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Review article

Observing memory encoding while it unfolds: Functional interpretation and current debates regarding ERP subsequent memory effects

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A B S T R A C T

Our ability to remember the past depends on neural processes set in train in the moment an event is experienced. These processes can be studied by segregating brain activity according to whether an event is later remembered or forgotten. The present review integrates a large number of studies examining this differential brain activity, labeled subsequent memory effect (SME), with the ERP technique, into a functional organization and discusses routes for further research. Based on the reviewed literature, we suggest that memory encoding is implemented by multiple processes, typically reflected in three functionally different subcomponents of the ERP SME elicited by study stimuli, which presumably interact with preparatory SME activity preceding the to be encoded event. We argue that ERPs are a valuable method in the SME paradigm because they have a sufficiently high temporal resolution to disclose the subcomponents of encoding-related brain activity. Implications of the proposed functional organization for future studies using the SME procedure in basic and applied settings will be discussed.

1. Introduction

Neural activity elicited by an event when it is initially encountered is an important predictor for its later memorability. This activity can be studied with an experimental approach in which brain activity elicited by the initial stimulus presentation is segregated according to whether the event is remembered or forgotten based on participants' performance in a subsequent memory test. In the first study using this approach, Sanquist and colleagues (1980) asked participants to study words in a semantic, a phonemic or in an orthographic encoding task. Those words which were later recognized tended to elicit larger positive event-related potential (ERP) amplitudes between 450 and 750 ms at midline posterior regions, followed by a more positive-going slow wave, than forgotten words. These effects were most pronounced for words from the semantic encoding task. Although these patterns were based on a very small number of participants and were not statistically confirmed, they lay the groundwork for a large body of research that has since used this so-called "subsequent memory paradigm" to shed new light on the complexity of memory encoding processes in the human brain and their neural underpinnings.

The differential brain activity between events later remembered and forgotten has sometimes been labeled Dm, for "difference due to memory" (e.g., Van Petten, Senkfor, 1996; Paller et al., 1987). However, as ERP activity predictive of subsequent memory can be decomposed into multiple subprocesses that play different roles during encoding (see Section 5), the label Dm, indicative for one general memory process, is misleading and has been largely replaced by the term "subsequent memory effect" (SME). SMEs can be analyzed in different types of brain activity such as electroencephalography (EEG), intracranial EEG recordings (iEEG), magnetoencephalography (MEG) or functional magnetic resonance imaging (fMRI), recorded while participants encode new information. In a subsequent test phase memory performance is assessed, for example using recall or recognition tests, and performance in these tests is used to back-sort the encoding trials according to subsequent retrieval. ERPs are a valuable method to monitor encoding activity in the subsequent memory paradigm because neurocognitive processes are fast and transient (Makeig et al., 2002; Nunez, 1981) and separating different subprocesses in most cases requires a good temporal resolution, which cannot be achieved with hemodynamic imaging methods like fMRI or by analyses of EEG oscillations (Nyhus and Curran, 2010). Separately quantifying each of the different subprocesses can, in turn, provide unique insight into the precise sequence of mechanisms

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underlying successful memory encoding in different learning contexts or populations. However, this requires prior knowledge on the kinds of ERP effects that are commonly observed and an understanding of their functional significance.

Given the wealth of SME studies that have been conducted since the initial report by Sanquist et al. (1980) and also in light of the fact that the last review of ERP SME dates back to 2000 (Friedman & Johnson) we consider a systematic review of the relevant literature as highly important. Rather than providing an inclusive review of ERP studies using the subsequent memory approach, the goal of the present article is to propose a functional organization of the SME that allows to integrate a large body of studies and to relate these studies to each other. We argue that the stimulus-elicited SME can be subdivided into three main components reflecting different processing principles in support of successful memory encoding: An early frontal SME between 300 and 600 ms post-stimulus reflecting semantic processing of a stimulus event, an early parietal SME that emerges between 350 and 500 ms post-stimulus and indicates the binding of multiple features of a study event into a single item representation as well as a sustained late frontal SME that onsets around 550 ms and reflects continued processing of associative and conceptual event features. These processes interact with preparatory mechanisms that are observable in ERPs already before stimulus onset.

The present article will focus on the following topics which we consider relevant for a comprehensive understanding of the SME, its subcomponents and the processing mechanisms they reflect. The second section explores whether and how SMEs differ according to the encoding tasks used to explore them. In the third section we evaluate how SMEs are modulated by the content to be retrieved and the way memory is tested. An event's distinctiveness is an important determinant for the SME, but it is still unclear by which mechanisms it enhances memory encoding. This will be discussed in the fourth section. The fifth section discusses the three-component structure of the SME and evaluates which processing mechanisms are reflected by these subcomponents. The sixth section evaluates whether the SME reflects merely intrinsic processes set in train by study events or is also altered by external factors, as for example neural activity tonically maintained throughout a task. In the seventh section we will discuss work showing that in addition to neural activity elicited by a study event, brain activity before the study event can also predict subsequent memory. The eighth section lists open issues and sketches age-related differences in successful encoding. Conclusions and proposals for future research on the processes underlying the SME are outlined in Section 9. Taken together, we hope that the present review will stimulate additional basic research testing and refining models on the functional significance of ERP SMEs, as well as applied research using ERP SMEs to mechanistically examine modulations on the neurocognition of memory in developmental and clinical contexts.

2. Do SMEs differ according to the encoding task?

A relevant question to start with is whether SMEs differ according to the type of study task. This question is of importance because it allows to assess whether encoding of a class of items relies on a single neural system that is engaged irrespective of study task or whether encoding is supported by multiple task specific systems. Prior studies generally support the latter view. For example, Cycowicz and Friedman (1999) reported a SME in an intentional, but not in an incidental encoding condition, suggesting that the SME may be (at least in part) indicative of higher-level processes that are affected by factors such as encoding mode, motivation or strategies.

Further support for the notion that SMEs differ according to the encoding task comes from studies that explored the SME during retrieval practice. Retrieval practice is an encoding manipulation by which participants are required to reinstate the episodic context of a prior study episode. Retrieval practice has been consistently shown to improve subsequent memory performance as compared to the mere re-studying of the prior episode without retrieval requirements (Karpicke and Roediger, 2008, for a review see Roediger and Karpicke, 2006). In an illustrative study, Liu et al. (2017) compared memory performance after two different encoding tasks: retrieval practice and re-studying. As expected, memory was enhanced after retrieval practice. In the ERPs there was a frontally distributed SME starting around 300 ms in the re-studying condition but not in the retrieval practice condition. Conversely, retrieval practice gave rise to a parietal SME between 500 and 700 ms, which was absent during re-studying. Another study by Jia et al. (2021), which explored the combined effect of retrieval practice and emotion on memory performance revealed a highly similar parietal SME selectively in the retrieval practice condition. A SME with similar spatio-temporal characteristics was also reported during retrieval practice in a study by Bai et al. (2015), that also demonstrated that this SME was spatio-temporally comparable to the parietal old/new effect, the ERP correlate of episodic recollection (see Rugg and Curran, 2007 or Friedman and Johnson, 2000 for reviews). Consistent with another study in which the parietal old/new effect, elicited by conceptual repetitions of study stimuli, was also correlated with subsequent recognition memory accuracy (Griffin et al., 2013), it can be concluded that retrieval practice engages recollection, that the parietal SME is pronounced when intrinsic features of a stimulus event are reinstated, and that the outcome of this process leads to better performance in a later memory test.

Another relevant study explored ERP SMEs during unitization encoding. Unitization refers to an encoding strategy that allows to flexibly bind components of an association to a single configuration that is similar to a single item representation and supports familiarity-based remembering (Parks and Yonelinas, 2015; Bader et al., 2010; see Mecklinger and Bader, 2020 for a review). In a study by Kamp et al., (2016, 2017) participants were presented with word pairs in the context of a definition that allows to encode the two words as a compound word. In a control condition the same word pairs were encoded in the context of a sentence frame that allows to process the two words associatively while maintaining separate representations in memory. While memory performance did not differ between the conditions, pronounced SME differences emerged: Only in the definition condition was there an early parietal and a frontal SME between 300 and 600 ms, whereas a late frontal SME between 1200 and 2000 ms was evident in both conditions. These findings hence support the view that the parietal SME reflects the encoding of item-specific information (Cohen et al., 2015; Otten and Donchin, 2000; Gonsalves and Paller, 2000; Fabiani and Donchin, 1995). The late frontal slow wave SME evident in both conditions was taken to reflect longer-lasting working memory processes supporting inter-item or item-context binding by which encoding gains memorability in the subsequent memory test (Kamp et al., 2017).

A parietal SME starting between 350 ms and 500 ms similar to the aforementioned unitization study has also been observed when novel face-name pairs were encoded and subsequently tested by cued recall (Folgueira-Ares et al., 2017) or associative recognition (Mangels et al., 2009; Guo, Voss and Paller, 2005), or when pairings of faces with occupations were encoded and subsequently retrieved (Yovel and Paller, 2004). Guo et al. (2006) reported a positive-going SME between 400 and 600 ms for Chinese characters successfully retrieved with figurative visual background information (squares and circles) for which a neural source analysis revealed generators in the parietal cortex. Under the assumption that a name and an occupation or a Chinese character together with a figurative background can be processed as an integral item feature, these findings support the view that the parietal SME is pronounced when unitized, item-like representations are formed.

Recent studies exploring SMEs during schema-based learning have investigated how knowledge structures composed of previously acquired information affect the processing of newly encountered information (see Gilboa and Marlatte, 2017 for a recent review). In an illustrative study by Höltje et al. (2019), participants studied words that were either congruent or incongruent with schema knowledge presented in a preceding sentence frame. Congruent words were remembered better than incongruent ones and an SME started to emerge at 300 ms and extended for several 100 ms. While sustained frontal SMEs were obtained for both, schema congruent and incongruent words, a parietal SME was evident in this time period only for congruent words. A related study used the Deese-Roediger-McDermott (DRM) false memory paradigm (Roediger and McDermott, 1995) to explore how semantically congruent information affects memory encoding (Packard et al., 2017). There was a topographically widespread SME for words presented in congruent and incongruent contexts. Supporting the view that semantically congruent information speeds up memory formation the SME in the congruent condition was present 400 ms earlier than in the incongruent condition. In another study on schema-based learning, Meßmer et al. (2021) also reported early onsetting frontal and parietal SME from around 300 ms onwards. Notably, as in the report by Höltje et al. (2019) the parietal effect was solely present for words presented in a semantically congruent context whereas a partly overlapping sustained frontal SME was not modulated by the encoding task. Fig. 1 displays the early onsetting parietal SME elicited by semantically congruent words in the Meßmer et al. (2021) study.

Taken together, these findings provide clear evidence that SMEs differ depending on task characteristics. They also suggest that the processes supporting schema-based encoding differ qualitatively from conditions in which encoding is not supported by a schema, and hence do not reflect a mere graded or quantitative difference between the encoding processes. Of note, even though the neural generators of scalp recorded ERP activity cannot unambiguously be determined, different scalp distributions of two SMEs as in the aforementioned studies allow for the conclusion that qualitatively different neurocognitive processes contribute to encoding in the two conditions (Rugg and Coles, 1995).

Otten and Rugg (2001) also report a qualitative task difference between the ERP correlates of successful memory encoding. When participants made animacy judgments about visually presented words, consistent with the aforementioned studies, a positive-going SME was obtained at frontal recording sites. The SME started immediately after stimulus onset, continued for almost two seconds and showed a fronto-central scalp topography. This early-onsetting frontal SME is illustrated in Fig. 2. Conversely, when alphabetic decisions were required during encoding, correctly recognized words were associated with a negative-going ERP modulation with similar temporal characteristics. The frontal scalp distribution of the effect in their animacy task bears high resemblance to the early-onsetting frontal SME reported in other studies using semantic tasks, including animacy or edibility judgments for study words (Van Petten, Senkfor, 1996) or animacy and manipulability judgements on object images (Duarte, 2004). Robichon et al. (2002) explored successful memory encoding during sentence reading and found a frontally focused SME between 200 and 1600 ms. This effect was strongly enhanced when the study words, which were semantically congruent with a sentential context, were presented within sentences presented at a slow rate, compared to a fast presentation rate. Presumably, slow presentation times allowed for deeper semantic processes to unfold. This is consistent with Angel et al. (2017), who reported an increased sustained late frontal SME when participants had to self-generate, rather than merely read, a to-be-learned word, also supporting the idea that more elaborative encoding is associated with an enhanced sustained late frontal SME (see also Guo et al., 2006).

As the frontal scalp distribution of these positive-going SMEs in semantic tasks corresponds with similar effects in tasks employing deep semantic processing (Staresina et al., 2005; Van Petten, Senkfor, 1996; Wagner et al., 1998), Otten and Rugg (2001) speculated that this effect may relate to left inferior prefrontal cortex (PFC) activation which has been found in a number of fMRI studies employing the subsequent memory approach (Wagner et al., 1998; Otten et al., 2001; for a review see Kim, 2011). This view also implies that the brain regions involved in deep semantic processing and successful memory encoding overlap.

Using a paired associate learning task, Kim (2009) also report a pronounced SME difference as a function of the encoding task. They employed a paired associate learning task with sequential presentation of two words. An interesting aspect of this paradigm is that associative inter-item processing cannot start before both words have been presented. Hence SMEs related to item encoding can be separated from associative encoding of the word pairs. There was an early positive-going SME in a 530–580 latency window (the parietal SME) with largest amplitudes over parietal brain regions reflecting item encoding for both words whereas a long-lasting frontal positive slow wave in a 1000–1600 ms time window (the sustained late frontal SME) was

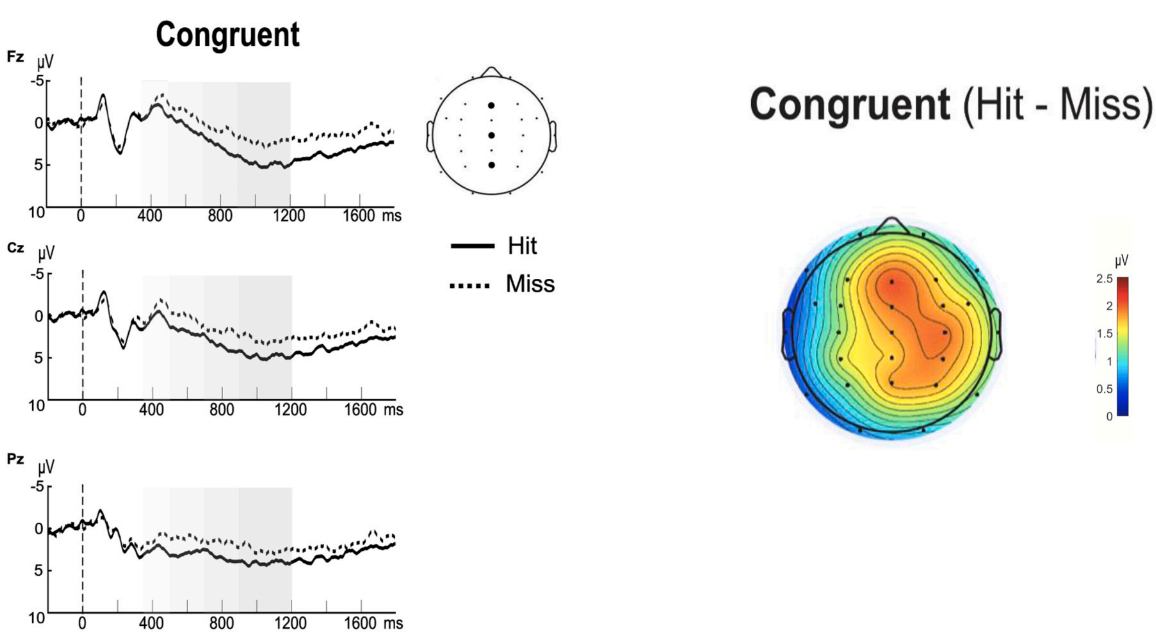

Fig. 1. The early onsetting parietal SME elicited by words preceded by semantically congruent sentential contexts in the study by Meßmer et al. (2021). The effect is present between 350 and 900 ms and shows a centro-parietal scalp topography. An additional sustained late frontal SME starts at around 900 ms and partly overlaps with the parietal SME. The topographic distribution in the 700–900 ms time window in which the parietal SME is significant is shown on the right.
Reprinted with permission from Meßmer et al. (2021).

