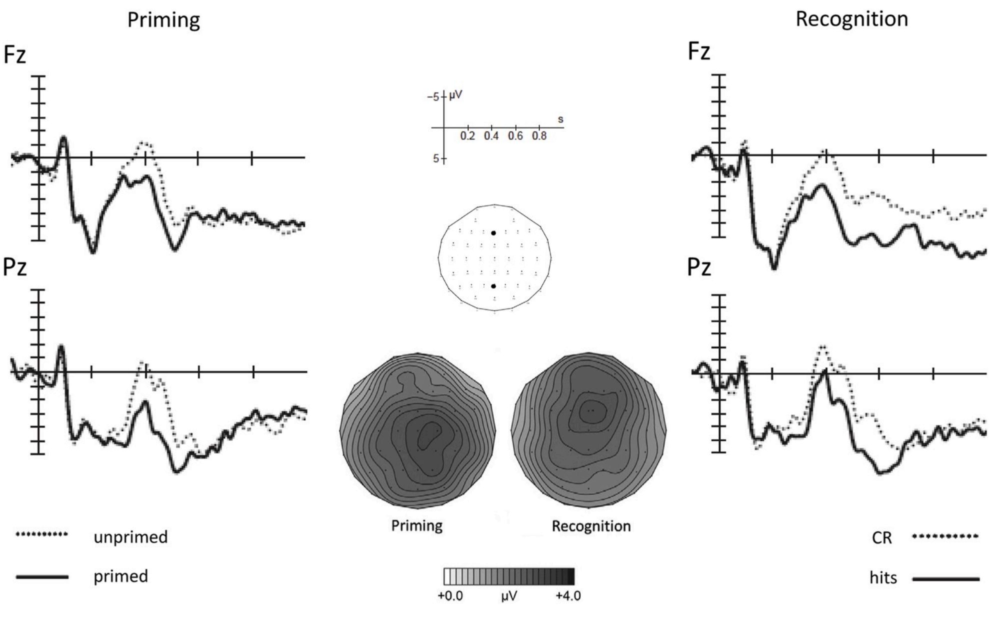

Fig. 1. ERP waveforms at a frontal and parietal recording site and topographic maps depicting the priming and old/new effects in the study and test phase in the Bridger et al. (2012) study. Left panel: The priming contrast (primed vs. unprimed words) revealed an N400 effect in the 300–500 ms time window with a centro-parietal maximum. Right panel: The recognition contrast (old vs. new words) showed an FN400 in the 300–500 ms time window with a frontal maximum. Reprinted with permission from Bridger et al. (2012).

semantic primes.

The claim that the FN400 cannot functionally be distinguished from the N400 brings to mind a series of prior reports in which it was argued that the FN400 rather than reflecting familiarity memory is a marker for implicit conceptual priming (Paller et al., 2007; Voss et al., 2009). In that debate, Paller, Voss and colleagues claimed that as most recognition memory studies use stimuli with inherent meaning such as words or pictures it cannot be excluded that conceptual information is implicitly reactivated together with explicit information when stimuli from a prior study phase are repeated in a laboratory setting. It is assumed that the FN400 is indicative of implicit conceptual priming and correlates with familiarity only when conceptual fluency co-varies with familiarity. Empirical support comes from studies showing that FN400 effects are elicited by recognition judgments for conceptually processed meaningful stimuli but not when recognition judgments are given for meaningless stimuli such as abstract visual patterns or nonsense words for which no conceptual priming occurs even though these items evoke a similar behavioral familiarity response (measured with know-responses) as meaningful stimuli (Voss and Paller, 2007; see also Voss et al., 2012, for a review). Therefore, the authors conclude that the FN400 is indicative of conceptual fluency and not familiarity. In further support of this view, pre-experimentally unfamiliar stimuli such as kaleidoscope stimuli only elicit an FN400 when they are subjectively perceived as meaningful (Voss et al., 2009).

It is arguable, however, whether this finding can be generalized to all studies using meaningless stimuli. Reliable FN400 effects were reported for nonsense visual figures (Groh-Bordin et al., 2006). Curran and Hancock (2007) showed that unfamiliar faces, which are recognized on the basis of familiarity alone elicit reliable FN400 effects and Speer and Curran (2007) found reliable FN400 effects for pairs of fractals when these stimuli were successfully recognized as an association. As we have outlined elsewhere (Bridger et al., 2012; Mecklinger et al., 2012), there are a number of observations of similar kind that cannot be accounted for with a pure conceptual priming account of the FN400. The FN400 has for example been shown to co-vary with the amount of perceptual overlap between study and test items (i.e., it was larger for perceptually identical than color-modified versions of the study items) even though conceptual processing should have remained the same for both classes of items (Groh-Bordin et al., 2006; Schloerscheidt and Rugg, 2004). The FN400 varies with task instructions, i.e. it was present in an explicit but not in an implicit memory task (Groh-Bordin et al., 2005), even though the amount of implicit conceptual priming should not vary as a function of task. Also, the FN400 was found to be influenced by top-down processing (Ecker and Zimmer, 2009; Rosburg et al., 2013), a finding which is difficult to reconcile with the view that the FN400 is indicative of implicit conceptual priming. In a similar vein, Stenberg et al. (2009) manipulated two stimulus dimensions, frequency and fame status of Swedish names, to dissociate familiarity and conceptual priming, respectively. There was a strong correlation between behavioral measures of familiarity (name frequency) and the FN400. No such correlation was obtained for behavioral measures of conceptual priming (fame status) and the FN400.

We will not reiterate the whole controversy regarding the conceptual implicit memory account of the FN400 here (for a detailed discussion see Curran and Hancock, 2007; Paller et al., 2007, and for a more recent debate Mecklinger et al., 2012; Paller et al., 2012). Even though this discussion is important as it shows that studies designed to test explicit memories often tap into implicit memory mechanisms (see Voss et al., 2012, for a review), we consider a pure implicit conceptual priming view as a too narrow conceptualization which cannot account for all FN400 findings without additional and not always valid assumptions. As will be outlined below, we consider implicit conceptual priming as one out of a multitude of mechanisms that can (but not necessarily have to) contribute to familiarity-based memory and give rise to an FN400 effect.

3. Familiarity is multiply determined and related to conceptual object knowledge

The view that familiarity is multiply determined was initially proposed by Mandler (1980). In his seminal paper he put forward the idea of two independent but interwoven familiarity mechanisms. His view was derived from the so-called word frequency mirror effect, the well-established finding that low frequency items elicit higher hit rates than high frequency ones whereas false alarms rates are higher for high frequency items (Glanzer and Bowles, 1976). Mandler (1980) proposed an explanation for this phenomenon according to which low frequency items receive a greater incremental change in memory strength due to their low pre-experimental baseline familiarity whereas high frequency items due to their high baseline familiarity are more prone to be erroneously classified as old. Their relatively small increment in memory strength is often not sufficient to discriminate recent from general occurrence. In other words, relative (incremental) familiarity is a mechanism that results from the repetition of an item in a particular experimental context and can be distinguished from baseline or pre-experimental familiarity (absolute familiarity).

In a recent study, we directly explored the interplay between two supposedly different familiarity mechanisms with different sensitivity to the general (absolute) and recent familiarity of events (Bridger et al., 2014). We used a recognition memory task with high and low frequency words because differences in word frequency can be regarded as a direct manipulation of absolute/baseline familiarity. We assumed that absolute familiarity should become manifest in the ERP contrast between high and low frequency words with no experimental history (unstudied words) whereas relative familiarity should be indexed by an early old/new effect that is larger for low than for high frequency words. The main results of the Bridger et al. (2014) study are depicted in Fig. 2.

Consistent with our assumptions, we found an FN400 effect which was larger for low than high frequency words (see Ye et al., 2019, for a similar effect with low frequency Chinese words and Curran, 1999, who found similar early frontal old/new effects for low frequency words and pronounceable pseudo words). In addition, a posteriorly distributed ERP difference between high and low frequency unstudied words was obtained in the same time interval (more positive ERPs for high frequency new words), presumably reflecting the higher semantic fluency (accessibility) of high than low frequency words (see Fig. 2). This suggests that absolute familiarity can be equated with conceptual fluency. In fact, the absolute familiarity effect in the Bridger et al. (2014) study is highly similar to the word frequency effect on the N400, i.e. a less pronounced N400 for high than low frequency words (Kutas and Federmeier, 2000; Van Petten and Kutas, 1990). Also, consistent with the idea that the level of pre-experimental absolute familiarity determines the relative increase in familiarity due to a recent presentation was the observation that the absolute familiarity effect preceded the mid-frontal effect by about 50 ms. The above-mentioned findings of the Bridger et al. (2014) study nicely resonate with the data from the Stenberg et al. (2009) study, which also reports a larger FN400 for rare (than frequent) Swedish names for which due to their low pre-experimental familiarity a larger increment in relative familiarity can be assumed.

The view that familiarity is multiply determined was additionally supported by a series of studies that showed that under some circumstances in recognition memory tasks old/new effects with a posterior topographic distribution can be observed in the FN400 (300–500 ms) time interval. Effects of this kind have been found in a series of recent studies in which we investigated unitization, an encoding strategy that allows to flexibly bind together components of an association to a single configuration in memory (Graf and Schacter, 1989; Parks and Yonelinas, 2015). Prior studies provided ERP evidence that unitization encoding increases the contribution of familiarity-based remembering to item (Ecker et al., 2007a) and source recognition (Diana et al., 2011). We set out to explore whether unitization encoding does also support associative recognition. In this study (Bader et al., 2010), two words (*smoke* –

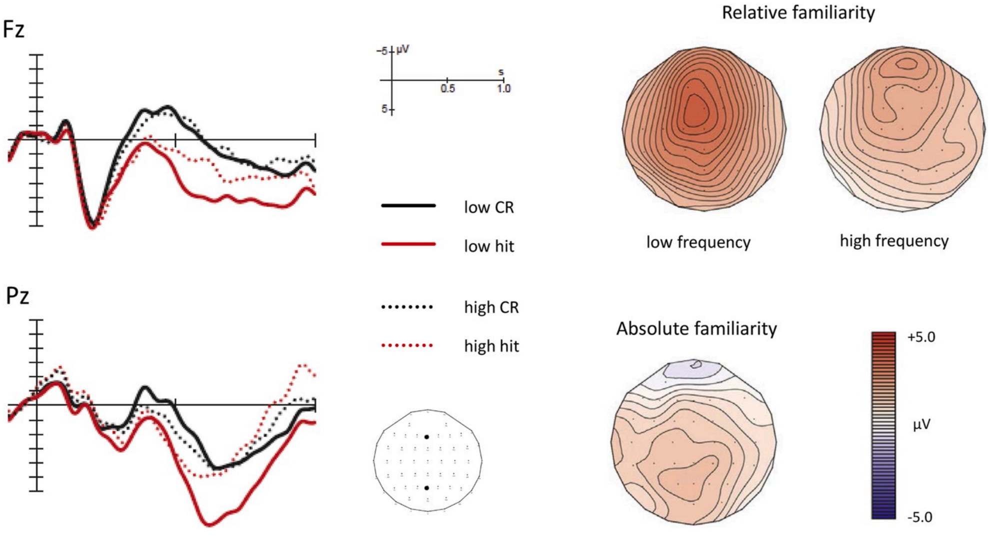

Fig. 2. Left panel: ERP waveforms at a frontal and parietal recording site depicting correct rejections and hits for low and high frequency words in the test phase of the Bridger et al. (2014) study. Right panel: Topographic maps show that the relative familiarity contrast (hits vs. correct rejections) in the 350–550 ms time window has a frontal maximum (FN400) and is more pronounced for low than high frequency words and that the absolute familiarity contrast (high vs. low correct rejections) in the 300–600 ms time window has a parietal maximum (N400). Reprinted with permission from Bridger et al. (2014).

apple) were presented together with a fictional definition that allows to create a new semantic entry for the fused items (*A fruit ripening above flames*). Correct recognition of these unitized pairs was associated with an early posterior positivity. In light of its high resemblance with the N400 this early posterior positivity will be referred to as an N400 in the following.[1] The posterior topographic distribution of the old/new effect was assumed to arise from the enhanced semantic (conceptual) fluency of the unitized word pairs relative to new and non-unitized pairs. We assumed that this N400 effect signifies the use of an absolute familiarity mechanism, which is presumably highly diagnostic for items which are presented for the first time in a laboratory setting in which all items are novel during learning. This mechanism is distinct from the relative familiarity mechanism, reflected in the FN400 and usually explored in standard recognition memory tasks that signifies the change of familiarity strength when a pre-experimentally familiar item was repeated in an experimental context.