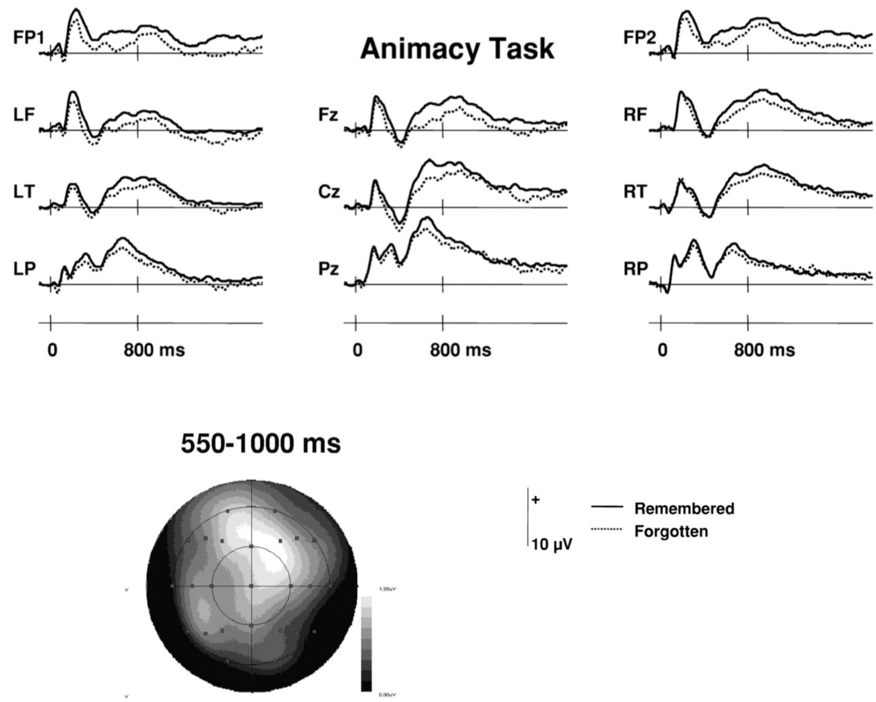

Fig. 2. The early-onsetting frontal SME elicited when participants made animacy judgments for visually presented words in the study by Otten and Rugg (2001). The effect is significant between 0 and 350 ms and between 550 and 1000 ms and shows a frontal scalp topography. Note that positive voltages are plotted upwards in this figure.
Reprinted with permission from Otten and Rugg (2001).

obtained selectively for successfully recalled word pairs. Similarly, Weyerts et al. (1997) reported that only associative, but not non-associative semantic encoding tasks of word pairs lead to a sustained late frontal SME. However, as this study only contrasted old pairs and completely new pairs, the task could also be performed on the basis of memory for the single words and therefore has lacked a clear associative processing component. Hence, the differential SME in both tasks may have even been more pronounced when memory performance on the basis of single items would have been controlled for. Forester and Kamp (2023) observed a similar dissociation of the SMEs related to successful item and associative encoding in a modified paired associates learning paradigm. While the parietal SME was related exclusively to subsequent item recognition, a sustained late frontal SME elicited when encoding entailed semantic elaboration was related to both item and associative recognition.

The studies discussed so far support the view that encoding is supported by multiple task-specific systems. In addition, they provide important hints regarding the functional significance of the different SMEs associated with each system. Thus, a common characteristic of the tasks eliciting pronounced early onsetting frontally distributed SMEs emerging at around 300 ms after the onset of the stimulus is the requirement to process semantic attributes of a stimulus. Accordingly, a tentative conclusion is that the early onsetting frontal SME reflects the processing and selection of semantic attributes of an event in order to incorporate them in an event's internal representation. Regarding the parietal SME with an onset around 300–500 ms, the aforementioned studies suggest that it is pronounced when encoding is enriched by the reinstatement of item features from prior study episodes, when the components of an association are integrated into a unitized, item-like representation, and with schema-based encoding. Finally, several studies have identified a third subcomponent of the SME, a late frontally distributed SME with an extended duration, that presumably reflects the use of elaborative encoding strategies with an emphasis on inter-item processing (see Section 5 for a detailed discussion of the functional characteristics of the subcomponents of the SME).

3. Are SME modulated by the content to be retrieved and the way memory is tested?

Besides its sensitivity to encoding tasks, another relevant question is whether ERP SMEs reflect processes that are modality independent or whether they are sensitive to the specific aspects of the memoranda that are encoded and subsequently tested. Furthermore, SMEs may simply reflect "encoding processes", but in this case they should be independent of what kind of test is subsequently used to probe memory. The present section evaluates prior literature regarding these points.

3.1. SME differ by the content of the study material

A number of studies have suggested that SMEs can be dissociated as a function of the content participants are subsequently required to retrieve. Mecklinger and Müller (1996) compared SMEs for spatial information and familiar object forms. Response times and accuracy did not differ between conditions. Remembered object forms gave rise to a frontal SME starting around 400 ms and a simultaneous parietal SME. This suggests that successful encoding of well-known object forms is supported by semantic processing and the extended processing of object features. Both effects were virtually absent for spatial locations under otherwise identical testing conditions. A post hoc analysis revealed that the absence of any SMEs in the spatial task most likely results from the use of shallower and less elaborative encoding strategies than in the object task.

In a study by Bridger and Wilding (2010) participants were presented with words at different screen locations and were required to make either a drawing difficulty judgment or a pleasantness judgement. In the test phase they were asked to either remember the screen location or the judgment task from the study phase. The analysis revealed broadly distributed SMEs in both tasks starting around 300 ms. Interestingly, there was a clear difference in the polarity of these effects from 900 ms onwards. Remembered locations were associated with negative-going waveforms whereas remembered study tasks gave rise to positive-going SMEs. This pattern of results indicates that SME can differ qualitatively as a function of the content to be retrieved even when all aspects of the study and test phases were held constant.

A polarity reversal of the SME dependent on the study content was also reported by Otten et al. (2007) when comparing SMEs for words and orthographically legal non-words. There was a positive-going frontal SME starting around 600 ms for remembered words whereas remembered non-words were associated with a topographically widespread negative going waveform from 1000 ms onwards. One interpretation for the polarity differences of the SME could be that the tasks differed in the relative engagement of semantic and perceptual processing during the generation of internal representations. Indeed, the studies reviewed so far suggest that SME with positive polarity and with frontal or parietal topographies are typically observed when study stimuli are familiar to the subjects and/or when encoding is supported by the processing of semantic attributes of study events. Conversely, negative going or absent SMEs are usually observed in situations characterized by processing of perceptual features of an event, like the encoding or retrieval of spatial stimulus characteristics (Bridger and Wilding, 2010; Mecklinger and Müller, 1996), non-word encoding (Otten et al., 2007), encoding together with alphabetic decisions (Otten and Rugg, 2001), encoding of meaningless shapes or letter strings (Khader et al., 2007), or relatively superficial encoding of an item without or with incorrect encoding of its temporal source (Angel et al., 2013). Reports of an early parieto-occipital SME with reversed (negative going) polarity in a recent study by Kamp (2020) using a shallow semantic judgment task with relatively low semantic processing demands, in a study by Spachtholz, Kuhbandner (2017) in which perceptual information of object features was encoded incidentally, and in a study in which meaningless visual patterns were encoded (Brodeur et al., 2011) are also consistent with this view. Hence, as a whole, this set of studies supports the view that positive- and negative-going SMEs reflect processes which are of importance for later remembering of conceptual and perceptual information, respectively.

Of relevance here is also an ERP SME study exploring how the congruency between processes engaged at study and test affects encoding related ERP activity (Bauch & Otten, 2012). Participants studied intermixed lists of pictures and words and in a subsequent memory test were either probed with the same mode of presentation (picture-picture; word-word) or in a different mode than at presentation (picture-word; word-picture). When a memory decision with a word cue required the recovery of perceptual details of a study episode (picture-word) a parietal SME was obtained from around 100 ms onwards, whereas in all other retrieval situations a frontal SME emerged with a similar time course (Bauch and Otten, 2007. This suggests that SMEs critically depend on the congruency between the processes initiated at study and at test and that the parietal SME is sensitive to the recovery of perceptual features form a prior study phase when memory is probed with words.

Other studies have shown that SMEs differ by the emotional content of the study material. For example, Righi et al. (2012) showed that in an encoding task in which participants had to discriminate between positive, negative and neutral facial expressions, followed by a recognition test in which all faces had neutral expressions, a parietal SME between 350 and 600 ms emerged, which was larger for negative than for positive or neutral facial expressions. Dolcos and Cabeza (2002) presented positive, negative and neutral images to participants in an intentional encoding task. Participants rated each picture's emotionality and subsequently completed a free recall task. In an early time window (400–600 ms), the SME was enhanced for emotional versus neutral images. Furthermore, Kamp et al. (2015) showed that negative words elicited enhanced parietal SME, while Weigl et al. (2020) reported an enhanced parietal (P300) SME for those words with more extreme (positive or negative) valence. Converging evidence thus suggests that emotional stimuli elicit an increased parietal SME.

3.2. SME differ as a function of how memory is tested

Two studies by Paller and colleagues (Paller, 1990; Paller et al., 1988) were the first to systematically investigate whether SME differ according to how memory is tested. Paller (1990) reports SMEs at frontal and central recordings from 400 ms onwards in two explicit tests of memory (cued and free recall) but not when memory was tested with an implicit (stem completion) test. This finding was confirmed in a study applying a more refined analysis to more systematically disentangle explicit from implicit memory (Schott et al., 2002). Several other studies have furthermore reported that SMEs were less pronounced or absent when recognition was tested, compared to recall (e.g., Batterink and Neville, 2011; Fabiani and Donchin, 1995; Münte et al., 1988; Karis et al., 1984).

A number of studies have examined whether ERPs at encoding differ for items later remembered on the basis of familiarity or recollection. Friedman and Trott (2000) examined this using a remember/know (R/K) recognition memory procedure (Tulving, 1985). They found that ERPs were more positive for subsequently remembered than both subsequently known and missed words starting around 500 ms. This effect lasted for several 100 ms and was broadly distributed over the scalp. Duarte et al. (2004) presented pictures of objects as study events, followed by a combined R/K and source memory procedure, and reported that subsequent familiarity-based recognition was associated with an attenuated left anterior negativity between 300 and 450 ms, whereas subsequent recollection gave rise to a topographically distinct early positivity followed by a frontal SME between 450 and 600 ms. Also using the R/K paradigm, Mangels et al. (2001) reported that words that were subsequently remembered based on familiarity and recollection were associated with a larger N340 at left frontal recording sites than words forgotten in the memory test. Remarkably, only words later recalled or remembered on the basis of recollection gave rise to an additional sustained SME with a duration of several hundred milliseconds at frontal sites. Meng et al. (2014) also found an early (300–400 ms) positive-going SME, followed by an additional later (500–600 ms) positive going parietal SME associated with familiarity, a similar SME that has been found to covary with a test phase ERP measure of retrieval success in another study (Chen et al., 2014). Subsequent recollection, by contrast, was characterized by a sustained positive-going frontal SME (Meng et al., 2014). Similarly, a late frontal SME sensitive to recollection was reported by Rollins and Riggins (2018) and Yovel and Paller (2004) using source memory tasks requiring relational processing among study items and by Porter et al. (2021a) using a R/K procedure. While these findings are heterogeneous, they do provide converging evidence that the two forms of remembering are dissociable at encoding. Subsequent recollection is most consistently characterized by a sustained SME at frontal sites. The evidence for subsequent familiarity is mixed, with some studies reporting an early left frontal SME and others reporting a positive-going parietal SME.

In a recent study by Forester and Kamp (2023), sequentially presented object pairs were encoded via interactive imagery. Additionally, upon presentation of the first object of a pair, participants either performed a semantic elaboration task, a visual task focusing on perceptual features of the image, or no particular task (control condition). In a subsequent test, item recognition memory for the individual objects as well as associative memory for the pairing was tested. In the semantic elaboration task, a frontal slow wave SME of positive polarity was linked to both item and associative recognition. Intriguingly, in the visual elaboration task, the same kind of SME was associated with item recognition, while a SME of negative polarity was associated with associative recognition. The early parietal SME was associated with subsequent item recognition, but not with associative recognition, in all task conditions. Taken together, SMEs differ depending on whether item information or an inter-item association has to be retrieved during the subsequent test.

In sum, different aspects about the study material as well as the manner in which memories are subsequently tested and retrieved have been consistently demonstrated to affect ERP SMEs. Notably, the influence of the manner of retrieval on the SME is strong evidence that SMEs cannot simply be interpreted as merely indexing “encoding processes”, even though it is often the simplest way to word SME patterns. Technically, SME index which processes set in train during encoding are associated with successful subsequent retrieval *in a given test format*. Hypothetically, processes engaged during encoding that are beneficial for one form of subsequent retrieval or one specific study content may hinder a different form of retrieval or content. This may contribute to polarity reversals in ERP SMEs. An interpretation of ERP SME should hence always consider which test was conducted and which content had to be retrieved.

4. What is the role of “distinctiveness” in ERP subsequent memory effects?

Section 2 has clearly shown that SMEs vary as a function of the encoding task, as for example tasks that entail the processing of conceptual versus perceptual features of a study event or tasks in which encoding is supported by the presence of schema knowledge versus tasks where it is not. Another important contextual factor known to influence memory encoding is the primary distinctiveness, or novelty, of a stimulus event in a given context (McDaniel and Geraci, 2006). As early as 1933, von Restorff developed an experimental paradigm that was designed to address Gestalt-theoretic research questions, but which also allows to investigate distinctiveness effects in memory. Participants are presented with lists of items which they have to retrieve in a subsequent memory test. Some of the items in the list (so-called “isolates”) are made distinctive by one or by a combination of attributes. Distinctive items are better recalled than the other items in the list, an effect that is nowadays known as the “von Restorff effect”. A number of studies in the mid-1980 s using the SME approach explored the relationship between ERPs during encoding and subsequent memory performance with a distinctiveness manipulation. The first study in this series found that words that deviated from their study list in a physical feature (font size) elicited a P300 and that those distinctive words that were subsequently freely recalled elicited a larger P300 than those that were not recalled (Karis et al., 1984). This P300 SME was explained such that the P300 reflects “context updating”, the degree to which memory is reorganized when a current model of the environment needs to be modified due to the encounter of unexpected or distinctive information, a process that occurs in interaction with long-term memory processes (e.g. Kamp and Donchin, 2015; Kamp et al., 2013; Otten and Donchin, 2000; Lian et al., 2002; Fabiani and Donchin, 1995; Fabiani e al, 1990; Donchin and Coles, 1988). The P300 SME resembles the early-onsetting parietal SME discussed before and has also been reported for emotional words which due to their emotional salience stand out in a given processing context (Kamp et al., 2015; Weigl et al., 2020).