The view that pre-experimentally unfamiliar items give rise to a unique absolute familiarity signal was corroborated in a second study in which the N400 effect was replicated and dissociated from the FN400 effect with its typical anterior distribution within the same test phase of a recognition memory study (Wiegand et al., 2010). As expected, unitized word pairs elicited an N400 in the 300–500 ms time interval. Notably, we also presented word pairs in reversed order as test cues (*apple – smoke*) assuming that with an unspecific cue of this kind, unitized presentations could not be assessed whereas familiarity of the single words should be preserved and give rise to the standard FN400 effect. Confirming our predictions, the reversed order test cues elicited an FN400 with its typical anterior distribution (Wiegand et al., 2010).

In a similar vein, MacKenzie and Donaldson (2007) reported an early, posteriorly distributed old/new effect for faces of unknown individuals which were correctly identified without recollection of study details. Consistent with the view forwarded here, the authors assume that it is the low level of pre-experimental familiarity that makes the repetition of these previously unknown faces within the experiment highly diagnostic and that this is indicated by a distinct familiarity mechanism with a unique electrophysiological signature.

In another study investigating memory for events with low pre-experimental familiarity, Voss et al. (2009) explored recognition memory for extremely uncommon English words (e.g., *cafard, epopt, romage*) which were sorted on the basis of participants' ratings in categories of high and low meaningfulness. ERPs to high meaningful (uncommon) words for which a know-response was given elicited a positive-going ERP response relative to correct rejections, which in its timing characteristics and its broad topographic distribution resembled the N400. This effect was absent for low meaningful events. Even though identified as an FN400 by the authors, the absence of an anteriority by condition interaction for this effect in the statistical analysis and its high similarity with the N400 supports the view that the repetition of uncommon meaningful events gives rise to a unique familiarity mechanism, reflected by an early and posteriorly distributed old/new effect, resembling the N400. It is conceivable that for stimuli which are extremely infrequent, first exposures contribute strongly to the accumulation of absolute familiarity (see Reder et al., 2007, for a similar argument), so that changes in absolute familiarity induced by a single presentation are large enough to be diagnostic for recognition memory decisions.

Lucas and Paller (2013) explored whether familiarity can also be driven by perceptual fluency sources. They used a letter segregation technique by which old words and lures are drawn from entirely separate letter pools. Hence, fluency was highly salient in this task because old and new items could be easily discriminated on the basis of letter and word level information. Interestingly, a posteriorly distributed old/new effect, resembling the N400, was obtained in the FN400 interval. In a second experiment, in which letter fluency alone did not suffice to discriminate old from lure words because old items and lures were drawn from overlapping letter pools and incremental differences in memory strength (relative familiarity) had to be assessed, an FN400 effect was obtained. This pattern of results suggests that the high perceptual fluency of studied items in the segregated condition provides an effective means to distinguish them from unstudied items and this may have bypassed the assessment of their relative familiarity.

Taken together, these findings indicate that changes in absolute familiarity as reflected in the N400 are diagnostic for recognition decisions under special circumstances. An absolute familiarity mechanism of this kind is highly useful particularly in situations in which all stimuli are novel and/or when the increase in fluency induced by an experimental encounter is highly salient and diagnostic for their prior occurrence.

The concept of absolute familiarity as introduced here bears similarities with conceptual knowledge or familiarity with respect to the lifetime of experiences. This involves the number of previous lifetime

[1] With labeling the early posterior positivity as N400 we do not intent to give a new account for the N400, a component which has been found in a large variety of language studies. With this label we rather want to take into account one important functional characteristic of the N400, namely its sensitivity to conceptual semantic processing in the language and memory domain. As for the FN400 and unless specified otherwise, with "N400" or "N400 effect" we will refer to the attenuation of the N400 in a given experimental condition.

encounters with an event or the experience a person has with an event. Bearing this resemblance in mind, the labels absolute and lifetime familiarity will be used interchangeable in the remaining sections. Studies that explore judgments of lifetime familiarity provide additional though indirect evidence for the multiply determined account of familiarity. Studies on lifetime familiarity probe recognition memory by asking participants to discriminate between stimuli with high and low pre-experimental familiarity. Hence, these tasks do not entail explicit memory judgments with respect to the prior experimental occurrence of a stimulus. In one of these studies, Leynes et al. (2017) contrasted ERPs to pictures of pre-experimentally familiar products (so-called name-brand products) with pictures of products which were novel to the participants (so-called off-brand products). The stimuli were only presented once and the participants performed a product classification task and – comparable to the absolute familiarity contrast in the Bridger et al. (2014) study - ERP differences between name-brand and off-brand products should reflect differences in absolute familiarity. There was an early (350–550 ms) positivity for name-brand relative to off-brand products with a broad topographic distribution along the anterior-posterior axis. With its broad topographic distribution, the positivity to name-brand relative to off-brand products shows high resemblance with the absolute familiarity effect in the Bridger et al. (2014) study. Notably, however, a re-analysis revealed that its topographic distribution did not differ statistically in anteriority from the FN400 to name brand products in the test phase, which is probably due to the relatively small electrode configuration of 29 electrodes (P. Andrew Leynes, personal communication).

In a similar manner, in a recent study from our own lab, in which we explored heuristic decision making and contrasted ERPs for well-known and little-known city names with no experimental history, we observed a similarly broadly distributed early positive difference between well-known and little known city names (Rosburg et al., 2011), which may index the higher absolute familiarity for well-known city names.[2] Even though these two aforementioned studies were not designed to directly test whether absolute and relative familiarity can electrophysiologically be dissociated, they showed ERP modulations with a stronger resemblance to the N400 than the FN400. Thereby, they provide at least indirect support for the view that both forms of familiarity can be dissociated and that the N400 effect co-varies with absolute/lifetime familiarity.

A recent ERP study directly contrasted ERP measures during frequency judgments for recent laboratory exposures with judgments of lifetime familiarity for object concepts (Yang et al., 2019). Both judgments are similar because they require an assessment of prior occurrence of events without recovering contextual details. However, judgments of lifetime familiarity depend on the perceived absolute familiarity of the objects whereas judging the number of recent experimental exposures requires an assessment of an object's relative familiarity. Verbal labels for object concepts with different levels of lifetime familiarity drawn from a normative database of object concepts were used as stimulus materials (Cree and McRae, 2003). Supporting the view that judgements of lifetime exposures depend on the assessment of absolute familiarity, an N400-like effect was obtained for this kind of judgment, whereas an effect with the same direction (frequent > infrequent) albeit with a more anterior scalp distribution (reminiscent of the FN400 but not as frontally distributed) was revealed for the frequency judgments.

As an additional dissociation, the FN400 effect for frequency judgments was decision-specific, i.e. it was only obtained when the degree of prior exposures was relevant for the decision to be given (frequency judgments) whereas the posterior N400 effect for lifetime familiarity was obtained irrespective of the decisions to be given. Even though the frequency judgments task in this study was different from the standard old/new recognition memory judgments usually employed to probe recognition memory, this study adds to the converging evidence for the view that relative and absolute familiarity can electrophysiologically be dissociated.

A recent brain imaging study that used the same procedure of directly contrasting frequency judgments with judgements of lifetime familiarity revealed important insights in the brain systems mediating both types of judgments (Duke et al., 2017). Consistent with brain imaging studies that showed that the perirhinal cortex (PrC) is involved in the processing of object concepts even in tasks that do not entail explicit memory judgments (Clarke and Tyler, 2014; Dew and Cabeza, 2013; Heusser et al., 2013; Wang et al., 2010), the PrC together with other brain regions showed a linear increase with lifetime (absolute) familiarity. Interestingly, however, the PrC was the only region that additionally showed a decreased response with increased relative familiarity (frequency judgments), a finding that has been reported in a variety of brain imaging studies (Daselaar et al., 2006; see Diana et al., 2007, for a review). As acknowledged by the authors, as the PrC is not only involved in memory retrieval but also in the formation of new episodic memories for objects, a contribution of episodic encoding to the increasing PrC response as a function of lifetime (absolute) familiarity cannot be ruled out. In support of this view, the authors found a high positive correlation between self-reported lifetime familiarity and object knowledge for specific object concepts in a behavioral follow-up study. Thus, it is possible that increased demands on episodic encoding associated with higher amounts of semantic feature knowledge led to the increased PrC response rather than the higher levels of lifetime familiarity per se.

There is also evidence from animal research showing that neurons in the anterior inferior temporal cortex, including the PrC, differ in their sensitivity to recent and lifetime familiarity in recognition tasks (Xiang and Brown, 1998). Some neurons show a reduced firing pattern to stimuli that have been seen recently (relative familiarity) whereas other neurons show a selective firing pattern to stimuli with a high absolute/lifetime familiarity (i.e. stimulus with frequent encounters on previous days). Notably, the latter neurons are not sensitive to stimuli that have been seen recently. These findings from animal studies together with the aforementioned results that the PrC supports the assessment of both, the absolute familiarity of objects with an increase in signal strength and their relative familiarity in an experimental context with a decrease in signal strength, corroborate the view that both familiarity mechanisms are functionally dissociable.

The PrC's important role in representing an object's familiarity acquired over the lifetime and familiarity with respect to recent experimental encounters receives additional support from a recent neuropsychological study that showed that a patient with a selective perirhinal lesion (NB), who was selectively impaired in making (relative) familiarity-based memory judgments (Bowles et al., 2007), was also impaired in the assessment of lifetime familiarity. Notably, this deficiency was sensitive to concept structure as it was only observed for objects with high amount of feature overlap as determined by an independent feature production task (Bowles et al., 2016). This is consistent with the view that the PrC hosts highly integrated object representations (e.g., Bussey et al., 2005) allowing for fine-grained discriminations between object concepts in semantic memory as required for judgments of lifetime familiarity. The findings from both aforementioned studies suggest that the discrimination between recently exposed and

[2] Of note, Schwikert & Curran (2014) also used a city-size comparison task to explore ERP correlates of heuristic decision making. As in the Rosburg et al. (2011) study, they found an early positive difference between well-known and little-known cities which, however, showed a more frontal and FN400 like topography than the corresponding effect in the Rosburg et al. (2011) study. We assume that these different topographies result from the unlike sorting procedures for the ERP trials in both studies. While Rosburg and colleagues contrasted ERP activity for a priori well-known and little-known cites, Schwikert and Curran used the participants' responses from a recognition test to contrast recognized and non-recognized cities. This latter sorting procedure may have enhanced the contribution of episodic (relative) familiarity to heuristic decisions which is accompanied by an FN400.

not-exposed items (required for successful relative familiarity assessments) also presupposes highly integrated object representations in the PrC, which dovetails with the notion that absolute/lifetime familiarity and relative familiarity are intertwined.