Not all forms of distinctiveness modulate the early parietal SME and improve memory. Thus, a study by Otten and Donchin (2000) showed that only words which were distinctive due to an integral feature of the word, like its color or font size, elicited a parietal SME, whereas words which were made distinctive by a nonintegral feature (i.e., being surrounded by a frame at far distance) elicited a positive-going SME at frontal recording sites. Nondistinctive words from all study lists were associated with frontal SME (Otten and Donchin, 2000). Similarly, Wiswede et al. (2006) reported a parietal SME for words isolated by their font color (integral distinctiveness), but not for words isolated by an emotional background picture (non-integral distinctiveness). Furthermore, Rangel-Gomez and Meeter (2013), induced distinctiveness by a tone co-occurring with the presentation of a word. No parietal SME was observed with this non-integral manipulation of distinctiveness (note, however, that a frontal SME was also not observed). It is important to note that in such circumstances, a P300 is still elicited by deviant stimuli, but its amplitude is not correlated with subsequent memory. These results are important in that they show that an event’s distinctiveness is not a general attribute that always enhances the memorability of an event, by virtue of enhanced allocation of attention to stimulus encoding or by otherwise deeper processing of stimulus features. Rather, only integral distinctive features that are relevant for the task at hand modulate the early-onsetting parietal SME. This again underscores the idea that SMEs do not merely reflect which processes are engaged during the initial encounter of events, but that they reflect which processes are *relevant* for successful subsequent retrieval in the given test.

The relationship between P300 and memory performance also critically depends on what other processes are engaged during memory encoding. In support of this view, the P300-memory relationship only holds when participants use relatively simple or rote memorization strategies, as for example, encoding words by silently repeating them (Fabiani et al., 1990; Lian et al., 2002). Conversely, when people apply elaborative strategies during encoding, as for example by building inter-item associations between the memorized materials, both the recall advantage for distinctive words and the parietal (P300) SME disappear. Instead, elaboratively encoded stimulus events elicit a frontally distributed SME (e.g., Mecklinger and Müller, 1996; Fabiani et al., 1990). A study that supports the view that distinctiveness-based encoding of isolates can be replaced by elaborative encoding was recently conducted by Koppehele-Gossel et al. (2019). Using a word list paradigm in which distinctive items differed in font type and size and participants were encouraged to use elaborative encoding strategies, they found a frontal positive-going SME, which was highly similar to the late frontal SME to nonintegral distinctive event in the report by Otten and Donchin (2000) or to frontal slow waves in other SME studies without distinctiveness manipulation in which elaborative memory strategies were used (e.g., Forester, Kroneisen et al., 2020; Höltje et al., 2019; Zerbes and Schwabe, 2019; Caplan et al., 2009; Weyerts et al., 1997; Mecklinger and Müller, 1996; Paller, 1990). These results together led to the idea that elaborative strategies reflected in frontally distributed slow wave SME can replace initial distinctiveness-based encoding as revealed by the P300 and the parietal SME (Fabiani and Donchin, 1995). Thus, such strategies are a powerful way to make study events memorable, rendering the outcome of this process more useful for successful subsequent memory retrieval than relatively low-level distinctiveness features of events.

To summarize, studies investigating the relationship between ERPs during encoding and subsequent memory using distinctiveness manipulations reveal that an event’s distinctiveness in a given context is not a general attribute of a stimulus event that supports memory formation by virtue of a uniform process. Rather, distinctiveness-based encoding can be replaced by elaborative encoding strategies, which are often a more powerful technique to support subsequent retrieval. A relative shift from distinctiveness-based encoding towards elaborative encoding is thus reflected in an enhanced magnitude of the sustained late frontal slow wave, relative to a decreased early parietal SME.

5. What are the components of the SME and which processing mechanisms do they reflect?

A critical aspect of this review concerns the functional organization of SMEs. Even though the precise functional significance of the SMEs needs to be determined there is increasing evidence that suggests that, when the encoded material has some conceptual representation in semantic memory, post-stimulus SME activity can be subdivided into three different types, which all typically show a positive polarity: An early frontal SME that emerges at around 300 ms at frontal or left frontal sites for verbal material, a simultaneously onsetting (300–500 ms) SME with a parietal scalp distribution which is usually brief in duration, but can also be extended over time, and a sustained frontal SME with a longer latency, observable when people use elaborative encoding strategies with an emphasize on inter-item processing. Examples of the three SMEs are given in Figs. 1 to 3. When encoding draws on perceptual or shallow

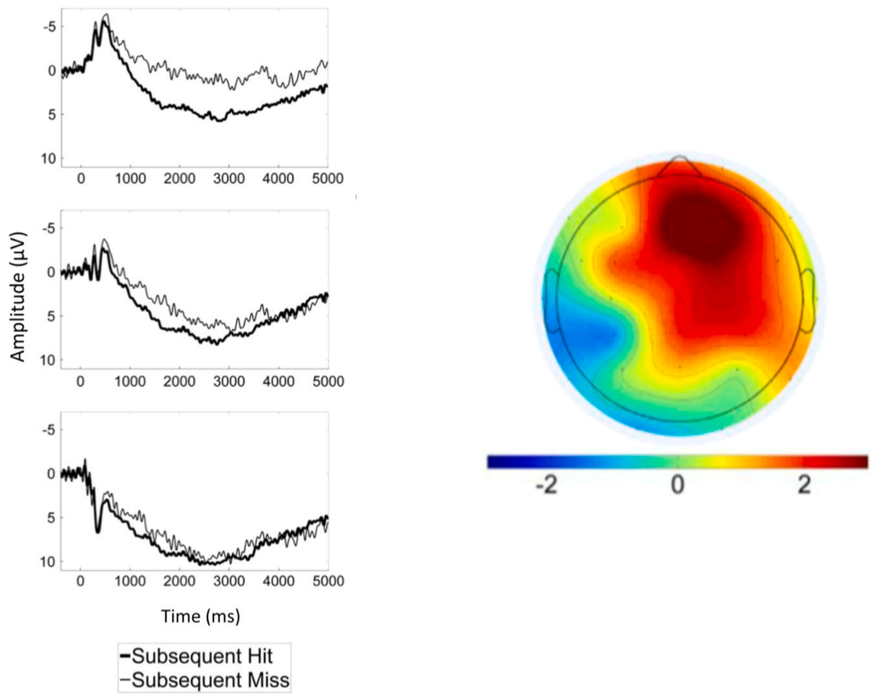

Fig. 3. The sustained late frontal SMA elicited by successfully encoded object picture pairs in the study by Kamp and Zimmer (2015). Participants used interactive imagery to encode the picture pairs and associative memory was assessed in an ensuing recognition memory task. The frontal topographic distribution between 1400 and 2200 ms post-stimulus is shown on the right.
Reprinted with permission from Kamp and Zimmer (2015).

processes, negative-going SME tend to be elicited, but the scarcity of prior literature does not yet allow for a detailed functional interpretation of this kind of SME.

5.1. The early frontal SME

As outlined in Section 2, studies reporting an early frontal SME typically employ tasks that emphasize the processing of semantic features. In most of these tasks the early frontal SME takes the form of an attenuated negativity resembling the N400, an ERP component related to semantic retrieval (Kutas and Hillyard, 1980). An exception is a study by Lian et al. (2002) that found an early SME to physical isolates that took the form of an enhanced P200 in a rote rehearsal task without explicit semantic processing requirements. It has been suggested that successful encoding can be supported by the processing of semantic features of a stimulus event (Otten and Rugg, 2001) and that the topographic distribution of the effect can be taken as evidence for the contribution of the left prefrontal cortex to efficient memory encoding (Wagner et al., 1998). Similar results that underscore the relevance of deep semantic processing for early memory encoding were obtained in an MEG study (Staresina et al., 2005). MEG SMEs were observed between 300 and 650 in frontal brain regions which also showed more pronounced MEG activity for semantic than for structural processing of words in an incidental encoding task. Notably, Friedman and Johnson (2000) in their initial review paper also raised the possibility that the left prefrontal cortex contributed to the early frontal SME.

Further support for the relevance of semantic processing for efficient memory encoding in this early time period and indications regarding the brain regions mediating successful encoding in this time interval come from studies employing intracranial ERP recordings in pre-surgical patients with temporal lobe epilepsy. Fernández et al. (1999) recorded ERPs from two medial temporal lobe structures, the anterior parahippocampal gyrus (in the vicinity of the rhinal cortex) and the hippocampus, while the patients studied words for a subsequent free recall test. There were reliable SME in both structures. They took the form of an attenuated negativity at 440 ms after word onset at the recording sites in the rhinal cortex, the so-called AMTL-N400 and a positive slow wave with a duration of several hundred ms which was present in the hippocampus from 500 ms onwards. An SME in the hippocampus, though of different polarity, has also been reported by Axmacher et al. (2010a) in a study exploring the impact of expectancy on memory formation. Notably, no evidence for a SME on hippocampal slow waves was obtained in another intracranial ERP study which contrasted the interplay of working memory and long-term memory in the hippocampus (Axmacher et al., 2010b). The lack of an SME could have resulted from the use of a recognition test and/or the relatively low memory performance resulting in too low trial numbers for ERP averaging. In any event, the sequential structure of the SMEs in the rhinal cortex and the hippocampus in the study by Fernández et al. (1999) suggests that both brain regions contribute successively to memory formation at least when memory is tested with free recall tests and memory performance is sufficiently high to allow reliable SME analyses.

As the results suggest that the rhinal cortex starts to contribute to successful memory encoding as early as 300 ms it is conceivable that it also supports the semantic processing reflected by the early frontal SME. Strong evidence for this view comes from another intracranial ERP study which investigated how a word frequency manipulation affects memory encoding (Fernández et al., 2002). High frequency words are rich in semantic context and allow for more associative semantic processing than low frequency words for which lexical representations are less readily accessible (Glanzer and Adams, 1990). Both word types generated reliable SME in the hippocampus. However, an SME in the rhinal cortex was only obtained for high frequency words. The AMTL N400 was selectively enhanced for subsequently remembered relative to forgotten high frequency words. Even though the study is limited by the fact that only nine patients participated, the results support the view that the rhinal cortex contributes to early memory formation by virtue of semantic processing that enhances the formation of durable declarative memories. Another SME study using a word frequency manipulation together with a word list free recall paradigm was reported by

Fernandez et al. (1998). Consistent with the intracranial ERP study an early SME in the vicinity of the N400 at fronto-temporal recordings was present for high frequency words and delayed by about 150 ms for low frequency words. Even though the early SME to high frequency words differed in polarity (an enhanced AMTL N400 in Fernández et al., 2002 and an attenuated N400 in Fernandez et al., 1998) and different word frequency criteria and list length manipulations were employed in both studies, the commonalities in the SMEs to low and high frequency words in intracranial and scalp recorded data are striking. Taken together, the results support the view that the contribution of semantic processing, mediated in part by the rhinal cortex and the left prefrontal cortex, to memory encoding is reflected in the early frontal SME.

5.2. The early parietal SME

As already suggested in Section 2, one theoretical interpretation of the early-onsetting parietal SME is that it reflects item-specific memory encoding (Kamp et al., 2017; Kim et al., 2009). However, speaking against the idea that the parietal SME reflects item-specific processing very generally are some studies that did not report an early parietal SME (Meßmer et al., 2021; Höltje et al., 2019) or reported a frontally distributed SME in the same time window instead (Guo et al., 2006) when item encoding likely played a role. It hence appears that a more refined view of the parietal SME is necessary. More specifically, the parietal SME may be observed when multiple features of an item are effectively bound together so that a rich and detailed item representation can be subsequently retrieved as a whole. From now on we will refer to this view as the "intra-item binding" view of the parietal SME.

In support of the aforementioned view, the parietal SME is often more pronounced in tasks that require shallower or less elaborate processing, compared to deeper, more elaborate study conditions in which associative information is processed (Forester, Kroneisen et al., 2020; Schott et al., 2002). Furthermore, Forester and Kamp (2023) reported direct evidence that the parietal SME relates to item but not inter-item associative memory. Notably, the parietal SME appears to require the availability and processing of prior semantic knowledge (see Section 3.1.). Indeed, item memory encoding should benefit from the recovery of prior semantic knowledge as this knowledge may facilitate intra-item binding processes and the memory representation may become richer and easier to retrieve. Typical item memory tasks involve relatively simple semantic or orthographic tasks that support intra-item binding processes (Yonelinas et al., 2010). The fact that the parietal SME is consistently found for familiar objects or words with well-known semantic attributes, as well as the fact that schema-based encoding elicits a parietal SME, are hence consistent with the intra-item binding view.

Strong support for the view that the early-onsetting parietal SME is pronounced under item-specific processing conditions also comes from a study exploring verbatim and gist encoding of word pairs (Cheng, Rugg, 2010). A parietal SME was found in an encoding situation in which word specific (verbatim) encoding was relevant for subsequent memory but not in a second condition that encouraged the encoding of gist-like semantic relations between words. The latter condition gave rise to a simultaneous frontal SME instead. Considerable further evidence comes from a study exploring the relationship between encoding and subsequent memory illusions using a modified version of the DRM false memory paradigm (Urbach et al., 2005). Words that were correctly recognized and did not lead to memory illusions in a subsequent memory test elicited more positive ERP waveforms at encoding than words that did induce false memories. This effect, which was referred to as DIM, (**d**ifference due to **i**llusionary **m**emory) was present between 500 and 1300 ms (and hence somewhat temporally drawn out), showed a maximum at parietal sites and was taken to reflect item-specific encoding processes that make memory representations of individual words more distinct and better discriminable from semantically related words (Urbach et al., 2005).

The parietal SME has been shown to emerge when subsequent retrieval in a recognition test is based on familiarity in the absence of recollection (Meng et al., 2014). By contrast, other studies have reported an association between the parietal SME with subsequent high confidence recognition judgments (Mangels et al., 2009) and this SME to be enhanced when recall rather than recognition is tested (Münte et al., 1988; Paller et al., 1988). Hence, it appears that the parietal SME cannot simply be mapped on either familiarity-based or recollection-based retrieval. Since item memory can be supported by both types of retrieval (Yonelinas et al., 2010), this inconsistent mapping of this SME with familiarity and recollection, however, does not contradict a role of this SME in item encoding.

As outlined in Section 4, events that stand out in a given processing context elicit a parietal (P300) SME, given that integral features of an event are used to induce distinctiveness, and that these features are relevant for subsequent retrieval (Otten and Donchin, 2000; Fabiani et al., 1990; Karis et al., 1984). It is not entirely understood how distinctiveness affects a memory representation of a stimulus event and enhances its memorability. It is conceivable, for example, that distinctive features of an event attract attention and that the additional allocation of attention, when it is directed at task-relevant information, results in facilitated processing of perceptual information and in deeper and elaborate processing of this event (Craik and Lockhart, 1972). This extended attentional processing may also modulate the parietal SME. A role of attentional processes in the parietal SME is supported by the finding that this SME is enhanced when successful encoding is rewarded, versus unrewarded (Marini et al., 2011). In the latter study a parietal SME was present as early as 300 ms selectively for faces preceded by a reward cue which presumably reflects enhanced motivation for face learning. The enhanced parietal SME for emotional stimuli (Section 3) and when a novel study event is task-relevant versus irrelevant (Cycowicz and Friedman, 1999) further supports this view. A role of attentional processes as outlined here is also in line with the intra-item binding view of the parietal SME, but it is important to note that the attention-grabbing feature of the study event must be goal-relevant, and the distinctive feature must be utilized to support subsequent retrieval in order for a parietal SME to occur.

Another process that contributes to the parietal SME is visual imagery. Imagery is an encoding technique known to improve long-term memory formation in particular for stimulus events for which preexisting (semantic) mnemonic representations exist, like famous faces (Ishai, 2002), or previously familiarized objects (Handy et al., 2004). Brain imaging studies have revealed that similar posterior and medial parietal brain regions are involved in visual imagery (Schott et al., 2018; Byrne et al., 2007) and memory encoding (Otten et al., 2002; Buckner et al., 2001; Henson et al., 1999). One of these regions is the precuneus, a medial parietal region that is crucial for visual imagery and also plays a role in memory formation (Otten et al., 2002; Henson et al., 1999) and together with other parietal brain regions is also involved in the generation of the P300 (Geng and Vossel, 2013; Bocquillon et al., 2011). Remarkably, a meta-analysis of brain imaging studies on successful memory formation (Uncapher and Wagner, 2009) revealed that 85% of the studies under investigation reported larger BOLD signals for subsequently remembered than forgotten items in dorsal posterior parietal regions that support goal-directed allocation of attention (Corbetta and Shulman, 2002) and partly overlap with the precuneus. Further support for the view that the parietal SME is related to imagery and/or visualization comes from three other SME studies (Gjorgieva et al., 2022; Gonsalves and Paller, 2000; Bauch and Otten, 2012).

Although there are still many details that need to be specified with respect to the parietal SME, on the basis of the observations presented above, we propose that the parietal SME is elicited when an item-specific memory trace is generated for study events with existing prior semantic knowledge. This item-specific trace can be enriched by processes supporting intra-item binding, like the active formation of visuo-spatial memory representations, the recollection and integration of details from prior experiences with the study event (see Section 2), and by enhanced attentional processing of task-relevant distinctive perceptual item features. The presented evidence from brain imaging suggests that the precuneus, a region in the medial posterior parietal cortex may be one of the brain regions critically involved in the generation of the parietal SME.

5.3. The sustained late frontal SME

A frontal SME with a longer onset latency and an extended duration is typically obtained when people use elaborative encoding strategies with an emphasis on relational processing of different information units (inter-item processing). In the earliest report of a frontal positive slow wave predictive of subsequent recall, Karis et al. (1984) employed a list learning paradigm and sorted participants according to their self-reported memorization strategy. Participants who reported elaborative rehearsal strategies, defined as "complex strategies, mainly involving combining the words into stories, or producing complex images or sentences" (Karis et al., 1984) showed a frontal slow wave SME from 540 ms onwards, which was clearly delayed relative to the early parietal SME displayed by those participants who reported the use of rote rehearsal strategies. Similar prolonged late frontal SMEs in association with elaborative memory strategies were reported in studies manipulating distinctiveness (Koppehele-Gossel et al., 2019; Fabiani et al., 1990) and without such a manipulation (Höltje et al., 2019; Zerbes and Schwabe, 2019; Kamp et al., 2017; Friedman & Trott, 2010; Mecklinger & Müller, 1993). As discussed in Section 3.2., this sustained late frontal SME (or frontal slow wave SME) has been relatively consistently linked with subsequent recollection-based retrieval.

Elaborative encoding emphasizing inter-item processing is typically engaged in associative memory tasks requiring relational processing among multiple items of a study episode (Kim, 2011; Yonelinas et al., 2010). Indeed, a sustained late frontal SME is frequently reported in paradigms in which the combination of two or more stimuli are encoded and subsequently retrieved (Kamp et al., 2019; Cheng and Rugg, 2010; Kim et al., 2009; Jäger et al., 2006; see Section 2). In an instructive study from our own lab (Kamp and Zimmer, 2015), participants used interactive imagery to encode pairs of familiar objects and associative memory was tested in a subsequent recognition memory task. As apparent from Fig. 3, there was a pronounced long-lasting late SME that displayed a frontal scalp distribution. The effect was most pronounced between 1400 and 2200 ms after onset of the picture pairs.

The frontal slow wave predictive of successful memory formation resembles frontal slow waves associated with long-term memory (Mecklinger, 2010; Rösler et al., 1997) and verbal working memory processes (Khader et al., 2007). Similarly, Bosch et al. (2001) found negative slow waves at frontal recording sites when different kinds of verbalizable materials (e.g., object forms and spatial locations) were maintained in working memory. Likewise, Khader et al., (2005, 2007) reported slow waves in a task that combined working memory maintenance with long-term memory formation. On the basis of these studies, Kamp and Zimmer (2015) argue that the sustained late frontal SME occurs when multiple information units are held and manipulated in working memory to elaboratively form an inter-item associative representation. In line with a role in forming associations between multiple information units, a sustained late frontal SME has been associated with memory for temporal source (Angel et al., 2013), with the amount of contextual information retrieved (Estrada-Manilla and Cansino, 2012), with correctly retrieved spatial study locations (Cansino and Trejo-Morales, 2008; but see Bridger and Wilding, 2010, for a different result), and with the combined retrieval of item and order information (Caplan et al., 2009).

Another study reported that this SME is observed when participants selectively encode task-relevant information, but less so, when task-irrelevant information is encoded relatively equally compared to task-relevant information (Richter and Yeung, 2016), potentially suggesting a role of executive control processes over encoding in the emergence of this SME. Fernandéz et al. (1998) reported that the late frontal SME was pronounced for high frequency, but absent for low frequency words, which they interpreted as the need to employ additional organizational or associative elaboration processes for high frequency words, which are low in distinctiveness. The aforementioned studies also suggest that the sustained late frontal SME can be observed when individual items are encoded elaboratively, and not only when combinations of multiple study items are encoded together.

An important question concerning the sustained late frontal SME is whether it can be dissociated from the earlier frontal SME or whether it is a continuation of the latter process. Indeed, in some studies, the ERP correlate of successful encoding takes the form of a sustained frontal positive slow wave that starts around 300–400 ms post-stimulus and extends for several hundred ms (Höltje and Mecklinger, 2022; Sundby et al., 2019; Meßmer et al., 2021; Bauch & Otten, 2012; Robichon et al., 2002; Friedman and Trott, 2000). A notable exception is a recent study from our own lab (Kamp et al., 2017) in which we showed that the early frontal SME is only present during the successful encoding of unitized items whereas the sustained late frontal SME emerges regardless of encoding condition, which speaks for a functional dissociation of the early and the sustained late frontal SME. Resolution of this issue thus has to await further research. Notably, Kamp et al. (2017)'s finding, as unitization encoding fosters item memory encoding, again supports the view that the sustained late frontal slow wave is not exclusively indicative of successful elaborative inter-item encoding. Rather, the sustained late frontal slow wave SME appears to be an index of associative processing of conceptual features of any kind, by which memory representations of items or inter-item associations gain memorability in a subsequent memory test. Evidence for this view also comes from the aforementioned study by Bauch & Otten, (2012), exploring the effects of study-test congruency on memory encoding (see Section 3.1). A sustained frontal SME extending from 100 to 1900 ms was obtained for studied words irrespective of whether memory was probed with words or pictures, and for studied pictures cued with pictures as test cues, presumably reflecting that an extended and continuous processing of conceptual features of words and pictures (in the latter case) supported subsequent retrieval.

In sum, even though it is not yet settled which processing mechanisms are reflected in the sustained late frontal SME, it is typically observed when elaborative encoding strategies emphasizing relational processing of multiple study items are employed. Furthermore, a large body of evidence suggests that this SME is not confined to inter-item associative processing, but rather reflects associative processing of conceptual information of any kind by which studied items gain memorability in a subsequent memory test. On this account, items whose conceptual features are processed more extensively are more likely to be remembered later on. These processes may be supported by maintenance and manipulation of information in working memory and, more generally, by cognitive control processes.

5.4. Caveats on identifying SME subcomponents

Caution is required when attributing an observed SME pattern to the specific subcomponents of the SME, in particular as in some studies the effects are broadly distributed across the scalp and do not unequivocally allow to identify a frontal or a parietal subcomponent. In an illustrative study, Bloom and collaborators set out to explore how epistemic curiosity, operationalized as tip-of-the-tongue (TOT) state (Brown, 1991), affects subsequent memory for facts (Bloom et al., 2018). Supporting the idea that being in a TOT state when feedback about a to-be-learned fact is given is associated with better subsequent memory, Bloom et al. (2018) report more positive going waveforms at central and parietal recoding sites for facts for which high TOT states were reported. Notably this TOT state ERP effect was topographically and temporally highly similar to the corresponding ERP difference between facts subsequently remembered and forgotten. A functional account for these similarities between TOT and SMEs in the ERP is difficult. On the one hand this could reflect that more prior information for to-be-learned facts is made available and that the availability of this semantic information is beneficial for effective memory encoding and gives rise to an early onsetting frontal SME. On the other hand, TOT states could enhance the motivation to remember, and this elevated motivational state could lead to increased attention to the to-be-learned facts, improve intra-item binding, and give rise to an early onsetting parietal SME. Perhaps the most likely possibility is that the broadly distributed positive-going ERP effects reflect a mixture of both processes and hence the co-occurrence of both SMEs.

A co-occurrence of both types of processes and an overlap of their ERP correlates could also be the case in situations in which item memory encoding as reflected by the parietal SME benefits from the availability of semantic knowledge, indicated by the early frontal effect. As outlined before, semantic knowledge may facilitate intra-item binding processes and the memory representation may become richer and easier to retrieve. One way to disentangle both effects and their contribution to successful memory formation could be the conjoined analysis of post-stimulus SMEs and the SMEs preceding the to-be-encoded event, so-called pre-stimulus SMEs (see Section 7). As an illustration, Höltje and Mecklinger (2022) report a positive correlation between a frontal pre-stimulus SME and a parietal post-stimulus SME in their study on schema-based learning. This led to the idea that item memory encoding may benefit from processes that make semantic information available even before the to-be encoded information is presented. Determining the relative proportion and the relative time scale with which each of the two SME subcomponents contributes to the ERP correlate of successful encoding in the early time interval remains a challenge for future research.

Another issue in identifying SME subcomponents concerns the sustained late frontal SME and its overlap with other frontal slow wave activity that may not directly be related to memory encoding. Kolisnyk et al. (2023) report a right frontal slow wave overlapping with the frontal SME that covaries with an event's memorability and presumably reflects memory retrieval initiated by to-be encoded images. Porter et al. (2021b) observed a late frontal positivity related to self-related information that also overlaps with a simultaneous sustained late frontal SME. Two studies in our own labs revealed frontal slow waves co-occurring with the sustained late frontal SME. One study disclosed a late frontal slow wave overlapping with the sustained late frontal SME that co-varies with the false alarm rate in a subsequent recognition memory test and presumably reflects memory suppression processes (Höltje et al., 2019). In the other study, we explored the interplay between episodic memory and affective attitude formation (Forester, Halbeisen et al., 2020) and found a compelling relationship between frontal slow wave activity related to affective attitude formation and successful subsequent memory indicative for a shared neural mechanism for both effects.

One account for the component overlap is that in some cases, elaborative processing may be generally elicited by the encoding task or context, and slow wave activity may index the general involvement of such processes, which, however, is not predictive of trial-by-trial variability in encoding success. Such an explanation is consistent with the observation that slow wave effects can emerge over the course of an entire study list and be predictive of the number of words recalled rather than showing an SME on the individual trial level (Kamp, Lehman et al., 2016). This idea is related to state-related encoding effects, a discussion which we will return to in Section 6. Alternatively, such slow wave effects may not be indicative of processes related to encoding per se but reflect activity that is separable from the frontal slow wave SME (as for example memory suppression or retrieval processing initiated by familiar study events). Further studies that independently manipulate encoding tasks leading to main effects on slow wave activity and SMEs are needed to further test the relationship between slow wave activity and the sustained late frontal SME.

Another way to disentangle temporally overlapping SME or ERP slow waves and to disclose the component structure of the SME is to use spatio-temporal (or temporo-spatial) principal components analysis (PCA; Dien, 2010; Spencer et al., 1999). This approach decomposes the correlational structure of ERP data into spatial and temporal factors, thus disentangling overlapping ERP components. Using this procedure, we could for example show that the early frontal and the parietal SME were simultaneously active in a unitization encoding condition (Kamp et al., 2017). While a few other ERP SME studies have used PCA (e.g., Kamp, Potts et al., 2015; Kamp and Donchin, 2015; Kamp et al., 2013; Otten and Donchin, 2000; Mecklinger and Müller, 1996), further studies employing spatio-temporal PCA or similar techniques are warranted to disclose the component structure underlying ERP SME. Source reconstruction methods that allow to localize the neural generators of ERP components (see Bocquillon et al., 2011 as an example) may also be promising tools to disentangle spatio-temporally overlapping SMEs.

Taken together, the current evidence suggests that three different types of SMEs with specific functional characteristics are commonly elicited by meaningful study materials. An early frontal SME arises when successful encoding is supported by the transient processing of semantic features of a stimulus event, with generators in the (left) inferior prefrontal cortex and the rhinal cortex in the anterior temporal lobe. An early-onsetting parietal SME reflects the formation of a rich and durable item memory trace, which entails the intra-item binding of multiple features of a study event into a single item representation. This form of item-specific processing is most evident for familiar items for which multiple perceptual attributes can be reinstated and posterior parietal brain regions critically involved in imagery and visuo-spatial memory are likely neural generators of this effect. A sustained late frontal SME is consistently found in studies in which people use elaborative encoding strategies and reflects the contribution of more general associative processing of conceptual item features to successful memory formation. Importantly, based on the present state of the literature, it appears that all three processes can either individually or in concert support memory formation. Disentangling and separately quantifying each SME, and determining their relative magnitudes, can thus provide important mechanistic insights into successful memory encoding in specific learning conditions or populations.

6. Beyond endogenous brain activity: Is efficient encoding modulated by external or state-related factors?

This review has thus far shown that studies analyzing neural activity during the encoding phase of a memory experiment have revealed reliable effects of successful memory encoding. However, there may be external factors diagnostic for successful remembering in addition to brain activity elicited by individual study events, which may be serious confounds in SME studies. Some of these factors have been tackled in a recent study by Weidemann and Kahana (2021) using time-frequency EEG analyses, and the principle may apply to ERP studies as well. The authors reanalyzed a large dataset comprising 100 participants who performed at least 20 sessions of a free recall test. Using spectral EEG power as dependent variable the authors showed that subsequently remembered words elicited enhanced gamma frequencies ($>$ 30 Hz) and reduced alpha frequencies (8–12 Hz) as compared to forgotten words. A logistic regression analysis was used to examine whether EEG power predicts residual memory performance after controlling for external memory-predictive factors (e.g., an item's serial position in the study list, its average recall probability, or its list number in the memory session). They found that the so-called corrected SME were still significant, even though the external factors accounted for a substantial amount of variance in the memory data. This observation supports the view that SMEs are endogenous effects and do not solely reflect the impact of external memory-predictive factors. Another implication of these findings is that even though external factors like encoding tasks, content to be remembered or item distinctiveness (as discussed in

Sections 2, 3 and 4) can account for the memorability of an event, SMEs mainly reflect individual variability in endogenous activity set in train in the moment an event is experienced (see Weidemann and Kahana, 2021 for further discussion). Since ERPs are derived from the EEG, we consider it likely that the same applies to ERP SME. However, this is yet to be confirmed empirically.

Evidence for another potentially confounding factor that contributes to successful encoding comes from a brain imaging study exploring how transient and tonically maintained neural activity (so-called state-related activity) modulates the efficient encoding of an event (Otten et al., 2002). Otten et al. (2002) report that state-related activity maintained over several task blocks, in addition to processes that act at the single item level, also support the memorability of an event. State-related SME were found across two different encoding tasks after item-specific activity related to successful memory encoding was controlled for. Worded differently, the mean level of hemodynamic activity across task blocks was correlated with the number of items remembered from that block. These state-related SME could be localized in three prefrontal and medial parietal brain and did not overlap between the two tasks. It can therefore be concluded, that similar to item-related SME, state-related SME do not reflect a uniform or general determinant of encoding efficiency (Otten et al., 2002), but rather are indicative of task-specific contributions of prefrontal and medial parietal brain regions to successful memory encoding.