Another recent brain imaging (fMRI) study that set out to explore the neural underpinnings of preexisting (absolute) and episodic (relative) familiarity revealed a mixed pattern of results (Gimbel et al., 2017). While relative familiarity operationalized as know-responses for re-exposed unfamiliar faces in a recognition memory task led to increased (rather than decreased) activation in the PrC, absolute familiarity, measured by know-responses for single exposures of famous faces, gave rise to increased activation in the parahippocampal cortex. These inconsistencies with the aforementioned study by Duke and colleagues may in part be due to differences in the stimulus materials. As argued before, in situations in which all stimuli to be learned are novel, as it was the case with the unfamiliar faces employed by Gimbel and colleagues, an absolute familiarity mechanism would be sufficiently diagnostic to differentiate the high recent familiarity of the re-exposed unfamiliar faces from the low familiarity of the other, not repeated faces. Hence, the increased PrC activity for re-exposed unfamiliar faces could reflect modulations of absolute familiarity rather than signifying relative familiarity. With this additional assumption, the PrC effects in the Gimbel et al. (2017) study could be reconciled with those from Duke et al. (2017), who also report increases in PrC activation with increasing absolute lifetime familiarity of object concepts. In any event, the results of the Gimbel et al. (2017) study again emphasize that special care has to be taken in order to find appropriate operational definitions for relative and absolute familiarity and to avoid confounding variables when interpreting the functional characteristics of brain activation patterns.

Taken together, empirical evidence from electrophysiological, neuroimaging and neuropsychological studies suggests that different and intertwined mechanisms exist for the judgment of recent exposures (relative familiarity) and the judgment of familiarity cumulated during lifetime (absolute familiarity). PrC activation increases with increases in lifetime familiarity of object concepts and decreases with increases in (relative) familiarity (Duke et al., 2017). Thus, both computational mechanisms rely on the PrC but in opposite directions. Also, judgments of lifetime familiarity and of recent exposures of object concepts give rise to dissociable ERP effects reminiscent of the N400 and the FN400, respectively (Yang et al., 2019). Together, these findings suggest that the processes required for the distinction between specific episodic object encounters (as required for remembering based on relative familiarity) and the identification of object concepts with highly integrated semantic features are functionally dissociable but have a close relationship.

Both mechanisms may be part of a recently proposed large-scale cognitive system centered in the PrC (Ranganath and Ritchey, 2012). This system is relevant for processing and representing specific classes of entities and which enables an ensemble of object-related processing functions such as familiarity-based remembering or the representation of semantic and salience knowledge acquired over the lifetime.

The exact nature of the relationship between object-related processing and episodic, familiarity-based processing and the roles of the PrC in representing both, conceptual and episodic information still have to be disclosed. An important direction for further research in this domain is to explore the temporal and neural dynamics of assessing different familiarity signals, i.e. those arising from recent exposures in laboratory settings and those underlying the assessment of object knowledge acquired during multiple encounters throughout the lifetime.

4. The unexpected fluency attribution account of familiarity

In most neuroimaging studies familiarity is characterized in an exclusive manner according to which any memory response that is not accompanied by recollection is ascribed to familiarity. This procedure of defining familiarity mainly in opposition to recollection, however, bears the risk of oversimplifying the situation by identifying any form of fluent processing that co-occurs with familiarity in some situations but not in others as a familiarity experience. This issue is also related to the broader question of how familiarity and processing fluency as an impression of implicit memory are related and why processing fluency does contribute to familiarity under some circumstances but can give rise to priming in other contexts. In other words, theoretical models and empirical procedures are required that draw a sharp distinction between fluency and familiarity and that can account for fluency influences on memory judgments. One such model is the fluency attribution account initially proposed by Jacoby and colleagues (Jacoby and Dallas, 1981; Jacoby et al., 1989). According to this model, fluency signals, which normally give rise to facilitated processing (priming), under some circumstances can be attributed to the past and drive recognition memory judgments. The concept of attribution is regarded as a rapid and unconscious inference based on enhanced fluency that gives rise to the feeling that the processing fluency results from a prior encounter with an event (Mayes et al., 1997).

Empirical evidence comes from a seminal study by Jacoby and Whitehouse (1989), who combined a recognition memory task for single words with a masked priming procedure. Each test word was preceded by a masked prime that was unidentifiable for the participants. The prime was either identical to the following word (masked priming condition) or a different word. Interestingly, even though the prime could not be identified, the probability of an old-response (hit and false alarm) was higher for primed than unprimed words suggesting that enhanced fluency that results from the priming procedure can guide recognition memory decisions. Further studies using variants of this masked priming paradigm revealed that the fluency manipulation mainly affects familiarity memory (Miller et al., 2008; Woollams et al., 2008; but see Kurilla and Westerman, 2008, or Taylor and Henson, 2012, and Gomes et al., 2017, for fluency effects on recollection). These findings support the fluency-attribution account of familiarity (Jacoby et al., 1989) according to which familiarity stems from an attribution of fluency to the past.

Notably, in a more recent conception of the fluency attribution account, the Discrepancy Attribution Hypothesis proposed by Whittlesea and Williams (2001a & 2001b), the feeling of familiarity is not inevitably based on fluency. Rather, the extent to which fluency is attributed to familiarity depends not on fluency per se but on the difference between actual fluency and the fluency that could be expected for a given item in a given situation. The Discrepancy Attribution Hypothesis assumes that in making recognition decisions people implicitly set up expectancies or norms against which they could compare the actual fluency of an item. Importantly, these norms do not only depend on the class of items which are used in a memory test (e.g. unfamiliar faces, meaningless stimuli or high and low frequency words) or the type of encoding. These norms can also develop during the remembering context and by this can take into account the characteristics of this context. Whittlesea and Williams (1998) have called this “norms on the fly”. In their seminal study, participants studied regular words, orthographically regular (pronounceable) and irregular nonwords. During a lexical decision and a pronunciation task pronounceable non-words were processed faster than irregular non-words, but slower than words. However, in a recognition test, in which old and new words of each type were presented, participants produced significantly more false alarms for the pronounceable nonwords (the so-called HENSION items) than for the irregular nonwords and words. The authors interpret this effect in terms of a violation of expectancies regarding the fluency of nonwords (“this was surprisingly easy for a nonword”) that has produced a perception of a discrepancy between fluency and meaninglessness, that was attributed to an erroneous feeling of familiarity (Whittlesea and Williams, 1998; see also Whittlesea and Williams, 2001b, for a discussion).

The idea that norms set up the basis for the experience of surprise and that these norms can be refined during a memory test (i.e. computed on the fly) was also confirmed by a recent study showing that the number of fluency-based memory illusions in a masked priming recognition memory study was inversely related to the proportion of primed stimuli, i.e. the memory illusion was much stronger when the surrounding stimuli were less fluent (Westerman, 2008). Thus, fluency is assessed relative to norms that are either set up a priori or which are formed during the memory test. When fluency is unexpected on the basis of these norms and people experience an unexpected discrepancy between their actual performance and how they expect to perform, this surprising divergence is attributed to the past and experienced as familiarity. Importantly, perceptions of surprising processing are not inevitably attributed to the past but can also be ascribed to other sources in the present, such as aesthetic preferences (e.g. the mere exposure effect, Jacoby, 1984), duration (Witherspoon and Allan, 1985) or other perceptual experiences.[3]

5. ERP evidence for fluency attribution in priming studies

A number of ERP studies were designed to explore the fluency attribution account of familiarity. A study by Woollams and colleagues (Woollams et al., 2008) was one of the first that combined the Jacoby & Whitehouse masked priming recognition memory paradigm with ERP recordings. Masked priming was associated with enhanced know-responses as a behavioral index of familiarity. As illustrated in Fig. 3, an FN400 effect (denoting relative familiarity) was apparent in a contrast between correct know-responses and misses. Interestingly, masked priming, as revealed by a primed vs. unprimed contrast did not yield an FN400 but was signified by an enhanced P200 between 150 and 250 ms followed by an N400 attenuation (see Nessler et al., 2005, for a similarly early and posterior effect of perceptual priming with face stimuli). In addition, a long-lasting priming effect operationalized as the contrast between misses and correct rejections was obtained in the time interval of the FN400 albeit with a posterior-positive topography.

Although these results are interesting in that they provide additional evidence that the FN400 as a measure of relative familiarity can topographically be dissociated from an ERP measure of processing fluency, a potential caveat of the Woollams et al. (2008) study and also some other ERP studies employing masked priming paradigms is the use of the know-response vs. miss contrast to identify relative familiarity and the FN400. Miss responses may reflect some level of implicit memory below the participant's decision criterion with a unique ERP signature (Rugg et al., 1998) and this may have blurred the FN400. Nevertheless, the study revealed different ERP effects for relative familiarity (as defined in the know-response vs. miss contrast) and fluency as induced by the masked primed vs. unprimed contrast. The familiarity effect showed a frontal distribution as would be expected for the ERP index of relative familiarity whereas the fluency effect resembled in its posterior distribution the N400, the ERP measure of absolute familiarity. Although behavioral measures suggest an attribution of fluency to familiarity (increased know-responses after priming), masked priming did not modulate the FN400. Moreover, the priming effects in the P200 and FN400 time interval were present for remember-responses, know-responses and correct rejections and therefore did not interact with behavioral measures of recognition memory. They presumably reflect facilitated processing induced by masked priming at different processing stages. Thus, the Woollams et al. (2008) study did not reveal an electrophysiological marker of fluency attribution.

To further explore the relationship between masked priming and familiarity, Lucas et al. (2012) employed a modified version of the recognition memory task used by Woollams et al. (2008) and investigated not only how fluency by masked priming affects studied words but also how fluency affects the processing of unstudied words and whether fluency can bias new words to be endorsed as old. The main results of the aforementioned study were replicated: An FN400 was found only for the (relative) familiarity contrast (know-responses vs. misses) and the ERP correlates of masked priming (the P200 and the N400) did not interact with behavioral measures of recognition memory. An intriguing new finding, however, was that an N400 effect was also obtained for primed new words endorsed as old (false alarms) relative to correct rejections. Under the assumption that the FN400 reflects the attribution of fluency to oldness, it is unclear why false alarms did not elicit an FN400 but gave rise to an N400 attenuation effect instead. It is conceivable that changes in absolute familiarity were mistakenly taken as evidence for prior occurrence and that this led to elevated false alarms and the N400 effect. The elevated false alarm rates for high frequency words (with high absolute familiarity scores) in studies on the word frequency mirror effect (Bader et al., 2014; Coane et al., 2011) would be consistent with this view.

The authors also consider the possibility that the anteriority of the effect indicated by the know-response vs. miss contrast might be explained by the effects of imagery as an encoding strategy (Lucas et al., 2012). Thus, the frontal effect for know-hits relative to misses may reflect the enhanced imagining-related processing of these events in contrast to unstudied items (i.e. primed new words). This view is based on the observation that concrete words or pictures as well as imagery instructions give rise to anteriorly distributed N400 effects (Ganis et al., 1996; Holcomb et al., 1999; West and Holcomb, 2000). However, the fact that FN400 effects have been reported for a large number of intentional and incidental encoding tasks with meaningful and meaningless stimuli (see Rugg and Curran, 2007, for a review) renders the view that the FN400 is an artefact of concreteness rather unlikely. Strong evidence against the concreteness view of the FN400 are findings by Strózak et al. (2016b), who recently showed that the topographic distributions of the FN400 effect elicited by abstract and concrete nouns do not differ in anteriority.