In sum, external factors predictive for successful memory encoding can have effects on brain activity at encoding in addition to brain activity elicited by individual study events. The studies reviewed here show that external factors and state-related brain activity at encoding independently contribute to effective memory encoding. They also show that ERP SMEs elicited by individual items are reliable measures of trial-by-trial variability of successful memory encoding beyond these factors. Notably, due to the scarcity of prior ERP studies on this topic, this section included fMRI studies and spectral EEG studies which are also better in capturing sustained neural activity than studies employing the ERP methodology. Further studies are urgently needed to extend these lines of research to ERP SME (see Kolisnyk et al., 2023 as an example).

7. How does activity preceding a study stimulus modulate memory encoding?

In the typical implementation of the subsequent memory paradigm, SME are examined as differences in neural activity elicited by to-be-remembered items and segregated according to whether the items are later remembered or forgotten. Interestingly, an increasing number of studies report that ERP activity preceding the to-be-encoded events can also be predictive of successful memory (so-called pre-stimulus SME; Koen et al., 2018; Yick et al., 2016; Galli et al., 2011, 2012, 2013, 2014; Padovani et al., 2013; Gruber and Otten, 2010; Otten et al., 2010; Otten et al., 2006; see Cohen et al., 2015 for a review).

7.1. Semantic preparation and motivational factors

Studies reporting pre-stimulus SME usually use a paradigm in which the to-be-studied items are preceded by a task cue that entails information about an upcoming study event or an action to be performed with a forthcoming item. In a seminal study by Otten et al. (2006) the task cue indicated whether a semantic or an orthographic decision had to be made for an upcoming word. The main finding was that the ERPs elicited by task cues indicating a forthcoming semantic decision differed according to whether the upcoming word was remembered or not. For words subsequently remembered the ERPs elicited by the task cue were more negative going than the ERPs preceding forgotten words and a significant pre-stimulus SME only emerged when the cue indicated that a semantic decision had to be performed with the upcoming word. The pre-stimulus SME started around 300 ms before word onset, reached largest negative amplitude at around word onset and was maximal at frontal sites. Notably, SME were also elicited by the study words which took the typical form of more positive-going ERPs for later remembered than forgotten words. These SMEs were also dissociable from the pre-stimulus SMEs in that they were present in conditions in which no pre-stimulus SME occurred. These results were replicated in a follow up study (Otten et al., 2010). Again, negative-going ERP preceding the onset of the to-be-encoded items predicted subsequent memory for these items. A negative-going SME over frontal scalp sites that preceded words subsequently recalled was also reported by Galli et al. (2012). In their study the pre-stimulus SMEs were specific for the first items in a study list, indicating that the preparatory processes they reflect are especially relevant for list initial items.

Further evidence for the view that pre-stimulus SME with negative polarity are associated with subsequent memory for the upcoming word was provided by a study in which a cue indexed whether a semantic (animacy) or an emotional (emotional/neutral) judgment was to be conducted on presented words, whereas recognition memory was subsequently tested (Padovani et al., 2011). Replicating the original findings by Otten et al. (2006), the pre-stimulus SMEs were negative-going for the semantic task, while the pre-stimulus SMEs for the emotional task were dissociable from the former by their topography.

In a study by Koen et al. (2018), differential benefits were placed on engaging in preparatory activity to a task cue. The task cue signaled which of two semantic tasks (manmade vs shoebox-size judgements) had to be performed with an upcoming word. Task cues that indicated a high benefit from engaging in preparatory processes elicited negative-going pre-stimulus SME, which were highly similar to the pre-stimulus SME reported by Otten and colleagues in the above-mentioned studies. Interestingly, for task cues indicating a lower benefit from preparatory processing, the pre-stimulus SME were of reversed polarity (more positive-going for subsequently remembered words) and were delayed by several hundred milliseconds. Finally, and also consistent with the results of the experiments reported by Otten and colleagues (2006, 2010), pre-stimulus SMAs were specifically tied to subsequent recollection, in this case operationalized as correct source judgments.

Using a monetary reward manipulation, Gruber and Otten (2010) shed further light on the factors that modulate pre-stimulus SMEs. Participants memorized series of words, which were preceded by task cues that indicated the monetary reward to be received if the upcoming word would be remembered. Pre-stimulus SMEs were obtained for high reward words only. Interestingly, and in contrast to the aforementioned pre-stimulus SME studies, this effect took the form of more positive going waveforms preceding subsequently remembered words. This pre-stimulus SME was present throughout the whole cue-target interval and, as in the above-mentioned studies, only present prior to words subsequently recollected. In contrast, reward-related preparatory activity in the cue interval (more positive going ERPs for high than low reward trials) was only revealed immediately after the reward cue.

The finding that the pre-stimulus SMA is elicited by cues signaling high rewards only allows for the conclusion that neural activity that aids the encoding of an upcoming stimulus event is influenced by motivational factors and consequently under voluntary control. The finding that post-stimulus SME are also modulated by motivational factors, as for example cues to upregulate memory encoding (Kolisnyk et al., 2023; Sundby et al., 2019), provides additional support for this view. Indirect further evidence for the beneficial effects of motivational and voluntary factors for memory formation comes from a positive-going pre-stimulus SME elicited by cues signaling the occurrence of negative study pictures when participants were instructed to explicitly feel their emotions upon presentation of the picture (Galli et al., 2014). A similar positive-going pre-stimulus SME was reported in anticipation of unpleasant pictures selectively for women in Galli et al. (2011).

What are the mechanisms by which pre-stimulus neural activity affects memory formation? According to one account the pre-stimulus effects could reflect spontaneous neural fluctuations or spontaneous variations in alertness that are of differential benefit for memory encoding (Ezzyat et al., 2017; Weidemann & Kahana 2020). In support of this view, a recent study found that ERP activity immediately preceding the onset of negative (but not neutral) images was predictive of their subsequent recognition (Yick et al., 2016). Since participants could not predict the valence of an upcoming image in this study, this finding was interpreted such that the pre-stimulus ERP activity reflects processing resources made available before image onset, which may play a larger role in resource-intensive encoding of negative emotional images. However, if the idea that some items are remembered better because people were more alert prior to processing them accounted entirely for pre-stimulus SMEs, one would expect these spontaneous fluctuations to occur randomly and to affect memory encoding in all trials. The observation that pre-stimulus SME vary consistently across conditions and are under voluntary control argues against this view.

A more likely account hence appears to be that pre-stimulus SME reflect the entering into a particular preparatory processing state which enhances the effectiveness of subsequent encoding. For example, task cues signaling reward or upcoming emotional information may elicit motivational processes that give rise to positive-going pre-stimulus SME and, as a consequence, lead to more engagement in the processing of the upcoming stimulus. The larger the engagement of these preparatory processes, the larger the likelihood that the upcoming event will be remembered later on. Consistent with the view that reward anticipation can initiate motivational states that boost memory encoding and elicit positive-going SMEs, Marini et al. (2011) report early and positive going post-stimulus SME effects of similar kind elicited by faces preceded by reward cues. Unfortunately, however, no pre-stimulus SME were computed in the latter study. In a similar vein, the negative-going pre-stimulus SME in anticipation of mainly semantic tasks may reflect semantic preparatory processes (see Galli et al., 2011 for a similar view). Thus, adapting a semantic preparatory state (or a semantic task set) may enable the creation of semantically more elaborate memory representations which in turn are more readily accessible in an ensuing memory test. The observation that pre-stimulus SMAs with negative polarity are exclusively found preceding items for which semantic discriminations have to be made is consistent with this view.

The semantic preparation account of the pre-stimulus SME receives additional support from recent EEG and ERP studies exploring semantic predictive mechanisms and their neural underpinnings during language comprehension (Grisoni et al., 2017; Piai et al., 2016; DeLong et al., 2005). Sentence contexts that strongly constrain semantic predictions for upcoming words (e.g., "*He opened the door with the…*") elicit negative slow waves at frontal recordings (called "semantic readiness potentials" by Grisoni et al., 2017), which show the largest amplitudes immediately before the sentence final word is presented. These slow waves may reflect preparatory processes, like predicting the upcoming word and keeping it in working memory to facilitate its processing and sentence comprehension in general (Grisoni et al., 2017; Fruchter et al., 2015). However, as no SME analysis was conducted for the semantic readiness potential, the relevance of the preparatory processes it reflects for memory formation remains elusive. A recent SME study in our own lab (Höltje and Mecklinger, 2022), exploring predictive processing during language comprehension, however, revealed a pre-stimulus SME elicited by a semantically constraining sentence context. This effect started as early as 800 ms prior to the onset of the word to be memorized and correlated positively with the ensuing post-stimulus parietal SME. Consistent with the semantic preparation account of the pre-stimulus SME, this effect bears high resemblance with the pre-stimulus SMEs elicited by task cues in the aforementioned memory studies.

7.2. Pre- and post-stimulus processing

An open issue concerns functional commonalities and differences between pre- and post-stimulus SME. The evidence on this issue is mixed: In the experiments reported by Otten et al. (2006) the pre- and post-stimulus activity supporting successful memory encoding did not emerge in the same experimental conditions and hence could be dissociated. Conversely, pre- and post-stimulus SME were positively correlated in the experiment reported by Höltje and Mecklinger (2022) suggesting that similar processes in support of successful memory encoding operate before and after a study item.

As highlighted by Cohen at colleagues (2015) in their recent review paper, when discussing pre- and post-stimulus SME it is important to keep in mind that memory encoding always entails the orchestration and integration of temporally overlapping neurocognitive processes. While these processes can be experimentally studied in isolation, in real life they never operate in isolation and for a complete understanding of encoding processes it is important to identify how pre- and post- stimulus effects are orchestrated together. Depending on the processing context, preparatory activity can facilitate memory formation of an upcoming stimulus event as it is the case when a cue is presented prior to the to-be-encoded activity. Conversely, preparatory processing as during language processing may lead to a top-down verification mode (Hubbard et al. (2019); Van Berkum (2010) in which people only verify that an actual event matches expectations. This form of shallow processing would lead to weak encoding and impoverished memory representations. Finally, it remains to be explored whether without entering a conscious preparatory state, spontaneous fluctuations of neural activity at the time of encoding can also influence memory encoding (see Guderian et al., 2009 or Griffin et al., 2004 for evidence).

An open question regarding pre-stimulus SMEs is what role their onset and timing play, since this timing has been somewhat variable in prior studies. Secondly, does the polarity reversal reflect that the same neural process is beneficial to subsequent retrieval under one set of circumstances (for example preparatory semantic processing), but impedes successful encoding in another set of circumstances (reward anticipation)? Or are completely separate sets of processes involved in the two kinds of effects?

To summarize, studies examining pre-stimulus SMEs have revealed several remarkable results: Pre-stimulus SMEs elicited by task cues signaling an upcoming semantic decision usually appear as more negative-going waveforms and are largest in the several hundred milliseconds preceding the study word. Depending on task characteristics pre-stimulus SMEs can also arise with positive polarity, presumably reflecting motivational preparatory states, entering into which enhances the likelihood that the upcoming event will be remembered later on. This suggests that multiple preparatory processes beyond the mere adaptation of semantic preparatory states, as for example the adaptation of specific motivational or reward-related states can contribute to memory formation. A further remarkable feature of pre-stimulus SMEs is that they appear to specifically support recollection at least when preparatory semantic processes are engaged.

8. Common confounds and individual differences

8.1. Confounding factors and open issues

Drawing conclusions from SME in different task contexts presupposes careful control of potentially confounding factors and consideration of alternative interpretations. Two tasks could for example differ in the time required to perform them and this could give rise to differences in the SME in the tasks under consideration (see for example the studies by Robichon et al., 2002 contrasting SME in sentences with fast and slow presentation rates or by Otten and Rugg, 2001 examining SME in two encodings tasks that differ in the time required to perform them). To cope with this issue, in a recent study we controlled for time-on-task effects by equating presentation times for study events between tasks (Meßmer et al., 2021). Hence, confounding effects of study duration can be avoided by taking appropriate measures and using such measures is highly recommendable for all SME studies.

Another open issue concerns the overlap of SMEs with other ERP effects, in particular in early time intervals. While SMEs are typically apparent in late time windows and not before about 300 ms post-stimulus, there are occasional reports of earlier SMEs. In an illustrative study, Brady et al. (2019) explored SMEs using fragmented stimuli that could either been seen as faces or not. The N170, an ERP index of face processing typically observed between 150 and 200 post-stimulus was larger for faces subsequently remembered than faces subsequently forgotten but only for ambiguous stimuli, suggesting that stimuli that are seen as meaningful (i.e., stimuli seen as faces, as indexed by a larger N170) are more likely to be efficiently encoded and latter remembered than non-meaningful stimuli. These results underscore the relevance of meaningfulness for the early encoding of visual features and also demonstrate that ERP SMEs due to their excellent temporal resolution allow to disclose these processes.

Exploring the interplay between feedback processing and memory encoding during reward-based learning, Höltje and Mecklinger (2020) found an SME overlapping with the Feedback-Related Negativity (FRN), an ERP component peaking between 200 and 350 ms which is sensitive to feedback processing (Bellebaum and Daum, 2008). This effect took the form of an attenuated FRN for events subsequently remembered that were presented together with delayed feedback. This suggests that feedback processing and early memory encoding compete for the same processing resources in this early time interval (for a similar relationship between the FRN and successful memory formation in a learning task see Arbel et al., 2013 and Arbel et al., 2014).

Finding early ERP signatures of effective memory encoding overlapping with other ERP components (see also Wolff et al., 2014) is an important endeavor for future studies, as it allows inferences on the neurocognitive mechanisms by which events are made memorable in different contexts, as for example the extraction of meaning that boosts initial encoding of faces (Brady et al., 2019), or by making use of mechanisms required for reward-based learning to allow more elaborative encoding (Höltje and Mecklinger, 2020). Thus, SMEs are a valuable tool for the exploration of the mechanisms that support successful memory encoding in different processing contexts.

8.2. Age-related changes

Given a thorough understanding of the functional significance of ERP SMEs, they are a useful tool to examine the neurocognitive basis of changes in memory functions in psychopathology (e.g., Kim and Yoo, 2005; Krauel et al., 2009), during childhood development (Rollins and Riggins, 2013, 2018), or in old age. As the most work has been done in the latter area, we briefly summarize the relevant results of this work here, as an example of how ERP SMEs can be used to understand individual differences in memory function. Thus, Kamp and Zimmer (2015) and Kamp et al. (2022) demonstrated that the sustained late frontal SME, while prominent in young adults during the encoding of object pairs via interactive imagery, was virtually absent in older adults, suggesting a reduction in the elaboration of a mental interactive image. Instead, Kamp et al. (2022) reported a negative-going SME in older adults with low associative memory performance, suggesting that these older adults engaged in superficial, perceptual processes, a non-optimal strategy for encoding associations. Other studies also reported absent (Bouazzaoui et al., 2022; Friedman et al., 1996; Kuo et al., 2014) or negative-going (Koen et al., 2018) sustained frontal SMEs for older adults, as opposed to the typical positive polarity SME in young adults, suggesting a lower engagement in elaborative processes or a lower efficiency of the processes supporting successful encoding in older adults. Finally, in a task in which evidently shallow, perceptual encoding was beneficial for subsequent memory performance, Kamp (2020) reported that a posterior, negative-going SME was pronounced for young, but not for older adults.