A similar dissociation between the ERP correlates of conceptual fluency and relative familiarity was reported by Wang et al. (2015), who combined masked priming for meaningful and non-meaningful pictographic Chinese characters with a recognition memory test. As in the aforementioned studies, fluency from masked priming gave rise to a broadly distributed positivity which was topographically different from FN400 effects in the same (300–500 ms) time interval. In contrast to Lucas et al. (2012), however, an FN400 effect rather than an N400 effect was observed when fluency (from masked priming) was erroneously attributed to oldness (as revealed by a false alarm vs. new contrast for primed high meaningful characters) implicating that in this study the FN400 was associated with the attribution of fluency to familiarity. An FN400 was also found in the contrast between high meaningful and low meaningful hits. This may suggest that the FN400 covaries with differences in conceptual fluency. However, the operational definition of conceptual fluency in this study is problematic as two different sets of words are contrasted. Thus, the high vs. low meaningful FN400 effect could also signify a larger increment in familiarity for high than low

[3] Of note, the Discrepancy Attribution Hypothesis (DAH) and the unexpected fluency account of familiarity proposed here (which is based on the DAH) have commonalities and differences with other models of recognition memory. For example, dual process models based on signal detection theory (SDT) assume that fluency is equivalent to the strength of evidence (memory strength) and that people set a response criterion on the basis of a top down inferential process which is in principle similar to the aforementioned attributional process. However, while SDT-based conceptions of recognition memory claim that items in a memory test situation differ only on the strength of evidence dimension, discrepancy attribution accounts assume that people base their memory decision not only on memory strength but take more stimulus characteristics and properties of the processing context into account that determine expectations and the assessment of fluency (see Whittlesea and Williams, 2001b). We do not think that other accounts such as the SDT account are invalid, we rather consider the unexpected fluency account as a more valid conception of familiarity in particular in complex situations in which stimulus-class-specific expectations exist or develop during the testing situation.

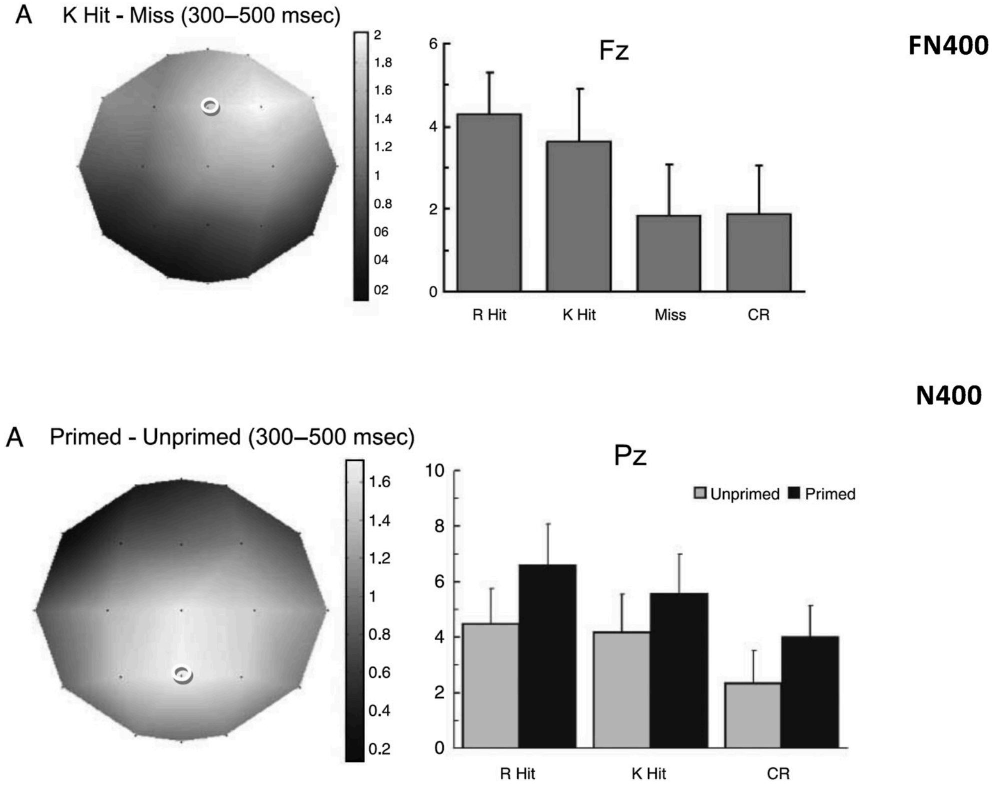

Fig. 3. Topographic distribution and mean amplitudes (+standard error) of the FN400 (upper panel) and the masked priming effects (lower panel) in the 300–500 ms time interval in the Woollams et al. (2008) study. The FN400 in the know-hit vs misses contrast shows a frontal distribution whereas the masked priming effect takes the form of an N400 difference between primed and unprimed words. The scales are in microvolt. Reprinted with permission from Woollams et al. (2008).

meaningful items.

A follow-up study by Wang and colleagues, which explored the separate contributions of conceptual and perceptual fluency on recognition memory and ERP measures, partly confirmed these findings: Conceptual fluency selectively enhanced remember-responses and know-false alarms and, as in the aforementioned studies, conceptual fluency was associated with an N400 effect (Wang et al., 2019). Unfortunately, no ERP contrasts between old and new items were conducted and no inferences can be made on the FN400 and its sensitivity to familiarity attributions.

To sum up, consistent with the unexpected fluency attribution account of familiarity, we take the frontal FN400 effect in the know-hits vs. misses contrast consistently found in studies combining masked priming with recognition memory to reflect the surprising discrepancy between expected and actual fluency that is attributed to a prior exposure and drives mnemonic judgments. In line with this, Wang et al. (2015) found an FN400 to primed new items erroneously endorsed as old. However, in the Lucas et al. (2012) study, false alarms were associated with an N400 effect suggesting that various processes might lead to misattributions of fluency and that the boundary conditions for each of them still need to be determined (see section 7 for a discussion of this issue).

Other ERP studies explored the interplay between familiarity and processing fluency by means of other fluency manipulations and task materials. These studies add to the increasing evidence that both processing aspects can be functionally and electrophysiologically dissociated and also provide (at least indirect) support for the unexpected fluency attribution account. Using Chinese characters as stimulus materials, Li et al. (2017) contrasted the effects of masked repetition priming and conceptual priming on recognition memory. Repetition priming increased behavioral measures of familiarity (false alarms given with a know-response) and conceptual priming increased correct remember-responses. Replicating earlier findings with this paradigm, the FN400 was present in the contrast between know-responses and misses and ERP effects of repetition priming were present in the P200 and N400 time intervals. Again, conceptual priming gave rise to an N400 attenuation effect in the same (300–500 ms) time interval and did not modulate the FN400. Notably, the N400 difference between primed and unprimed characters was larger for hits than for correct rejections suggesting that fluency due to oldness and fluency due to priming do not operate independently.

In an ERP study combining semantic priming with recognition memory, Wolk et al. (2004) explored recognition memory for single words that were either primed or unprimed by a preceding sentence. Priming increased old responses and a semantic priming effect, i.e. a smaller N400 for primed than unprimed words, was obtained between 300 and 500 ms for old and new words. Surprisingly, this N400 effect was smaller for old words and no old/new effects were obtained in the N400 time interval. Old/new differences were only present in a late time window, beyond 800 ms, where new responses elicited more positive going slow wave activity (see Kurilla and Gonsalves, 2012, for a similar effect). As this slow wave was negatively correlated with a behavioral measure of processing fluency, it is interpreted to reflect the processing consequences of an erroneous fluency attribution. As we have argued elsewhere (Bader and Mecklinger, 2017), this interpretation is problematic because in light of the robust effect of priming on old responses which was obtained in this study, an ERP measure of familiarity and/or its processing consequences should be present well before responses were made.

Semantic priming was also used as fluency manipulation in a recent study by Strózak et al. (2016a). ERP differences between primed and unprimed old words and between old and new (primed) words were found between 300 and 500 ms. However, these two effects showed a highly similar central maximum and did not differ topographically from each other as one would expect if both effects differ qualitatively. As acknowledged by the authors, their old/new analysis was problematic as it was confined to primed items and by this potentially confounded because hits in the related condition may have reflected contribution from both, conceptual fluency and familiarity. Thus, no firm conclusions can be drawn from the absence of a topographic difference between the priming and the recognition old/new effect.

In light of the difficulties of directly comparing ERP old/new and priming effects when both effects are embedded in a recognition test, in a recent ERP study we developed and used a new approach to disentangle relative familiarity and conceptual fluency. We manipulated conceptual priming (words were preceded by a semantically related or unrelated auditory prime word) and episodic familiarity (hits vs correct rejections) orthogonally in an incidental recognition memory test. Our approach was to contrast conceptual priming with a conceptual priming plus familiarity contrast (Bader and Mecklinger, 2017). The logic behind this analysis strategy was that if conceptual priming and episodic familiarity can be dissociated electrophysiologically, the priming contrast for correct rejections (CR related – CRs unrelated) and the priming plus familiarity contrast (hits in the related condition – CRs in the unrelated condition) should differ qualitatively. Importantly, the priming contrast was confined to correct rejections to avoid any confounds between priming and episodic familiarity, which by definition is absent for correct rejections. As conceptual priming similarly contributes to both contrasts, any differences between the contrasts can be unambiguously attributed to episodic familiarity. Given that conceptual fluency is indexed by a posterior N400 and relative familiarity resulting from an attribution of fluency to the past by an FN400, we expected the combined contrast to display a significantly more frontal scalp topography than the priming contrast. The results of the Bader and Mecklinger (2017) study are depicted in Fig. 4.

Our predictions were confirmed. First, supporting the view that fluency can be attributed to oldness when perceived fluency and expected fluency differ (Leynes et al., 2017), we found higher proportions of old responses for primed than unprimed words. Second, while the priming contrast for correct rejections displayed a posterior scalp topography, resembling the N400 effect, the combined contrast (priming plus familiarity) was characterized by an additional frontal focus, as would be expected if relative familiarity only contributed to the combined but not to the priming contrast. Interestingly and also illustrated in Fig. 4, not only the combined (priming and familiarity) contrast but also the priming contrast for hits (i.e. hits related – hits unrelated) had a more anterior distribution than the pure priming contrast for correct rejections. This implicates that in case of old responses, fluency induced by priming enhanced relative familiarity (more positive-going amplitudes for hits in the related than in the unrelated condition at frontal sites) which was not the case for correct rejections. Thus, these findings confirm the view that conceptual fluency and relative familiarity are associated with different electrophysiological signatures between 300 and 500 ms after a retrieval cue and do also interact in form of a fluency attribution to familiarity which is reflected in a stronger FN400 attenuation for primed hits than correct rejections.