A reduced sustained late frontal SME does not appear to be a general feature of SME patterns in older adults, but appears to be task-dependent. For example, Després et al. (2017) reported no significant age differences in ERP SMEs in a word encoding task requiring an edibility judgment, followed by a recognition test. Both age groups showed SMEs of positive polarity. Kamp et al. (2018) also reported no age differences in the sustained late frontal SME in young and older adults in unitization or associative encoding tasks. However, the early frontal and parietal SME were selective to the unitization condition in young adults, but were condition-invariant in older adults, suggesting that encoding processes were not tuned to the specific demands of the encoding task in older adults. Friedman and Trott (2000) also report a broadly distributed late SME with typical polarity in both young and older adults when individual words were encoded within sentence structures. This SME, however, differentiated between trials retrieved based on recollection versus familiarity in young, but not in older adults, suggesting that differential encoding and retrieval processes were engaged only in the young. Similarly, Gutchess et al. (2007) reported a sustained late frontal SME for both age groups, which, however differed according to subsequent recognition confidence only in young adults. Taken together, age differences in ERP SMEs thus far support the view that older adults often engage less efficiently in task specific encoding strategies, such as elaborative encoding or in some cases proactive processing or perceptual encoding. Furthermore, several studies suggest that older adults do not tend to differentially tune encoding processes to the specific task demands or retrieval outcomes. Future research using the SME paradigm to compare different groups of participants will enable further mechanistic insights into changes in the efficiency of memory processes due to factors such as aging.

9. Summary and conclusions

Our ability to remember the past depends on neural processes set in train in the moment the event is experienced. These neural processes elicited by an event can be an important predictor for its subsequent remembrance and the subsequent memory paradigm, a procedure that allows to separate encoding-related activity from ongoing brain activity is a powerful method to explore the neural underpinnings of successful memory formation. Although there are still many unresolved questions regarding the structure and function of ERP SMEs, the literature presented in the current review suggests that multiple processes relevant to memory encoding can be tracked by ERP SMEs. Specifically, three functionally different, positive-going ERP SMEs are most commonly set in train by a study event, which index early semantic processing, intra-item feature binding and elaboration, respectively. While these positive-going SME reflect processes relevant for remembering conceptual contents, SMEs of negative polarity are indicative of later memory for perceptually or shallowly processed contents from a study episode. Furthermore, SMEs can also be present prior to a study event, in which case they index preparatory semantic processing states or motivational states that support memory formation and later remembering. Although the functional relationship among the different ERP SMEs remains to be determined, it appears that the different mechanisms can be recruited either individually or in concert, together determining which memory contents are remembered and how. An examination of the relative magnitude of ERP SMEs can hence provide unique mechanistic insights into the nature and timing of memory processes in different learning contexts or populations.

This article made unequivocally clear that for the dissociation of the subcomponents of successful memory formation a very good temporal resolution as afforded by ERP is essential. Depending on the experimental manipulation at hand, SMEs can differ in their onset or temporal extension by a few dozen millisecond while the magnitude and topography of the effect remains the same. Examples are the SME for semantically congruent and incongruent information which differed in onset by about 200 ms (Packard et al., 2017) or the report of a parietal SME which was delayed for about 150 ms for low frequency as compared to high frequency words (Fernandez et al., 1998). The longer persistence of the SME to low as compared to high vividness mental images (Gjorgieva et al., 2022) or the 200 ms earlier onset of a parietal

SME when participants anticipated the occurrence of an electric shock (Wiemer et al., 2021) also underscore the need of a high temporal resolution for the exploration of these effects. In all of these examples the comparable scalp distributions suggest that the same type of SME simply differed in its onset or extension. Furthermore, different subprocesses of memory encoding, which occur within milliseconds of one another – as is the case for the ERP SME reviewed in the present article – cannot be disentangled with methods that exhibit a low temporal resolution like fMRI or spectral analyses of EEG oscillation. In other words: Studies on memory encoding and the underlying brain activity require a strong focus on high temporal resolution as provided by the ERP methodology or by MEG. Only these methodologies have the appropriate temporal resolution to disclose subtle temporal differences between SMEs.

In conclusion, the present review proposes a functional organization and interpretation of ERP SMEs as they have been reported in prior studies. Future research should be specifically designed to test the proposed functional organization of the ERP SME to further refine or modify this view. For example, one could parametrically manipulate the number of perceptual features available during encoding to examine the interplay between of intra-item binding during encoding and perceptual reinstatement during retrieval as reflected in the parietal SME. Given a thorough functional understanding of the different types of SME, the ERP subsequent memory technique is not only useful to understand neurocognitive mechanisms underlying memory phenomena, but it can also be applied to develop methods to optimize individual memory encoding for desired information and suppress memory encoding of undesired information (Cohen et al., 2015). Another valuable outcome is the examination of the locus and underlying neurocognitive mechanisms of age-related changes, childhood development and psychopathology of memory processes. We thus hope that the present review will stimulate further basic and applied research using this technique.

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Declarations of interest

None.

References

Angel, L., Isingrini, M., Bouazzaoui, B., Fay, S., 2013. Neural correlates of encoding processes predicting subsequent cued recall and source memory. NeuroReport 24 (4), 176–180. https://doi.org/10.1097/WNR.0b013e32835d8452.

Angel, L., Fay, S., Bouazzaoui, B., Taconnat, L., 2017. What can ERPs tell us about the generation effect? Neurosci. Lett. 658, 171–176. https://doi.org/10.1016/j.neulet.2017.08.053.

Arbel, Y., Goforth, K., Donchin, E., 2013. The good, the bad, or the useful? The examination of the relationship between the feedback-related negativity (FRN) and long-term learning outcomes. J. Cogn. Neurosci. 25 (8), 1249–1260. https://doi.org/10.1162/jocn_a_00385.

Arbel, Y., Murphy, A., Donchin, E., 2014. On the utility of positive and negative feedback in a paired-associate learning task. J. Cogn. Neurosci. 26 (7), 1445–1453. https://doi.org/10.1162/jocn_a_00617.

Axmacher, N., Cohen, M.X., Fell, J., Haupt, S., Dümpelmann, M., Elger, C.E., Schlaepfer, T.E., Lenartz, D., Sturm, V., Ranganath, C., 2010a. Intracranial EEG correlates of expectancy and memory formation in the human hippocampus and nucleus accumbens. Neuron 65 (4), 541–549. https://doi.org/10.1016/j.neuron.2010.02.006.

Axmacher, N., Lenz, S., Haupt, S., Elger, C.E., Fell, J., 2010b. Electrophysiological signature of working and long-term memory interaction in the human hippocampus. Eur. J. Neurosci. 31 (1), 177–188. https://doi.org/10.1111/j.1460-9568.2009.07041.x.

Bader, R., Mecklinger, A., Hoppstädter, M., Meyer, P., 2010. Recognition memory for one-trial-unitized word pairs: evidence from event-related potentials. NeuroImage 50 (2), 772–781. https://doi.org/10.1016/j.neuroimage.2009.12.100.

Bai, C.-H., Bridger, E.K., Zimmer, H.D., Mecklinger, A., 2015. The beneficial effect of testing: an event-related potential study. Front. Behav. Neurosci. 9 https://doi.org/10.3389/fnbeh.2015.00248.

Batterink, L., Neville, H., 2011. Implicit and explicit mechanisms of word learning in a narrative context: an event-related potential study. J. Cogn. Neurosci. 23 (11), 3181–3196. https://doi.org/10.1162/jocn_a_00013.

Bauch, E.M., Otten, L.J., 2012. Study–test congruency affects encoding-related brain activity for some but not all stimulus materials. J. Cogn. Neurosci. 24 (1), 183–195. https://doi.org/10.1162/jocn_a_00070.

Bellebaum, C., Daum, I., 2008. Learning-related changes in reward expectancy are reflected in the feedback-related negativity. Eur. J. Neurosci. 27 (7), 1823–1835. https://doi.org/10.1111/j.1460-9568.2008.06138.x.

Bloom, P.A., Friedman, D., Xu, J., Vuorre, M., Metcalfe, J., 2018. Tip-of-the-tongue states predict enhanced feedback processing and subsequent memory. Conscious. Cogn. 63, 206–217. https://doi.org/10.1016/j.concog.2018.05.010.

Bocquillon, P., Bourriez, J.-L., Palmero-Soler, E., Betrouni, N., Houdayer, E., Derambure, P., Dujardin, K., 2011. Use of swLORETA to localize the cortical sources of target- and distracter-elicited P300 components. S1388245711002367 Clin. Neurophysiol.. https://doi.org/10.1016/j.clinph.2011.03.014.

Bosch, V., Mecklinger, A., Friederici, A.D., 2001. Slow cortical potentials during retention of object, spatial, and verbal information. Cogn. Brain Res. 10 (3), 219–237. https://doi.org/10.1016/S0926-6410(00)00040-9.

Bouazzaoui, B., Angel, L., Sacher, M., Fay, S., Alibran, E., Pylouster, J., Gautier, R., Taconnat, L., 2022. The age-related effect on electrophysiological correlates of successful episodic memory encoding supports the hypothesis of a deficit in self-initiated encoding processes in aging. Neurosci. Lett. 781, 136676 https://doi.org/10.1016/j.neulet.2022.136676.

Brady, T.F., Alvarez, G.A., Störmer, V.S., 2019. The role of meaning in visual memory: face-selective brain activity predicts memory for ambiguous face stimuli. J. Neurosci. 39 (6), 1100–1108. https://doi.org/10.1523/JNEUROSCI.1693-18.2018.

Bridger, E.K., Wilding, E.L., 2010. Requirements at retrieval modulate subsequent memory effects: an event-related potential study. Cogn. Neurosci. 1 (4), 254–260. https://doi.org/10.1080/17588928.2010.484882.

Brodeur, M.B., Debruille, J.B., Renoult, L., Prévost, M., Dionne-Dostie, E., Buchy, L., Lepage, M., 2011. The influence of contour fragmentation on recognition memory: an event-related potential study. Brain Cogn. 76 (1), 115–122. https://doi.org/10.1016/j.bandc.2011.02.010.

Brown, A.S., 1991. A review of the tip-of-the-tongue experience. Psychol. Bull. 109 (2), 204–223. https://doi.org/10.1037/0033-2909.109.2.204.

Buckner, R.L., Wheeler, M.E., Sheridan, M.A., 2001. Encoding processes during retrieval tasks. J. Cogn. Neurosci. 13 (3), 406–415. https://doi.org/10.1162/08989290151137430.

Byrne, P., Becker, S., Burgess, N., 2007. Remembering the past and imagining the future: a neural model of spatial memory and imagery. Psychol. Rev. 114 (2), 340–375. https://doi.org/10.1037/0033-295X.114.2.340.

Cansino, S., Trejo-Morales, P., 2008. Neurophysiology of successful encoding and retrieval of source memory. Cogn. Affect. Behav. Neurosci. 8 (1), 85–98. https://doi.org/10.3758/CABN.8.1.85.

Caplan, J.B., Glaholt, M.G., McIntosh, A.R., 2009. EEG activity underlying successful study of associative and order information. J. Cogn. Neurosci. 21 (7), 1346–1364. https://doi.org/10.1162/jocn.2008.21167.

Chen, Y.Y., Lithgow, K., Hemmerich, J.A., Caplan, J.B., 2014. Is what goes in what comes out? Encoding and retrieval event-related potentials together determine memory outcome. Exp. Brain Res. 232 (10), 3175–3190. https://doi.org/10.1007/s00221-014-4002-1.

Cheng, S., Rugg, M.D., 2010. Event-related potential correlates of gist and verbatim encoding. Int. J. Psychophysiol. 77 (2), 95–105. https://doi.org/10.1016/j.ijpsycho.2010.04.010.

Cohen, N., Pell, L., Edelson, M.G., Ben-Yakov, A., Pine, A., Dudai, Y., 2015. Peri-encoding predictors of memory encoding and consolidation. Neurosci. Biobehav. Rev. 50, 128–142. https://doi.org/10.1016/j.neubiorev.2014.11.002.

Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. Nat. Rev. Neurosci. 3 (3), 201–215. https://doi.org/10.1038/nrn755.

Craik, F.I.M., Lockhart, R.S., 1972. Levels of processing: a framework for memory research. J. Verbal Learn. Verbal Behav. 11 (6), 671–684. https://doi.org/10.1016/S0022-5371(72)80001-X.

Cycowicz, Y.M., Friedman, D., 1999. The effect of intention to learn novel, environmental sounds on the novelty P3 and old/new recognition memory. Biol. Psychol. 50 (1), 35–60. https://doi.org/10.1016/S0301-0511(99)00004-6.

DeLong, K.A., Urbach, T.P., Kutas, M., 2005. Probabilistic word pre-activation during language comprehension inferred from electrical brain activity. Nat. Neurosci. 8 (8), 1117–1121. https://doi.org/10.1038/nn1504.

Després, O., Lithfous, S., Tromp, D., Pebayle, T., Dufour, A., 2017. Gamma oscillatory activity is impaired in episodic memory encoding with age. Neurobiol. Aging 52, 53–65. https://doi.org/10.1016/j.neurobiolaging.2016.12.019.

Dien, J., 2010. The ERP PCA toolkit: an open source program for advanced statistical analysis of event-related potential data. J. Neurosci. Methods 187 (1), 138–145.

Dolcos, F., Cabeza, R., 2002. Event-related potentials of emotional memory: encoding pleasant, unpleasant, and neutral pictures. Cogn., Affect., Behav. Neurosci. 2 (3), 252–263.

Donchin, E., Coles, M.G.H., 1988. Is the P300 component a manifestation of context updating? Behav. Brain Sci. 11, 355–372.

Duarte, A., Ranganath, C., Winward, L., Hayward, D., Knight, R.T., 2004. Dissociable neural correlates for familiarity and recollection during the encoding and retrieval of pictures. Cogn. Brain Res. 18 (3), 255–272. https://doi.org/10.1016/j.cogbrainres.2003.10.010.

Estrada-Manilla, C., Cansino, S., 2012. Event-related potential variations in the encoding and retrieval of different amounts of contextual information. Behav. Brain Res. 232 (1), 190–201. https://doi.org/10.1016/j.bbr.2012.04.012.

Ezzyat, Y., Kragel, J.E., Burke, J.F., Levy, D.F., Lyalenko, A., Wanda, P., O'Sullivan, L., Hurley, K.B., Busygin, S., Pedisich, I., Sperling, M.R., Worrell, G.A., Kucewicz, M.T., Davis, K.A., Lucas, T.H., Inman, C.S., Lega, B.C., Jobst, B.C., Sheth, S.A., Kahana, M. J., 2017. Direct brain stimulation modulates encoding states and memory performance in humans. Curr. Biol. 27 (9), 1251–1258. https://doi.org/10.1016/j.cub.2017.03.028.

Fabiani, M., Donchin, E., 1995. Encoding processes and memory organization: a model of the von Restorff effect. J. Exp. Psychol.: Learn., Mem., Cogn. 21 (1), 224–240. https://doi.org/10.1037/0278-7393.21.1.224.

Fabiani, M., Karis, D., Donchin, E., 1990. Effects of mnemonic strategy manipulation in a Von Restorff paradigm. Electroencephalogr. Clin. Neurophysiol. 75 (1–2), 22–35. https://doi.org/10.1016/0013-4694(90)90149-E.

Fernandez, G., Weyerts, H., Tendolkar, I., Smid, H.G.O.M., Scholz, M., Heinze, H.-J., 1998. Event-related potentials of verbal encoding into episodic memory: dissociation between the effects of subsequent memory performance and distinctiveness. Psychophysiology 35 (6), 709–720. https://doi.org/10.1111/1469-8986.3560709.