Notably, in contrast to the aforementioned study by Strózak and colleagues (Strózak et al., 2016a), our study shows that conceptual fluency and episodic familiarity can be dissociated when both factors are manipulated in the same test phase. The differences between both studies can be reconciled by the observation that in addition to differences in data analysis (i.e. restricting the priming contrast to memory-free correct rejection responses), our test phase design included mere old/new judgments as compared to combined valence and old/new judgments in the Strózak et al. study. This may have promoted the impact of memory processing over conceptual processing on the test phase ERPs.

Taken together, in this section, we review studies that combine priming manipulations with recognition memory tasks in order to explore how different forms of fluency interact and translate in feelings of familiarity. Behavioral measures in studies combining masked priming with memory decisions revealed that when perceived fluency differs from the fluency in the present task context, this surprising fluency experience resulting from a mixture of study-induced fluency and priming induced fluency is attributed to familiarity. There is also evidence that fluency attribution to familiarity gives rise to the FN400 (Bader and Mecklinger, 2017; Wang et al., 2015) which can be dissociated from fluency signals that did not lead to familiarity attributions and revealed an N400 effect instead.

6. Familiarity memory is context dependent and modulated by top down processing

Models on episodic recognition memory generally assume that the retrieval of episodic information is the progression from a retrieval cue to a target memory. Global matching models, for example, presume that test cues are not used to retrieve particular items from memory but access memory in a broader sense by activating multiple features of a memory trace (Clark & Gronlund, 1996). Memory retrieval in accordance with current goals or task demands therefore presupposes an ensemble of memory control processes which can occur prior to or during the access of the memory trace that allow to prioritize task-relevant over irrelevant memory contents (Rugg and Wilding, 2000; Mecklinger, 2010). Similarly, the fluency attribution account outlined above entails the assumption that memory signals which are triggered by a retrieval cue are continuously monitored and updated by top down control processes and if a discrepancy is encountered between actual

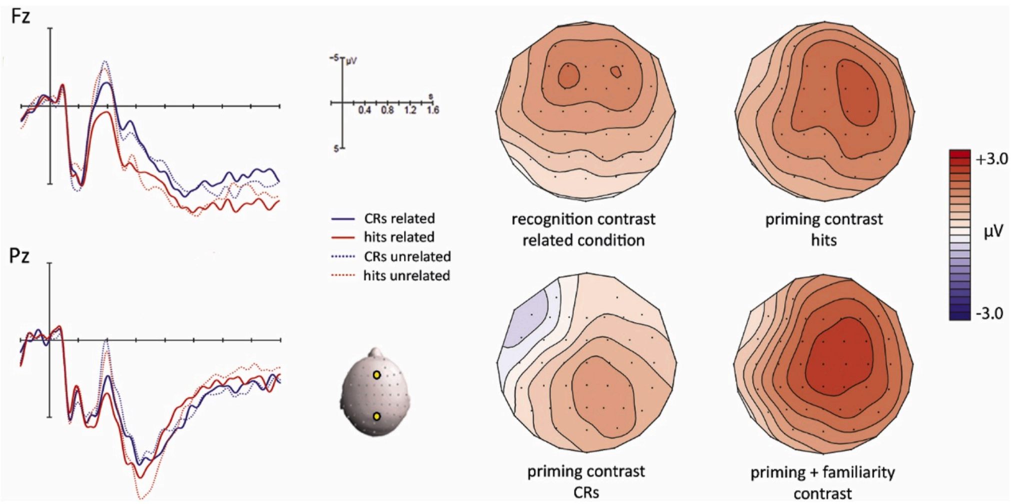

Fig. 4. Left panel: ERP waveforms at a frontal and parietal recording site depicting correct rejections and hits words preceded by related or unrelated primes in the test phase of the Bader et al. (2017) study. Right panel: Topographic maps (time window 300–500 ms) show that the pure priming contrast for correct rejections (CRs related – CR unrelated) has a more posterior distribution than the priming plus familiarity contrast (hits related – CRs unrelated) suggestive of independent fluency and familiarity signals. Also, the priming contrast for hits (hits related – hits unrelated) has a more frontal distribution than the priming contrast for CRs in line with the view that fluency and familiarity signals are interwoven in this time interval. Reprinted with permission from Bader et al. (2017).

processing and processing as expected in the given context, this discrepancy is evaluated and attributed to a memory (familiarity) or depending on the task context to another source (see also Bastin et al., 2019, for a similar distinction between representational memory systems and an attribution system that modulates memory representations as a function of task context). Showing that familiarity is modulated by expectations and other forms of top-down processing would provide important and additional evidence for the unexpected fluency attribution account of familiarity. Studies of this kind would underscore the assumption that familiarity is not necessarily an inherent characteristic of a memory trace but can arise from a processing discrepancy that is noticed and attributed to the past.

In an illustrative study, Leynes and Zish (2012) manipulated perceptual fluency by presenting test words in a recognition test either in a clear or blurry visual format. The critical manipulation was that visual clarity either varied randomly from trial to trial by presenting clear (high fluency) and slightly blurry words (low fluency) in random order in the test phase. In another condition, visual clarity was blocked by grouping clear and blurry words in different test phases in which either all words were blurry or all words were clear. To reduce the contribution of recollection on recognition judgments, all test words were presented after a shallow encoding task. Memory performance was not affected by the visual clarity manipulation when clarity was blocked. However, when clarity varied randomly participants showed a more conservative response criterion for blurry than for clear words. This shift in response criterion can be taken as evidence that modulations of memory and decision processes by top down processes (criterion setting) differed between clarity conditions. The interesting ERP finding was that when clarity was blocked, old words elicited a larger early negative component at parietal recording sites than new words that started at around 280 ms. Early negative components of similar kind have been taken as indices of perceptual fluency or implicit memory contribution to recognition (Voss and Paller, 2010), although, as discussed before, other studies reported more positive going ERP waveforms at posterior recording sites related to implicit memory (Nessler et al., 2005; Rugg et al., 1998; Woollams et al., 2008).[4] When visual clarity was varying randomly from trial to trial, old words elicited an FN400 effect but did not affect the early posterior ERP effect (Fig. 5). This means that familiarity memory is context dependent: In situations in which fluency from various sources (repetition and clarity) varies across trials, fluency presumably pops out because it is unexpected in a context in which other stimuli are less fluent. This may create more processing discrepancies and more feelings of familiarity. The observation that fluency differences between old and new items in some situations can be experienced as facilitated perceptual processing and are reflected in a fluency-related ERP effect (the early parietal negativity in the blocked clarity test) or in other cases are attributed to the past and experienced as episodic familiarity and give rise to an FN400 (random clarity test) is evidence that familiarity is not an intrinsic feature of a stimulus or a class of stimuli (the stimuli only differed in their old/new status and were otherwise identical in the blocked and random condition) but rather reflects the outcome of a top-down attributional process.

It is unclear, however, why in the blocked conditions the relative difference in repetition-related fluency did not elicit a familiarity signal and an FN400 effect. Even when fluency is blocked, the repetition of stimuli from the study phase - as it is usually the case in recognition memory experiments - should result in a change of relative familiarity and be reflected in an FN400 modulation. An interpretation could be derived from what Whittlesea and Williams (2001) have called “norms on the fly”. The blocked test may have constituted a specific testing condition. Different from lots of other recognition memory studies, due to shallow encoding the memory traces were weak and expectations for fluency were low. Therefore, fluency attributions to a perceptual experience were presumably more likely than in the random condition and this may have served as diagnostic basis for the memory judgments. Random presentation may have shifted the trial-by-trial norms and rendered fluency perceptions more surprising so that a familiarity experience was produced. In other words, participants may have developed different processing expectations in the random and the blocked test conditions and these different attributions led to different ERP effects. The ERP perceptual priming effect in the blocked condition and the FN400 effect in the random condition would be consistent with this view.[5]

Also, if the random condition creates a context in which fluency is particularly surprising because it can result from various sources (clarity and oldness), the discrepancy between perceived and expected fluency should be larger for old-clear than for old-blurry items and be reflected in a larger FN400 in the former condition. Unfortunately, however, interactions between fluency and repetition for the FN400 have not been investigated in this study.

The findings from the Leynes and Zish (2012) study were replicated and extended in a recent study by Bruett and Leynes (2015). They manipulated fluency by presenting pre-experimentally familiar (name-brand) and unfamiliar (off-brand) products. During a recognition memory test in which name-brand and off-brand products were shown randomly intermixed (as in the random clarity test in the Leynes & Zish study), off-brand products elicited an FN400 (more positive going waveforms for old than new off-brand products). A fluency-related ERP effect (an early posterior negativity) followed by a late parietal old/new effect was obtained for off-brand products in a test in which - analogous to the blocked test in the aforementioned study - brand status was constant within each block and only old/new status was varying from trial to trial. Notably, no FN400 was obtained in this condition. This absence of an FN400 at the first glance may be surprising because due to the low absolute familiarity of the novel off-brand products the increment in relative familiarity must have been particularly high when these items were repeated even in the blocked conditions and an FN400 should have been manifest in this condition as well. Alternatively, it could be argued that similarly to the Leynes and Zish study mentioned before, in the blocked condition participants relied on a fluency heuristic and attributed fluency to a perceptual source because due to shallow encoding the memory traces were weak and there was no other basis for memory judgements. In addition, for some off-brand products recognition decisions were supported by recollection and this may have created a unique testing situation being reflected by a bimodal distribution of ERP effects with an early posterior negativity and a late LPC. The fact that average ERPs are not trial-unique measures of cognitive processes but rather reflect the average processing for a class of stimuli may have additionally contributed to this pattern of results.

These lines of reasoning imply that fluency attributions are difficult to reveal in some experimental settings. Participants may refine their expectation regarding fluency based on their experiences with test probes in a particular testing condition and this may alter the attribution process from a familiarity attribution to an attribution to a perceptual source. The different attributions produce different ERP effects and also alter the diagnostic basis for the memory judgements, from episodic familiarity in the random condition to perceptual fluency in the blocked condition.

Taken together, the results of both studies provide support for the view that familiarity assessment is under top down control and that the extent to which fluency pops out in a particular testing context is an important determinant for the attribution process.

This viewpoint, however, does not imply that the attribution of

[4] The reasons for these discrepant perceptual fluency effects in the aforementioned studies are unknown. It is conceivable that the reversed polarity effects reflect the differential contribution of explicit memory to implicit memory processes (see Leynes and Zish, 2012, for a more extended discussion).

[5] We want to thank P. Andrew Leynes for pointing this out.

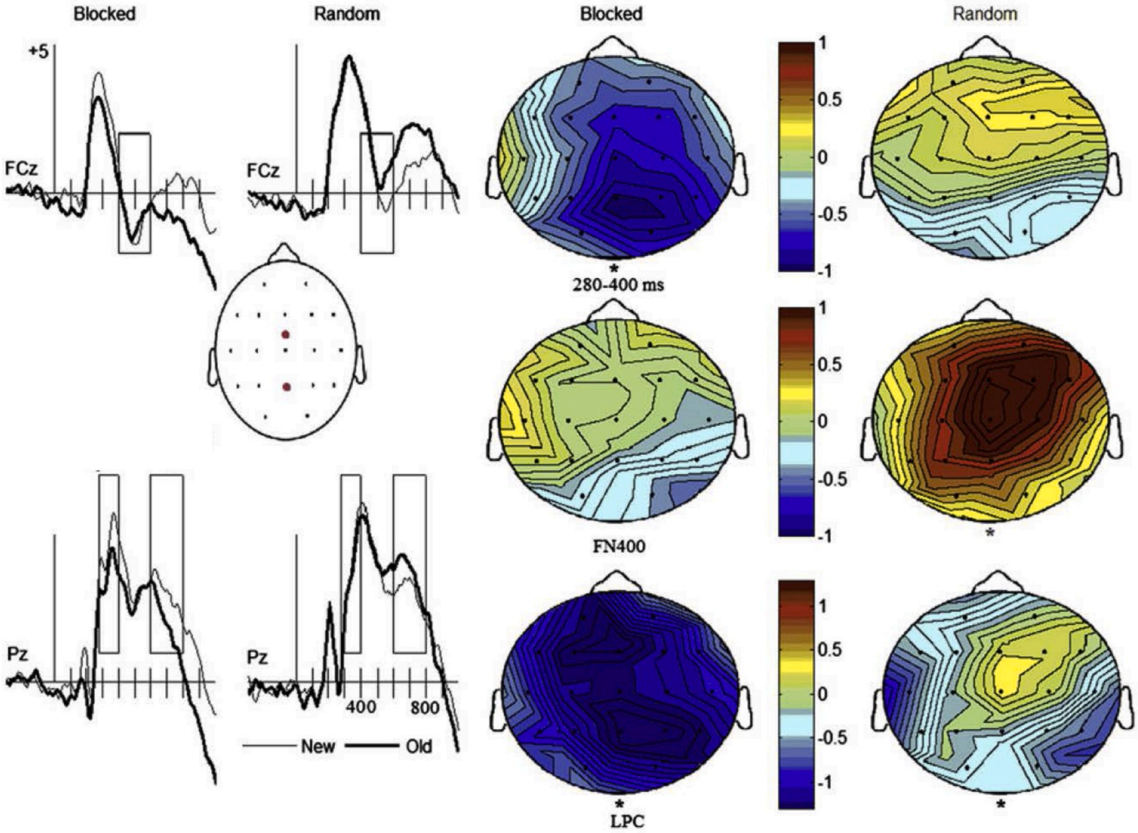

Fig. 5. ERP waveforms at a fronto-central and parietal recording site (left panel) and topographic maps depicting the old/new effects in the blocked and random condition (right panel) in an early, middle (FN400) and late time interval in the Leynes and Zish (2012) study. In the random condition repeated (old) words elicited an FN400, whereas in the blocked condition old words elicited an early negative component most pronounced at parietal sites. Reprinted with permission from Leynes and Zish (2012).

fluency is the only way by which familiarity can be modulated by top-down processes and adjusted to concrete task demands. In an illustrative study, Ecker et al. (2007b) used a cueing technique to explore how the allocation of attention modulates the FN400. In this study, object images superimposed on background images were presented at study and in the ensuing test phase, old (repeated) objects had to be classified as old, irrespective of the context in which they were repeated. Participants were either cued with a rectangular frame that encased the upcoming test probe or they classified the object in the foreground without cueing. Interestingly, in the cueing condition, in which attention was allocated to the target object, all old objects elicited an FN400 effect relative to new objects in new contexts whereas without cueing the FN400 was only present in conditions entailing old or rearranged object-context pairings. This finding suggests that in the cueing condition the objects attracted more attention and the background was treated as "truly contextual", so only repeated objects in the foreground elicited an FN400 whereas without cueing the background scenes may have captured more attention, so these stimuli were treated more like new objects and only highly salient old pairings (old or rearranged) elicited a familiarity signal (Ecker et al., 2007b). This supports the view that contextual factors such as the potential of background stimuli to capture attention do affect how familiarity is assessed and how this contributes to recognition memory judgments.

Further underscoring the sensitivity of the FN400 to contextual factors, in a recent study we found that the FN400 is modulated by the format of the test display (Bader et al., 2019). In two test conditions of a recognition memory task, participants had to discriminate studied pictures from similar foils. Familiarity-based judgments are usually deemed unreliable in such a situation as differences in familiarity strength between these two item classes are relatively small (e.g., Morcom, 2015). However, we showed that when studied pictures and corresponding similar foils were presented in a forced-choice test format, in which familiarity values for studied pictures and foils can be directly compared (so-called corresponding foils), studied pictures were associated with an FN400. In contrast, when the forced-choice display contained foils which were similar to other studied items (i.e. non-corresponding foils) and did not allow a direct comparison of the familiarity values of studied pictures and foils, no FN400 was obtained. This result is in line with the notion that the FN400 occurs in laboratory settings only when differences in relative familiarity provide an effective means to discriminate studied from unstudied items. Therefore, it does not signify an intrinsic characteristic of a stimulus but reflects an attributional process.

Another way to examine how contextual factors modulate familiarity-based remembering and the FN400 is to explore how manipulations of decision criterion alter recognition and the ensuing ERP components. In an illustrative study, Azimian-Faridani and Wilding (2006) required participants to adopt a conservative decision criterion by instructing them to respond "old" only when confident about the correct response and to give a "new" response otherwise. In the liberal condition, they were to respond "new" only when they were sure that this is the correct response. In line with these instructions, there were more old responses with the liberal criterion. An FN400 effect was obtained in both conditions but confirming the view that the level of familiarity associated with correctly classified old and new items is higher in the conservative than the liberal condition, the ERPs to correct decisions were more positive going than in the conservative condition. A similar pattern of results, i.e. more positive ERPs in the FN400 time window in the conservative than in the liberal condition was also reported in two other studies by Hill and Windmann (2014) and Leynes et al. (2019). These studies provide strong evidence that manipulations that alter decision criteria or more general processing expectancies do modulate recognition ERPs in general and the FN400 in particular.

The high relevance of contextual factors for FN400 elicitation was recently also demonstrated in another study by Leynes and colleagues. They manipulated expectancies for fluent processing by informing participants about the proportions of old and new items they could expect in different testing blocks, even though the proportion of old and new items was exactly the same in all three blocks. Meaningless stimuli were used for which a low fluency expectation can be assumed and it was predicted that fluency should be ascribed to perceptual processing rather than to familiarity. Consistent with these predictions, no FN400 was obtained under normal testing conditions but only in test blocks with high expectations for old items. This nicely illustrates that top down processes govern whether or not fluency is attributed to familiarity or to another source as the testing conditions were physically identical in all three test blocks.

Other studies have shown that the FN400 is affected by a memory control process, called retrieval orientation, i.e. a specific form of processing that – when applied to a test cue – facilitates the recovery of information from specific prior experiences (Bridger and Mecklinger, 2011; Rugg and Wilding, 2000). In an illustrative study, Ecker and Zimmer (2009) presented object pictures in a study phase and, in a subsequent memory test, participants made old/new judgments for studied pictures, new pictures or pictures from the same category as the studied pictures. Two test conditions were employed: In a specific test, only studied pictures had to be classified as old whereas in a general test old pictures and same-category pictures had to be classified as old. The idea behind this manipulation was that the specific test should initiate a retrieval orientation that facilitates the recovery of highly specific perceptual object details from the study episode whereas the general test should allow to focus retrieval processing on conceptual (categorical) aspects of the studied objects. Consistent with the view that the FN400 is modulated by retrieval orientation, Ecker and Zimmer (2009) found an FN400 (more positive going waveforms) only for studied pictures but not for same-category pictures in the specific test in which item-specific details had to be recovered whereas in the general test the FN400 was graded (studied > same-category > new). These findings show that the FN400 can be flexibly adapted to particular retrieval situations, i.e. situations in which retrieval processing was focused on specific perceptual details or on more general conceptual characteristics.

Confirming and extending these findings, Rosburg et al. (2013) explored ERP correlates of memory retrieval in a variant of a memory exclusion task (Jacoby, 1991). In this task, subjects studied items in different conditions in which they should either identify the word as the subject of a sentence (identify condition) or generate the word from a word fragment (generate condition). At test, items from one condition were denoted as targets and the items of the other category were denoted as non-targets and together with new items had to be rejected.

As apparent from Fig. 6, an FN400 attenuation to non-targets was only obtained in the condition in which items from the identify condition were targets. In this condition, target representations due to their shallow encoding were presumably weak and difficult to retrieve. This shows that the FN400 can be modulated by top down processing, such as retrieval orientation, in particular in situations in which the critical target information is only weakly encoded and non-target retrieval can be used to enhance overall memory performance (Rosburg et al., 2013; Rosburg and Mecklinger, 2017).

In sum, different forms of top down processing during recognition memory tasks such as allocation of attention, setting of decision criteria or adapting retrieval orientations have been shown to modulate familiarity assessment and its ERP correlate. Familiarity experiences and FN400 effects are also affected by test expectations which can be set pre-experimentally or be refined on the basis of experiences in a memory test as it is for example the case when testing conditions change. This alters

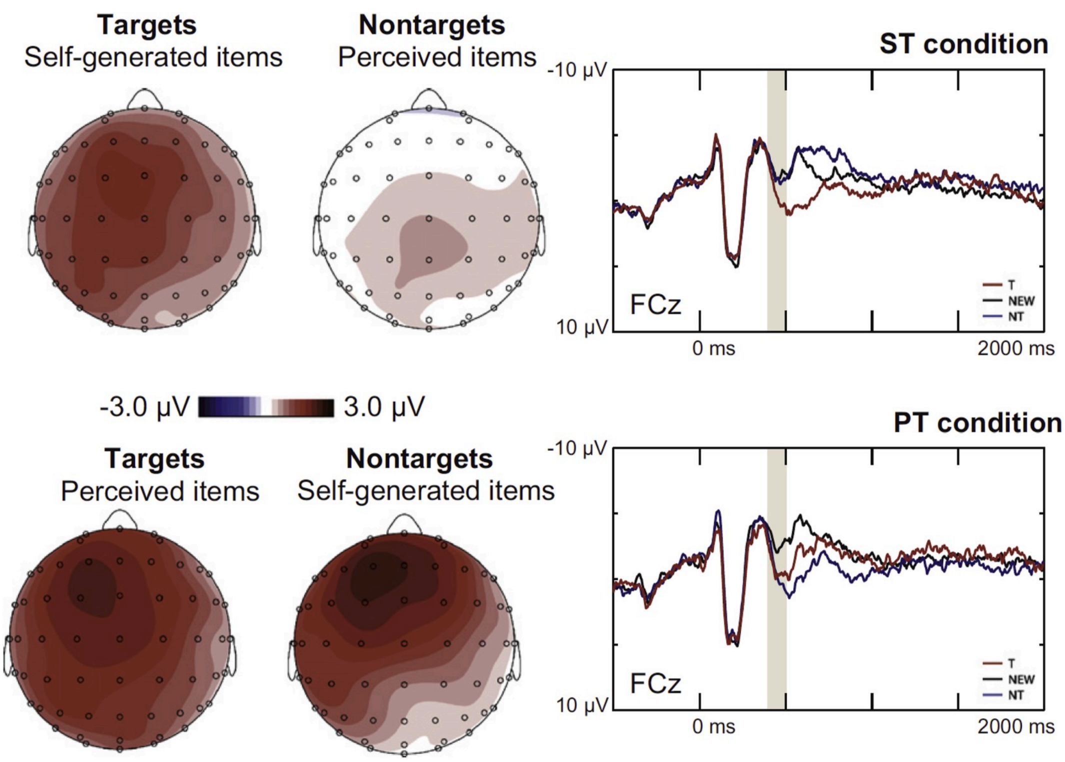

Fig. 6. The old/new effects for targets and non-targets in the 400–500 ms time interval in the generate condition (Upper Panel) and the identify condition (lower panel) of the Rosburg et al. (2013) study. The left side shows the difference maps and the right site shows the ERPs to targets (red line), non-targets (blue line) and new items (black line). FN400 effects for targets were present in both conditions whereas an FN400 to non-targets was only obtained in the identify condition in which targets items were difficult to retrieve. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

the extent to which fluency is attributed to and experienced as familiarity. This dovetails with the claim that a plurality of mechanisms contributes to familiarity memory and that these top-down processes determine whether or not mnemonic attribution takes place.