Fernández, G., Effern, A., Grunwald, T., Pezer, N., Lehnertz, K., Dümpelmann, M., Roost, D.V., Elger, C.E., 1999. Real-time tracking of memory formation in the human rhinal cortex and hippocampus. Science 285 (5433), 1582–1585. https://doi.org/10.1126/science.285.5433.1582.

Fernández, G., Klaver, P., Fell, J., Grunwald, T., Elger, C.E., 2002. Human declarative memory formation: Segregating rhinal and hippocampal contributions: segregating Human Declarative Memory Formation. Hippocampus 12 (4), 514–519. https://doi.org/10.1002/hipo.10050.

Folgueira-Ares, R., Cadaveira, F., Rodríguez Holguín, S., López-Caneda, E., Crego, A., Pazo-Álvarez, P., 2017. Electrophysiological anomalies in face–name memory encoding in young binge drinkers. Front. Psychiatry 8, 216. https://doi.org/10.3389/fpsyt.2017.00216.

Forester, G., Kamp, S.-M., 2023. Pre-associative item encoding influences associative memory: behavioral and ERP evidence. Cogn. Affect. Behav. Neurosci. 1–17. https://doi.org/10.3758/s13415-023-01102-7.

Forester, G., Kroneisen, M., Erdfelder, E., Kamp, S.M., 2020. Survival processing modulates the neurocognitive mechanisms of episodic encoding. Cogn. Affect. Behav. Neurosci. 20 (4), 717–729.

Forester, G., Halbeisen, G., Walther, E., Kamp, S.-M., 2020. Frontal ERP slow waves during memory encoding are associated with affective attitude formation. Int. J. Psychophysiol. 158, 389–399. https://doi.org/10.1016/j.ijpsycho.2020.11.003.

Friedman, D., Johnson, R., 2000. Event-related potential (ERP) studies of memory encoding and retrieval: a selective review. Microsc. Res. Tech. 51, 6–28.

Friedman, D., Trott, C., 2000. An event-related potential study of encoding in young and older adults. Neuropsychologia 38 (5), 542–557. https://doi.org/10.1016/S0028-3932(99)00122-0.

Friedman, D., Ritter, W., Snodgrass, J.G., 1996. ERPs during study as a function of subsequent direct and indirect memory testing in young and old adults. Cogn. Brain Res. 4 (1), 1–13. https://doi.org/10.1016/0926-6410(95)00041-0.

Fruchter, J., Linzen, T., Westerlund, M., Marantz, A., 2015. Lexical preactivation in basic linguistic phrases. J. Cogn. Neurosci. 27 (10), 1912–1935. https://doi.org/10.1162/jocn_a_00822.

Galli, G., Wolpe, N., Otten, L.J., 2011. Sex differences in the use of anticipatory brain activity to encode emotional events. J. Neurosci. 31 (34), 12364–12370. https://doi.org/10.1523/JNEUROSCI.1619-11.2011.

Galli, G., Leng Choy, T., Otten, L.J., 2012. Prestimulus brain activity predicts primacy in list learning. Cogn. Neurosci. 3 (3–4), 160–167. https://doi.org/10.1080/17588928.2012.670105.

Galli, G., Gebert, A.D., Otten, L.J., 2013. Available processing resources influence encoding-related brain activity before an event. Cortex 49 (8), 2239–2248. https://doi.org/10.1016/j.cortex.2012.10.011.

Galli, G., Griffiths, V.A., Otten, L.J., 2014. Emotion regulation modulates anticipatory brain activity that predicts emotional memory encoding in women. Soc. Cogn. Affect. Neurosci. 9 (3), 378–384. https://doi.org/10.1093/scan/nss145.

Geng, J.J., Vossel, S., 2013. Re-evaluating the role of TPJ in attentional control: contextual updating? Neurosci. Biobehav. Rev. 37 (10), 2608–2620. https://doi.org/10.1016/j.neubiorev.2013.08.010.

Gilboa, A., Marlatte, H., 2017. Neurobiology of schemas and schema-mediated memory. Trends Cogn. Sci. 21 (8), 618–631. https://doi.org/10.1016/j.tics.2017.04.013.

Gjorgieva, E., Geib, B.R., Cabeza, R., Woldorff, M.G., 2022. The influence of imagery vividness and internally-directed attention on the neural mechanisms underlying the encoding of visual mental images into episodic memory. Cereb. Cortex 1–14. https://doi.org/10.1093/cercor/bhac270.

Glanzer, M., Adams, J.K., 1990. The mirror effect in recognition memory: data and theory (o. J.). J. Exp. Psychol.: Learn., Mem., Cogn. 16 (1), 5.

Gonsalves, B., Paller, K.A., 2000. Neural events that underlie remembering something that never happened. Nat. Neurosci. 3 (12), 1316–1321. https://doi.org/10.1038/81851.

Griffin, A.L., Asaka, Y., Darling, R.D., Berry, S.D., 2004. Theta-contingent trial presentation accelerates learning rate and enhances hippocampal plasticity during trace eyeblink conditioning. Behav. Neurosci. 118 (2), 403–411. https://doi.org/10.1037/0735-7044.118.2.403.

Griffin, M., DeWolf, M., Keinath, A., Liu, X., Reder, L., 2013. Identical versus conceptual repetition FN400 and parietal old/new ERP components occur during encoding and predict subsequent memory. Brain Res. 1512, 68–77. https://doi.org/10.1016/j.brainres.2013.03.014.

Grisoni, L., Miller, T.M., Pulvermüller, F., 2017. Neural correlates of semantic prediction and resolution in sentence processing. J. Neurosci. 37 (18), 4848–4858. https://doi.org/10.1523/JNEUROSCI.2800-16.2017.

Gruber, M.J., Otten, L.J., 2010. Voluntary control over prestimulus activity related to encoding. J. Neurosci. 30 (29), 9793–9800. https://doi.org/10.1523/JNEUROSCI.0915-10.2010.

Guderian, S., Schott, B.H., Richardson-Klavehn, A., Düzel, E., 2009. Medial temporal theta state before an event predicts episodic encoding success in humans. Proc. Natl. Acad. Sci. USA 106 (13), 5365–5370. https://doi.org/10.1073/pnas.0900289106.

Guo, C., Voss, J.L., Paller, K.A., 2005. Electrophysiological correlates of forming memories for faces, names, and face–name associations. Cogn. Brain Res. 22 (2), 153–164. https://doi.org/10.1016/j.cogbrainres.2004.08.009.

Guo, C., Duan, L., Li, W., Paller, K.A., 2006. Distinguishing source memory and item memory: brain potentials at encoding and retrieval. Brain Res. 1118 (1), 142–154. https://doi.org/10.1016/j.brainres.2006.08.034.

Gutchess, A.H., Ieuji, Y., Federmeier, K.D., 2007. Event-related potentials reveal age differences in the encoding and recognition of scenes. J. Cogn. Neurosci. 19 (7), 1089–1103. https://doi.org/10.1162/jocn.2007.19.7.1089.

Handy, T., Miller, M., Schott, B., Shroff, N., Janata, P., Van Horn, J., Inati, S., Grafton, S., Gazzaniga, M., 2004. Visual imagery and memory: Do retrieval strategies affect what the mind's eye sees? Eur. J. Cogn. Psychol. 16 (5), 631–652. https://doi.org/10.1080/09541440340000457.

Henson, R.N.A., Rugg, M.D., Shallice, T., Josephs, O., Dolan, R.J., 1999. Recollection and familiarity in recognition memory: an event-related functional magnetic resonance imaging study. J. Neurosci. 19 (10), 3962–3972. https://doi.org/10.1523/JNEUROSCI.19-10-03962.1999.

Höltje, G., Mecklinger, A., 2020. Feedback timing modulates interactions between feedback processing and memory encoding: Evidence from event-related potentials. Cogn. Affect. Behav. Neurosci. 20 (2), 250–264. https://doi.org/10.3758/s13415-019-00765-5.

Höltje, G., Mecklinger, A., 2022. Benefits and costs of predictive processing: How sentential constraint and word expectedness affect memory formation. Brain Res. 1788, 147942 https://doi.org/10.1016/j.brainres.2022.147942.

Höltje, G., Lubahn, B., Mecklinger, A., 2019. The congruent, the incongruent, and the unexpected: event-related potentials unveil the processes involved in schematic encoding. Neuropsychologia 131, 285–293. https://doi.org/10.1016/j.neuropsychologia.2019.05.013.

Hubbard, R.J., Rommers, J., Jacobs, C.L., Federmeier, K.D., 2019. Downstream behavioral and electrophysiological consequences of word prediction on recognition memory. Front. Hum. Neurosci. 13, 291 https://doi.org/10.3389/fnhum.2019.00291.

Ishai, A., 2002. Visual imagery of famous faces: effects of memory and attention revealed by fMRI. NeuroImage 17 (4), 1729–1741. https://doi.org/10.1006/nimg.2002.1330.

Jäger, T., Mecklinger, A., Kipp, K.H., 2006. Intra- and inter-item associations doubly dissociate the electrophysiological correlates of familiarity and recollection. Neuron 52 (3), 535–545. https://doi.org/10.1016/j.neuron.2006.09.013.

Jia, X., Gao, C., Li, B., Shinkareva, S.V., Guo, C., 2021. Effects of retrieval and emotion on within-item associative memory – Evidence from ERP and oscillatory subsequent memory effects. Biol. Psychol. 166, 108222 https://doi.org/10.1016/j.biopsycho.2021.108222.

Kamp, S.M., Endemann, R., Domes, G., Mecklinger, A., 2019. Effects of acute psychosocial stress on the neural correlates of episodic encoding: Item versus associative memory. Neurobiol. Learn. Mem. 157, 128–138.

Kamp, S.-M., 2020. Neurocognitive mechanisms of guided item and associative encoding in young and older adults. Brain Cogn. 145, 105626 https://doi.org/10.1016/j.bandc.2020.105626.

Kamp, S.-M., Donchin, E., 2015. ERP and pupil responses to deviance in an oddball paradigm. Psychophysiology 52 (4), 460–471.

Kamp, S.-M., Zimmer, H.D., 2015. Contributions of attention and elaboration to associative encoding in young and older adults. Neuropsychologia 75, 252–264. https://doi.org/10.1016/j.neuropsychologia.2015.06.026.

Kamp, S.-M., Brumback, T., Donchin, E., 2013. The component structure of ERP subsequent memory effects in the Von Restorff paradigm and the word frequency effect in recall. Psychophysiology 50 (11), 1079–1093.

Kamp, S.-M., Potts, G.F., Donchin, E., 2015. On the roles of distinctiveness and semantic expectancies in episodic encoding of emotional words: Emotional word encoding. Psychophysiology 52 (12), 1599–1609. https://doi.org/10.1111/psyp.12537.

Kamp, S.-M., Lehman, M., Malmberg, K.J., Donchin, E., 2016. A buffer model account of behavioral and ERP patterns in the Von Restorff paradigm. AIMS Neurosci. 3 (2).

Kamp, S.-M., Bader, R., Mecklinger, A., 2017. ERP subsequent memory effects differ between inter-item and unitization encoding tasks. Front. Hum. Neurosci. 11 https://doi.org/10.3389/fnhum.2017.00030.

Kamp, S.-M., Bader, R., Mecklinger, A., 2018. Unitization of word pairs in young and older adults: Encoding mechanisms and retrieval outcomes. Psychol. Aging 33 (3), 497–511. https://doi.org/10.1037/pag0000256.

Kamp, S.-M., Forester, G., Henken, M., Vittinghoff, M., Knopf, L., 2022. On the role of item encoding mechanisms in associative memory in young and older adults: a mass univariate ERP study. Neurobiol. Learn. Mem. 189, 107588 https://doi.org/10.1016/j.nlm.2022.107588.

Karis, D., Fabiani, M., Donchin, E., 1984. P300″ and memory: Individual differences in the von Restorff effect. Cogn. Psychol. 16 (2), 177–216. https://doi.org/10.1016/0010-0285(84)90007-0.

Karpicke, J.D., Roediger, H.L., 2008. The critical importance of retrieval for learning. Science 319 (5865), 966–968. https://doi.org/10.1126/science.1152408.

Khader, P., Burke, M., Bien, S., Ranganath, C., Rösler, F., 2005. Content-specific activation during associative long-term memory retrieval. NeuroImage 27 (4), 805–816.

Khader, P., Ranganath, C., Seemüller, A., Rösler, F., 2007. Working memory maintenance contributes to long-term memory formation: Evidence from slow event-related brain potentials. Cogn. Affect. Behav. Neurosci. 7 (3), 212–224. https://doi.org/10.3758/CABN.7.3.212.

Kim, A.S.N., Vallesi, A., Picton, T.W., Tulving, E., 2009. Cognitive association formation in episodic memory: Evidence from event-related potentials. Neuropsychologia 47 (14), 3162–3173. https://doi.org/10.1016/j.neuropsychologia.2009.07.015.

Kim, E.N., & Yoo, S.Y. (2005). Event-Related Potentials Study of Incidental Encoding in Obsessive-Compulsive Disorder.

Kim, H., 2011. Neural activity that predicts subsequent memory and forgetting: a meta-analysis of 74 fMRI studies. NeuroImage 54 (3), 2446–2461. https://doi.org/10.1016/j.neuroimage.2010.09.045.

Koen, J.D., Horne, E.D., Hauck, N., Rugg, M.D., 2018. Age-related differences in prestimulus subsequent memory effects assessed with event-related potentials. J. Cogn. Neurosci. 30 (6), 829–850. https://doi.org/10.1162/jocn_a_01249.

Kolisnyk, M., Pereira, A.E., Tozios, C.J., Fukuda, K., 2023. Dissociating the impact of memorability on electrophysiological correlates of memory encoding success. J. Cogn. Neurosci. 35 (4), 603–627.

Koppehele-Gossel, J., Khosrowtaj, Z., Gibbons, H., 2019. Effects of distinctiveness and memory on lateralized and unlateralized brain-electrical activity during visual word encoding. Brain Cogn. 134, 9–20. https://doi.org/10.1016/j.bandc.2019.04.005.

Krauel, K., Duzel, E., Hinrichs, H., Lenz, D., Herrmann, C.S., Santel, S., Rellum, T., Baving, L., 2009. Electrophysiological correlates of semantic processing during encoding of neutral and emotional pictures in patients with ADHD. Neuropsychologia 47 (8–9), 1873–1882. https://doi.org/10.1016/j.neuropsychologia.2009.02.030.

Kuo, M.C.C., Liu, K.P.Y., Ting, K.H., Chan, C.C.H., 2014. Age-related effects on perceptual and semantic encoding in memory. Neuroscience 261, 95–106. https://doi.org/10.1016/j.neuroscience.2013.12.036.

Kutas, M., Hillyard, S.A., 1980. Reading senseless sentences: Brain potentials reflect semantic incongruity. Science 207 (4427), 203–205.

Lian, J., Goldstein, A., Donchin, E., He, B., 2002. Cortical potential imaging of episodic memory encoding. Brain Topogr. 15 (1), 29.

Liu, Y., Rosburg, T., Gao, C., Weber, C., Guo, C., 2017. Differentiation of subsequent memory effects between retrieval practice and elaborative study. Biol. Psychol. 127, 134–147. https://doi.org/10.1016/j.biopsycho.2017.05.010.

Makeig, S., Westerfield, M., Jung, T.-P., Enghoff, S., Townsend, J., Courchesne, E., Sejnowski, T.J., 2002. Dynamic brain sources of visual evoked responses. Science 295 (5555), 690–694. https://doi.org/10.1126/science.1066168.