7. A comprehensive neurocognitive account of the FN400

The goal of this article was to critically examine current claims and assumptions about the FN400, an ERP component which has been related to familiarity memory even though there is an ongoing debate regarding the detailed cognitive processes captured by the FN400. This article also highlights new developments in the understanding of the functional characteristics of the FN400. The relevant literature suggests that the FN400 is qualitatively distinct from the N400 when adequate operational definitions are used for the critical ERP contrasts and confounds between episodic recognition and semantic priming are avoided. This review also revealed that attributing the FN400 solely to implicit conceptual priming cannot account for many FN400 effects and that the observation that the FN400 co-varies with implicit conceptual memory in some situations but not in others requires a broader theoretical account. In a first step, intended to avoid a polarized debate on whether the FN400 reflects familiarity or conceptual fluency (Mecklinger et al., 2012; Paller et al., 2012; Rugg and Curran, 2007) and aimed to obtain a broader conceptualization of the memory processes reflected in ERP old/new differences present at around 400 ms after stimulus onset, we reviewed recent studies that show that familiarity can be multiply determined and that an important distinction has to be made between a recent-exposure, relative familiarity mechanism indexed by the FN400 and a pre-existing absolute familiarity mechanisms being reflected by a coincidental but topographically distinct ERP effect resembling the N400. This important distinction between relative and absolute familiarity is substantiated by brain imaging and neuropsychological studies showing that judgments of lifetime (absolute) familiarity and of experimental (relative) familiarity rely on highly integrated representations of object features housed by the PrC. The PrC tracks the frequency of recent exposures with a decreasing signal and cumulative lifetime/absolute familiarity with an increasing signal suggesting that the mechanisms underlying the computation of relative and absolute familiarity rely on PrC integrity in opposite directions.

The main assumptions of the unexpected fluency account of the FN400 are summarized in Fig. 7. To reiterate, familiarity can be driven by a multitude of signals that relate to different forms of processing fluency. Relative familiarity and the FN400 result from a surprising difference between perceived and expected fluency and a mnemonic attribution process that ascribes this enhanced fluency to a prior experience with that event. The mnemonic attribution process presumes that there are at least two possibilities for an attribution and an intention to retrieve. Top down processes operating upstream regulate the attribution process (illustrated by the upper branch in Fig. 7). An exception to this process are contextual conditions with explicit requirements to retrieve episodic information in which all stimuli are novel and changes of their absolute familiarity after first exposures in a laboratory setting are highly diagnostic for their prior occurrence. In this situation, absolute familiarity is sufficiently diagnostic and hit responses are

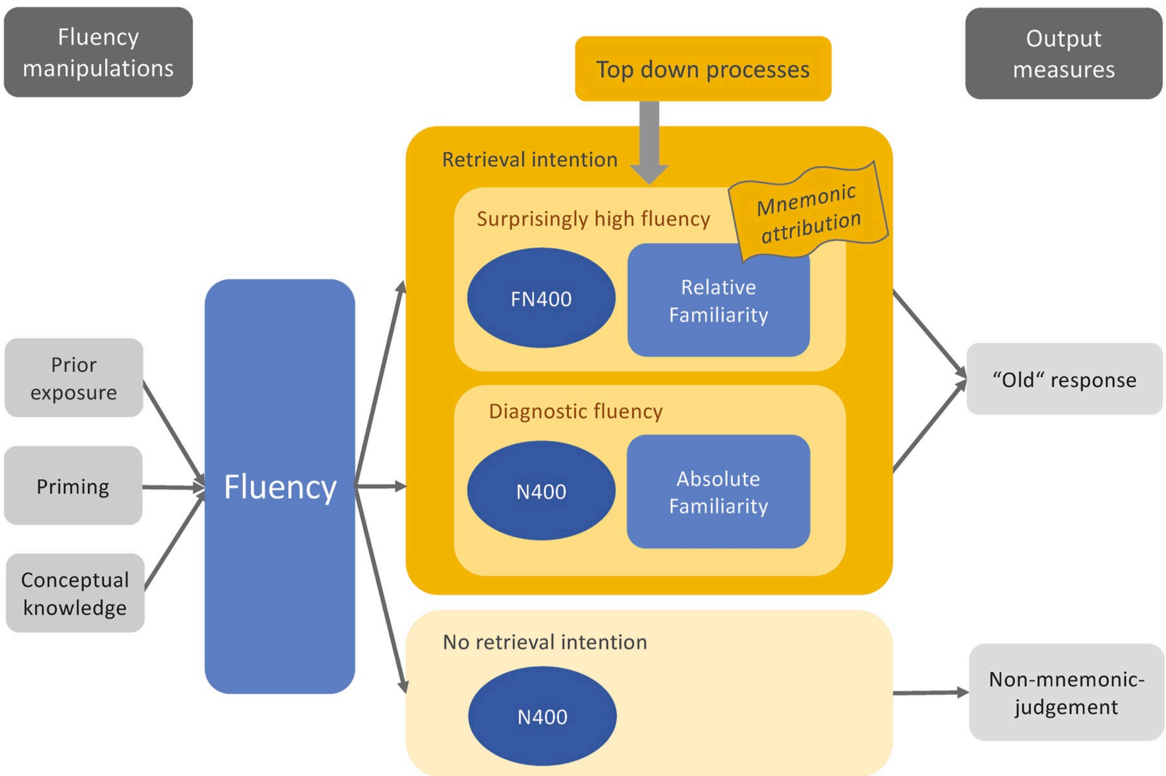

Fig. 7. The unexpected fluency attribution account of the FN400: According to our proposal familiarity can be driven by a multitude of signals that relate to different forms of processing fluency. An important distinction has to be made between relative familiarity which tracks the increment in familiarity from a recent to the present exposure and the pre-experimental absolute familiarity of events (equivalent to conceptual knowledge). The mnemonic attribution process presumes an intention to retrieve and is regulated by top-down processes. Relative familiarity and the FN400 result from a surprising difference between perceived and expected fluency and an attributional process that ascribes this enhanced fluency to a prior experience (upper branch). An exception are situations with retrieval intentions in which absolute familiarity is sufficiently diagnostic and memory judgments are accompanied by an N400 (middle branch). Without explicit retrieval requirements (retrieval intentions) and when expectancies for fluency are high, ongoing processing is fluent and depending on the way fluency was manipulated gives rise to an N400 or other fluency-related ERP effects (lower branch). The computations underlying the mnemonic attribution process and relative familiarity are closely intertwined.

accompanied by an N400 effect (cf. middle branch in Fig. 7). This also holds for situations in which the salience of fluency is so high that its ensuing absolute familiarity provides an effective means to distinguish studied from unstudied items. In these situations, no discrepancy between an expected and experienced fluency signal is perceived and no FN400 is elicited. This could for example have been the case in the Lucas and Paller (2013) study in which studied and unstudied items were drawn from different letter pools and the fluency of studied items was presumably salient enough to trigger a correct old response. Perceptions of fluent processing are not necessarily ascribed to the past but can also be attributed to other sources and produce a variety of feelings about a current stimulus and might alter the diagnostic basis for recognition decisions. This holds true also for situations in which people have an intention to retrieve but due to weak memory signals presumably rely on a fluency heuristic and attribute fluency to a perceptual experience, as in the studies by Leynes and colleagues discussed in section 6. Due to the shallow encoding task semantic elaboration may have been low in the study phase so that conceptual fluency was not sufficiently enhanced in the test phase. In this situation, perceptual fluency was the sole basis for recognition decisions and “old” responses were accompanied by an ERP effect of perceptual fluency rather than an N400 attenuation effect.

Without explicit retrieval intentions (i.e. old judgments) or when fluency is not surprising or when non-mnemonic decisions are made, ongoing processing is fluent and depending on the way fluency was manipulated can give rise to fluency-related ERP effects such as the N400 or the P200. Notably this latter form of fluency is detached from episodic memory and no FN400 is generated under these circumstances (cf. Lower branch in Fig. 7).

The unexpected fluency attribution account which we propose as a valid account of the FN400 and the processes it reflects allows to interpret a large breadth of FN400 findings without additional assumptions and enables to make testable predictions on the FN400. It also extends the multiply-determined view of the FN400 that we proposed earlier (Bader et al., 2010; Bridger et al., 2014; Wiegand et al., 2010) in important ways:

First, our proposal can account for the findings from studies combining (masked) semantic priming with recognition memory reviewed above. Fluency induced by priming consistently modulates the N400 without affecting the FN400 whereas fluency induced by prior study exposure (relative familiarity) gives rise to FN400 effects (Bader and Mecklinger, 2017; Lucas et al., 2012; Wang et al., 2015, 2019; Woollams et al., 2008). The high resemblance of the N400 in the aforementioned priming studies with the ERP correlate of absolute familiarity suggests that the conceptual priming it reflects is disconnected from episodic memory and presumably reflects facilitated conceptual processing characteristic for high frequency words (Bridger et al., 2014) or concept names with high concept familiarity (Yang et al., 2019).

By our view, the FN400 and the relative familiarity mechanism it reflects stem from the same fluency mechanism that underlies conceptual implicit memory but is not identical with it. This dovetails with a recently proposed view according to which the FN400 reflects a conceptual fluency-related precursor to familiarity (Lucas et al., 2012). However, different from the latter claim, we propose that conceptual fluency alone does not suffice to generate an FN400 effect: An intention to retrieve, unexpectedness of the fluency signal in the task context, and an attributional process that ascribes the surprising fluency to the past are prerequisites for the generation of this effect.

Second, an important implication of the unexpected fluency attribution account is that the computations underlying the attribution process may be related to those that characterize the relative familiarity mechanism, i.e. the change in familiarity strength relative to pre-experimental familiarity when items are repeated in an experimental context (see Gimbel et al., 2017, for a similar argument). It is conceivable that the mnemonic attribution process is closely intertwined with the relative familiarity mechanism. For unexpected events embedded in a context of other events, the perceived increment in familiarity may be highly surprising and this discrepancy may increase the likelihood that fluency is attributed to the past and that familiarity is experienced. Likewise, Coane et al. (2011) also refer to an analogy between a relative familiarity mechanism and the discrepancy attribution process. Exploring recognition memory for high and low frequency words, the authors found evidence that the recognition of low frequency words was based on an early relative familiarity mechanism. They argued that the difference between expected and perceived fluency was particularly strong for low frequency words and that participants were more likely to attribute this surprising fluency to a recent exposure. In other words, the difference between perceived fluency and expected fluency may be in general particularly high for words with a low frequency of occurrence (Bridger et al., 2014) and this large discrepancy could be analogous to the large increment in relative familiarity (and the large FN400) for this class of stimuli. A similar argument holds for the results of the Leynes and Zish (2012) study. In their random condition, in which fluency from different sources varied from trial to trial, the discrepancy between actual and expected fluency was presumably particularly high and surprising and this may have led to a large increment in relative familiarity.