Mangels, J.A., Picton, T.W., Craik, F.I.M., 2001. Attention and successful episodic encoding: an event-related potential study. Cogn. Brain Res. 11 (1), 77–95. https://doi.org/10.1016/S0926-6410(00)00066-5.

Mangels, J.A., Manzi, A., Summerfield, C., 2009. The first does the work, but the third timeˆs the charm: the effects of massed repetition on episodic encoding of multimodal face–name associations. J. Cogn. Neurosci. 22 (3), 457–473.

Marini, F., Marzi, T., Viggiano, M.P., 2011. Wanted!" The effects of reward on face recognition: electrophysiological correlates. Cogn. Affect. Behav. Neurosci. 11 (4), 627–643. https://doi.org/10.3758/s13415-011-0057-7.

McDaniel, M.A., Geraci, L., 2006. Encoding and retrieval processes in distinctiveness effects: toward an integrative framework. In: Hunt, R.R., Worthen, J.B. (Eds.), Distinctiveness and Memory. Oxford University Press, New York, pp. 65–88. https://doi.org/10.1093/acprof:oso/9780195169669.003.0004.

Mecklinger, A., 2010. The control of long-term memory: brain systems and cognitive processes. Neurosci. Biobehav. Rev. 34 (7), 1055–1065. https://doi.org/10.1016/j.neubiorev.2009.11.020.

Mecklinger, A., Bader, R., 2020. From fluency to recognition decisions: a broader view of familiarity-based remembering. Neuropsychologia 146, 107527. https://doi.org/10.1016/j.neuropsychologia.2020.107527.

Mecklinger, A., Müller, N., 1996. Dissociations in the processing of "what" and "where" information in working memory: an event-related potential analysis. J. Cogn. Neurosci. 8 (5), 453–473. https://doi.org/10.1162/jocn.1996.8.5.453.

Meng, Y., Ye, X., Gonsalves, B.D., 2014. Neural processing of recollection, familiarity and priming at encoding: Evidence from a forced-choice recognition paradigm. Brain Res. 1585, 72–82. https://doi.org/10.1016/j.brainres.2014.08.024.

Meßmer, J.A., Bader, R., Mecklinger, A., 2021. The more you know: Schema-congruency supports associative encoding of novel compound words. Evidence from event-related potentials. Brain Cogn. 155, 105813 https://doi.org/10.1016/j.bandc.2021.105813.

Münte, T.F., Heinze, H.J., Scholz, M., Künkel, H., 1988. Effects of a cholinergic nootropic (WEB 1881 FU) on event-related potentials recorded in incidental and intentional memory tasks. Neuropsychobiology 19 (3), 158–168. https://doi.org/10.1159/000118453.

Nunez, P.L., 1981. Electrical Fields of the Brain: The Neurophysics of EEG. Oxford University Press, New York.

Nyhus, E., Curran, T., 2010. Functional role of gamma and theta oscillations in episodic memory. Neurosci. Biobehav. Rev. 34 (7), 1023–1035. https://doi.org/10.1016/j.neubiorev.2009.12.014.

Otten, L.J., Donchin, E., 2000. Relationship between P300 amplitude and subsequent recall for distinctive events: Dependence on type of distinctiveness attribute. Psychophysiology 37 (5), 644–661. https://doi.org/10.1111/1469-8986.3750644.

Otten, L.J., Rugg, M.D., 2001. Electrophysiological correlates of memory encoding are task-dependent. Cogn. Brain Res. 12 (1), 11–18. https://doi.org/10.1016/S0926-6410(01)00015-5.

Otten, L.J., Henson, R.N.A., Rugg, M.D., 2001. Depth of processing effects on neural correlates of memory encoding: Relationship between findings from across- and within-task comparisons. Brain 124 (2), 399–412. https://doi.org/10.1093/brain/124.2.399.

Otten, L.J., Henson, R.N.A., Rugg, M.D., 2002. State-related and item-related neural correlates of successful memory encoding. Nat. Neurosci. 5 (12), 1339–1344. https://doi.org/10.1038/nn967.

Otten, L.J., Quayle, A.H., Akram, S., Ditewig, T.A., Rugg, M.D., 2006. Brain activity before an event predicts later recollection. Nat. Neurosci. 9 (4), 489–491. https://doi.org/10.1038/nn1663.

Otten, L.J., Sveen, J., Quayle, A.H., 2007. Distinct patterns of neural activity during memory formation of nonwords versus words. J. Cogn. Neurosci. 19 (11), 1776–1789. https://doi.org/10.1162/jocn.2007.19.11.1776.

Otten, L.J., Quayle, A.H., Puvaneswaran, B., 2010. Prestimulus subsequent memory effects for auditory and visual events. J. Cogn. Neurosci. 22 (6), 1212–1223. https://doi.org/10.1162/jocn.2009.21298.

Packard, P.A., Rodríguez-Fornells, A., Bunzeck, N., Nicolás, B., de Diego-Balaguer, R., Fuentemilla, L., 2017. Semantic congruence accelerates the onset of the neural signals of successful memory encoding. J. Neurosci. 37 (2), 291–301. https://doi.org/10.1523/JNEUROSCI.1622-16.2016.

Padovani, T., Koenig, T., Brandeis, D., Perrig, W.J., 2011. Different brain activities predict retrieval success during emotional and semantic encoding. J. Cogn. Neurosci. 23 (12), 4008–4021. https://doi.org/10.1162/jocn_a_00096.

Padovani, T., Koenig, T., Eckstein, D., Perrig, W.J., 2013. Sustained and transient attentional processes modulate neural predictors of memory encoding in consecutive time periods. Brain Behav. 3 (4), 464–475. https://doi.org/10.1002/brb3.150.

Paller, K.A., 1990. Recall and stem-completion priming have different electrophysiological correlates and are modified differentially by directed forgetting. J. Exp. Psychol.: Learn., Mem., Cogn. 16 (6), 1021–1032. https://doi.org/10.1037/0278-7393.16.6.1021.

Paller, K.A., McCarthy, G., Wood, C.C., 1988. ERPs predictive of subsequent recall and recognition performance. Biol. Psychol. 26 (1–3), 269–276. https://doi.org/10.1016/0301-0511(88)90023-3.

Parks, C.M., Yonelinas, A.P., 2015. The importance of unitization for familiarity-based learning. J. Exp. Psychol.: Learn., Mem., Cogn. 41 (3), 881–903. https://doi.org/10.1037/xlm0000068.

Piai, V., Anderson, K.L., Lin, J.J., Dewar, C., Parvizi, J., Dronkers, N.F., Knight, R.T., 2016. Direct brain recordings reveal hippocampal rhythm underpinnings of language processing. Proc. Natl. Acad. Sci. USA 113 (40), 11366–11371. https://doi.org/10.1073/pnas.1603312113.

Porter, N.A., Fields, E.C., Moore, I.L., Gutchess, A., 2021a. Late frontal positivity effects in Self-referential Memory: Unique to the Self? Soc. Neurosci. 16 (4), 406–422. https://doi.org/10.1080/17470919.2021.1929460.

Porter, N.A., Fields, E.C., Moore, I.L., Gutchess, A., 2021b. Late frontal positivity effects in Self-referential memory: unique to the self? Soc. Neurosci. 16 (4), 406–422. https://doi.org/10.1080/17470919.2021.1929460.

Rangel-Gomez, M., Meeter, M., 2013. Electrophysiological analysis of the role of novelty in the von Restorff effect. Brain Behav. 3 (2), 159–170. https://doi.org/10.1002/brb3.112.

Richter, F.R., Yeung, N., 2016. ERP correlates of encoding success and encoding selectivity in attention switching. PLOS ONE 11 (12), e0167396. https://doi.org/10.1371/journal.pone.0167396.

Righi, G., Peissig, J.J., Tarr, M.J., 2012. Recognizing disguised faces. Vis. Cogn. 20 (2), 143–169.

Robichon, F., Besson, M., Habib, M., 2002. An electrophysiological study of dyslexic and control adults in a sentence reading task. Biol. Psychol. 59 (1), 29–53. https://doi.org/10.1016/S0301-0511(01)00118-1.

Roediger, H.L., Karpicke, J.D., 2006. The power of testing memory: basic research and implications for educational practice. Perspect. Psychol. Sci. 1 (3), 181–210. https://doi.org/10.1111/j.1745-6916.2006.00012.x.

Roediger, H.L., McDermott, K.B., 1995. Creating false memories: remembering words not presented in lists. J. Exp. Psychol.: Learn., Mem., Cogn. 21 (4), 803.

Rollins, L., Riggins, T., 2013. Developmental changes in memory encoding: Insights from event-related potentials. Dev. Sci. 16 (4), 599–609. https://doi.org/10.1111/desc.12072.

Rollins, L., Riggins, T., 2018. Age-related differences in subjective recollection: ERP studies of encoding and retrieval. Dev. Sci. 21 (3), e12583 https://doi.org/10.1111/desc.12583.

Rösler, F., Heil, M., Röder, B., 1997. Slow negative brain potentials as reflections of specific modular resources of cognition. Biol. Psychol. 45 (1–3), 109–141.

Rugg, M.D., Coles, M.G.H. (Eds.), 1995. Electrophysiology of mind: Event-related brain potentials and cognition. Oxford University Press.

Rugg, M.D., Curran, T., 2007. Event-related potentials and recognition memory. Trends Cogn. Sci. 11 (6), 251–257. https://doi.org/10.1016/j.tics.2007.04.004.

Sanquist, T.F., Rohrbaugh, J.W., Syndulko, K., Lindsley, D.B., 1980. Electrocortical Signs of Levels of Processing: Perceptual Analysis and Recognition Memory. Psychophysiology 17 (6), 568–576. https://doi.org/10.1111/j.1469-8986.1980.tb02299.x.

Schott, B., Richardson-Klavehn, A., Heinze, H.-J., Düzel, E., 2002. Perceptual priming versus explicit memory: dissociable neural correlates at encoding. J. Cogn. Neurosci. 14 (4), 578–592. https://doi.org/10.1162/08989290260045828.

Schott, B.H., Wüstenberg, T., Lücke, E., Pohl, I.-M., Richter, A., Seidenbecher, C.I., Pollmann, S., Kizilirmak, J.M., Richardson-Klavehn, A., 2018. Gradual acquisition of visuospatial associative memory representations via the dorsal precuneus. Hum. Brain Mapp. 40 (5), 1554–1570. https://doi.org/10.1002/hbm.24467.

Spachtholz, P., Kuhbandner, C., 2017. Visual long-term memory is not unitary: Flexible storage of visual information as features or objects as a function of affect. Cogn. Affect. Behav. Neurosci. 17 (6), 1141–1150. https://doi.org/10.3758/s13415-017-0538-4.

Spencer, K.M., Dien, J., Donchin, E., 1999. A componential analysis of the ERP elicited by novel events using a dense electrode array. Psychophysiology 36 (3), 409–414. https://doi.org/10.1017/S0048577299981180.

Staresina, B.P., Bauer, H., Deecke, L., Walla, P., 2005. Neurocognitive correlates of incidental verbal memory encoding: a magnetoencephalographic (MEG) study. NeuroImage 25 (2), 430–443. https://doi.org/10.1016/j.neuroimage.2004.11.035.

Sundby, C.S., Woodman, G.F., Fukuda, K., 2019. Electrophysiological and behavioral evidence for attentional up-regulation, but not down-regulation, when encoding pictures into long-term memory. Mem. Cogn. 47 (2), 351–364. https://doi.org/10.3758/s13421-018-0871-z.

Tulving, E., 1985. Memory and consciousness. Can. Psychol. /Psychol. Can. 26 (1), 1.

Uncapher, M.R., Wagner, A.D., 2009. Posterior parietal cortex and episodic encoding: Insights from fMRI subsequent memory effects and dual-attention theory. Neurobiol. Learn. Mem. 91 (2), 139–154. https://doi.org/10.1016/j.nlm.2008.10.011.

Urbach, T.P., Windmann, S.S., Payne, D.G., Kutas, M., 2005. Mismaking memories: neural precursors of memory illusions in electrical brain activity. Psychol. Sci. 16 (1), 19–24. https://doi.org/10.1111/j.0956-7976.2005.00775.x.

Van Berkum, J.J., 2010. The brain is a prediction machine that cares about good and bad-any implications for neuropragmatics? Ital. J. Linguist. 22, 181–208. ⟨https://linguistica.sns.it/RdL/2010.html⟩.

Van Petten, C., Senkfor, A.J., 1996. Memory for words and novel visual patterns: Repetition, recognition, and encoding effects in the event-related brain potential. Psychophysiology 33 (5), 491–506. https://doi.org/10.1111/j.1469-8986.1996.tb02425.x.

Wagner, A.D., Schacter, D.L., Rotte, M., Koutstaal, W., Maril, A., Dale, A.M., Rosen, B.R., Buckner, R.L., 1998. Building memories: remembering and forgetting of verbal experiences as predicted by brain activity. Science 281 (5380), 1188–1191. https://doi.org/10.1126/science.281.5380.1188.

Weidemann, C.T., Kahana, M.J., 2021. Neural measures of subsequent memory reflect endogenous variability in cognitive function. J. Exp. Psychol.: Learn. Mem. Cogn. 47 (4), 641–651. https://doi.org/10.1037/xlm0000966.

Weigl, M., Pham, H.H., Mecklinger, A., Rosburg, T., 2020. The effect of shared distinctiveness on source memory: an event-related potential study. Cogn., Affect., Behav. Neurosci. 20 (5), 1027–1040. https://doi.org/10.3758/s13415-020-00817-1.

Weyerts, H., Tendolkar, I., Smid, H.G.O.M., Heinze, H.-J., 1997. ERPs to encoding and recognition in two different inter-item association tasks. NeuroReport 8 (7), 1583–1588. https://doi.org/10.1097/00001756-199705060-00007.

Wiemer, J., Leimeister, F., Pauli, P., 2021. Subsequent memory effects on event-related potentials in associative fear learning. Soc. Cogn. Affect. Neurosci. 16 (5), 525–536. https://doi.org/10.1093/scan/nsab015.

Wiswede, D., Rüsseler, J., Hasselbach, S., Münte, T.F., 2006. Memory recall in arousing situations – an emotional von Restorff effect? BMC Neurosci. 7 (1), 57 https://doi.org/10.1186/1471-2202-7-57.

Wolff, N., Kemter, K., Schweinberger, S.R., Wiese, H., 2014. What drives social in-group biases in face recognition memory? ERP evidence from the own-gender bias. Soc. Cogn. Affect. Neurosci. 9 (5), 580–590. https://doi.org/10.1093/scan/nst024.

Yick, Y.Y., Buratto, L.G., Schaefer, A., 2016. Variations in prestimulus neural activity predict the emotion-enhanced memory effect. NeuroReport 27 (11), 864–868. https://doi.org/10.1097/WNR.0000000000000628.

Yonelinas, A.P., Aly, M., Wang, W.-C., Koen, J.D., 2010. Recollection and familiarity: examining controversial assumptions and new directions. Hippocampus 20 (11), 1178–1194. https://doi.org/10.1002/hipo.20864.

Yovel, G., Paller, K.A., 2004. The neural basis of the butcher-on-the-bus phenomenon: when a face seems familiar but is not remembered. NeuroImage 21 (2), 789–800. https://doi.org/10.1016/j.neuroimage.2003.09.034.

Zerbes, G., Schwabe, L., 2019. Across time and space: spatial-temporal binding under stress. Learn. Mem. 26 (12), 473–484. https://doi.org/10.1101/lm.050237.119.