Third, the premise that familiarity results from an attributional process that determines whether processing fluency is ascribed to the past or to another source highlights the importance of the processing context and of top-down inferential processing for creating a familiarity experience. As reviewed in section 6, top down processes determine whether or not mnemonic attributions take place and attributing fluent processing to the past presumes an intention to retrieve. When people make recognition judgments, people set up expectancies (or norms) against which the actual fluency of an item is compared. The feeling of familiarity depends critically on the characteristics of the processing context because the context can change the norms which in turn can set up a new basis for surprise.

Having the goal to remember may lead to more elaborated processing of retrieval cues and may also enable a more precise attribution of fluency. Of note, in other contexts in which no explicit memory decisions are required, attributions of fluency resulting from prior experience are made to other processing qualities. For instance, subjects show preferences for stimuli that occurred in an earlier phase of an experiment when aesthetic judgments are required (the “mere exposure effect”, Jacoby, 1984) or when judgments of the loudness of stimuli or the duration they were visible on the screen were required (Witherspoon and Allan, 1985). In such situations, no FN400 is elicited. Such misattributions of the prior exposure as a quality of the task at hand (be it an aesthetical or a physical dimension) rather than an attribution to familiarity underscores the idea that the experience of familiarity may be similar to the experience of an emotion (Schachter and Singer, 1962), given that an emotional experience is also the result of an interaction between an unspecific arousal signal and a cognitive, attributional process about the arousing situation (see Jacoby et al., 1989, for an elaboration of this view).

Fourth, the fluency attribution account does not mean to imply that fluency attributions are the only means by which familiarity memory can be generated. For example, active memory search is a mechanism involved in direct tests of memory such as recognition tests by which participants search their episodic memory for cues that reactivate a target memory automatically (Gillund and Shiffrin, 1984). In some situations, successful remembering requires a prolonged and active search through semantic and episodic memories assisted by active retrieval. Active search and retrieval activate memory representations for items and item-context associations and can also lead to familiarity experiences. However, such a process would be different from the fast reactivation based on fluency attributions outlined above. Hence, uncertainty remains whether all judgments of familiarity result from memory attributions based on enhanced fluency (see Jacoby et al., 1989, for such a view) or whether familiarity can also be generated by other processes such as active search in memory combined with a fluency attribution mechanism or active search without any attributional processes being involved.

An open issue and a worthwhile enterprise for future research that arises from the unexpected fluency attribution account concerns the boundary conditions under which fluency is attributed to familiarity. Such attributions likely depend on a number of factors, such as the strength of the memory signal or the amount of semantic processing in a testing condition. As outlined above, situations with weak memory signals and low semantic processing may constitute unique testing conditions in which fluency is used as the basis for recognition decisions. In such exceptional situations, there is a retrieval intention and correct old responses are given. As no FN400 but ERP evidence for facilitated perceptual processing is present (Leynes and Zish, 2012; Bruett and Leynes, 2015), it can be assumed that fluency is not attributed to familiarity but to a perceptual source.

Another factor that impacts the attribution process is the expectancy for fluency. When expectations for fluency are low, as for example when low frequency words are repeated in an experimental context (Bridger et al., 2014; Coane et al., 2011) or when fluency is surprising due to random trial-by-trial fluctuations of fluency (Leynes and Zish, 2012; Bruett and Leynes, 2015) as well as in tasks in which priming and recognition memory are combined in the test phase (e.g., Bader and Mecklinger, 2017; Wang et al., 2015), processing may be surprisingly fluent and may activate the attributional process to a stronger extent than in situations characterized by less surprising fluency.

In fact, when fluency is encountered in a context in which events are highly expected due to their high pre-experimental familiarity or due to their contextual congruency, fluency may not be as surprising and familiarity attributions are less likely to occur. Consistent with this view, in studies exploring recognition memory for words with different frequencies of occurrence (Bridger et al., 2014; Ye et al., 2019), FN400 effects were attenuated for high-frequency words. It is also conceivable that in some testing conditions, words are erroneously judged on the basis of their absolute familiarity. Under these circumstances high absolute familiarity signals could mistakenly be taken as evidence for prior occurrence. This could account for the finding that elevated false alarm rates in the Lucas et al. (2012) study did not elicit an FN400 but gave rise to an N400.

Also, when subjects are required to make non-mnemonic decisions such as fame or liking judgments rather than recognition judgments or in experimental settings in which recognition decisions are combined with other tasks (Strózak et al., 2016a; Voss and Federmeier, 2011), fluency is less likely attributed to the past. Leynes and Addante (2016) explored the effects of repetition and perceptual fluency on recognition memory and liking judgments which had to be given in one and the same trial. They found no electrophysiological effects of fluency for recognition judgments suggesting that the requirement to make liking judgments may have rendered the repetition of these items less surprising, lowered the likelihood that their enhanced fluency was attributed to the past and attenuated the FN400. In other words, a strong emphasis on the recognition memory task over other forms of processing seems to be an important measure to avoid an overshadowing of memory processes by semantic priming and constitutes an important boundary condition under which fluency is attributed to familiarity.

Attributions are influenced by task instructions and processing contexts. This can mask fluency attribution effects in some experimental contexts which makes it difficult to isolate these effects in laboratory studies (see Leynes et al., 2017, for a similar argument). This indicates that effects of task goals (i.e. is one's goal remembering?) and context (i.e. can an event be easily predicted by its context?) have to be carefully controlled in studies testing the boundary condition of the fluency attribution account in ERP studies. In the FN400 time interval, the ERP signal is characterized by multiple sources of fluency and the interpretation of these multiple fluency signals will determine the memory experience. In sum, the FN400 is present for stimuli which are judged familiar on the basis of a relative (incremental) familiarity mechanism and the expectedness of an event's fluency is one of the main factors governing this mechanism. Conversely, fluency emanating from conceptual priming is associated with an N400, which can be indicative of more fluent processing of events with higher absolute familiarity.

The present proposal bears similarities with a recent conceptualization of the FN400 proposed by Andrew Leynes and colleagues (Leynes et al., 2017). As in the present framework, familiarity is considered to arise from surprisingly fluent processing of an event and an attribution process that ascribes this fluency to a prior experience. In their view, familiarity arising from a discrepancy attribution (called familiarity perception) is associated with an FN400 response whereas in other processing contexts, expectations for fluency may differ and fluency can be ascribed to other (perceptual) sources which gives rise to other (fluency-related) ERP responses (see Leynes et al., 2017, for a more detailed description). As outlined in section 6, it would be desirable to see an interaction analysis of fluency and repetition for the FN400 in testing situations with fluency from various sources, as such effects would further substantiate the authors' account. Nonetheless, the proposal that familiarity is a perception based on a processing discrepancy that is attributed to oldness can account for a variety of findings: These findings include the reliance of familiarity attributions on top down processes such as retrieval orientation or setting of decision criteria or the dependency of the familiarity perception on contextual factors as the expectancy of fluency or the kind of decision (mnemonic vs. non-mnemonic) required in a particular task situation. The present unexpected fluency account, however, picked out the multiply determined view of familiarity as a central theme and elaborates the interplay between relative (experimental) familiarity and absolute (lifetime) familiarity and their distinct electrophysiological manifestations. It also makes relevant claims on the close relationship between the memory attribution mechanism and the relative familiarity mechanisms and last but not least identifies putative brain systems involved in the generation of relative and absolute (baseline) familiarity signals (see below). Thus, the proposal by Leynes and colleagues and the present one are complementary but the present one can be considered as a broader conceptualization of the FN400 as it postulates multiple familiarity signals not just those that give rise to the FN400.

A final point to be addressed concerns the neural underpinnings of relative and absolute familiarity signals and the supposed fluency attribution process. As outlined in section 3, the PrC plays a key role in the computation of relative familiarity signals as well as in the computation of fine-grained object representations. These representations constitute object knowledge in semantic memory and are also the computational basis for the judgment of lifetime (absolute) familiarity. Evidence for this view comes from a brain imaging study showing that the assessment of absolute familiarity of objects is associated with an increase in signal strength in the PrC whereas judgments of relative familiarity are related to a decrease in PrC signal strength (Duke et al., 2017). Decreases in PrC signal strength accompanying correct judgments of prior exposures in recognition memory studies have also been reported in a variety of recent brain imaging studies (Daselaar et al., 2006; Dew and Cabeza, 2013; Henson et al., 2003). Also, the finding that a patient with a selective perirhinal lesion (NB), who was selectively impaired in making familiarity-based memory judgments, was also impaired in the assessment of lifetime familiarity (Bowles et al., 2016) supports the view that the PrC is critically involved in the computation of absolute and relative familiarity signals. Of note, deactivation of the PrC has not only been found for correct old judgments. Studies combining masked priming with a recognition memory task found decreased PrC activity for new items which were misattributed to oldness (Dew and Cabeza, 2013; Gomes et al., 2019) which supports the view that PrC deactivations play a critical role not only in accurate memory judgments but also in erroneous decisions which are influenced by fluency (Dew and Cabeza, 2013).

Despite this evidence for common generators for absolute and relative familiarity in the PrC, the apparent difference in anteriority in the topography of their respective ERP correlates (the FN400 and the N400) indicates that additional brain regions (presumably those which are specifically involved in explicit judgments of prior exposures) contribute to the generation of the FN400. As we have discussed previously, a likely candidate is the lateral PFC (Bader and Mecklinger, 2017; Bader et al., 2014). In fact, there is evidence from various brain imaging studies indicating that the dorsolateral PFC is critically involved in familiarity-based decision making (Angel et al., 2013; Bader et al., 2014; Henson et al., 1999; Yonelinas et al., 2005) and the generation of the FN400 (Hoppstädter et al., 2015). Henson et al. (1999) found that know-responses were associated with more pronounced lateral and medial PFC activity than both, remember- and new-responses. Using a recognition paradigm that allows to contrast recency judgments which depend on relative familiarity with source judgments requiring recollection, Dobbins et al. (2003) found enhanced activation in the right PFC during relative familiarity judgments relative to source memory judgments which were independent of retrieval success. Aly et al. (2011) showed that lesions to the lateral PFC lead to an increase in familiarity-based false alarms. A recent multimodal imaging study employing simultaneous EEG/fMRI recordings revealed that the BOLD signal in the lateral PFC in an item recognition memory task was predicted by the size of the simultaneous FN400 effect (Hoppstädter et al., 2015). Interestingly, in the aforementioned study by Dew and Cabeza (2013), a PFC index of successful retrieval showed enhanced connectivity with fluency modulated PrC activation for correct memory decisions. This suggests that the PrC and lateral PFC act in concert when increments in fluency are correctly attributed to oldness, a situation that also gives rise to an FN400 effect. The PFC may be critically involved in the comparison between the actual fluency signal and the one expected in a given task context which gives rise to a relative familiarity signal and the FN400. In other words, interactions between the PrC and the lateral PFC seem to play a pivotal role when fluency is attributed to prior exposures and experienced as familiarity.

These results are promising and elucidating the neuronal networks involved in the generation of absolute and relative familiarity signals and the fluency attribution process remains an important endeavor for future research. Multimodal imaging approaches combining brain imaging with ERP data are favorable in this regard as they allow to track the relevant neural activation with sufficiently high temporal and spatial resolution. Also, combined analyses of brain imaging (fMRI) and oscillatory EEG data would be a valuable approach to identifying the brain regions and networks generating functionally relevant oscillations underlying mnemonic processes (see Herweg et al., 2016, as an example). The analysis of EEG oscillations can add important insights into the mnemonic functions of particular brain regions which are not present in local patterns of neural activity such as ERP components and will be a worthwhile endeavor for further research on familiarity memory and its relation to other memory processes.

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