Reduced memory-related ongoing oscillatory activity in healthy older adults

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A B S T R A C T

Age-related impairments in episodic memory have been linked to alterations in encoding-induced neural activity. In young individuals, even prestimulus activity has been shown to influence the encoding of an upcoming stimulus, with ongoing theta and beta oscillations being predictive of subsequent recognition. The present study investigated if these memory-related ongoing oscillations are also affected by aging. In an EEG experiment, healthy older and young individuals performed an encoding task with a subsequent recognition test on picture and word stimuli. The group of younger participants showed an increased oscillatory activity in the lower frequency range (ranging from 3 to 17 Hz) in the pre- and post-stimulus period compared with the older adults. Only in young participants, ongoing beta power during encoding was related to later memory in both stimulus categories, whereas in older participants, this effect was diminished. Interestingly, there was no general age-related decrease in recognition performance. These results indicate that ongoing low beta oscillations might constitute a functional indicator of cognitive aging that reveals itself even before a strong decline in behavioral performance is noticeable, and that could be a potential target for neuromodulatory interventions.

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1. Introduction

Ongoing neural activity can modulate the way we perceive and process incoming sensory input (Hanslmayr et al., 2007; Keil et al., 2014; Salari et al., 2012). The state of the nervous system before the onset of a stimulus influences the successful encoding of an upcoming stimulus into long-term memory (e.g., Otten et al., 2006). Differences in brain activity at the stage of encoding that are associated with later remembering of stimuli have been detected in the prestimulus time range using a variety of methods investigating neural activity on several scales, such as event-related potentials (Galli et al., 2013; Gruber and Otten, 2010; Otten et al., 2006) and functional magnetic resonance imaging (fMRI; Park and Rugg, 2010). Regarding oscillatory brain states, an increased prestimulus power in the theta frequency range (3–7 Hz) has been found to be associated with later memory using MEG (Guderian et al., 2009), EEG (Fellner et al., 2013) and intracranial recordings from the hippocampus and rhinal cortex (Fell et al., 2011). Theta effects were reported under conditions of high motivation (Gruber et al., 2013) and before the successful learning of an association (Scholz et al., 2017). Other studies also reported prestimulus effects in alpha

(8–12 Hz) and gamma (>30 Hz) frequencies (Fell et al., 2011; Noh et al., 2014; Park et al., 2014).

Recently, Salari and Rose (2016) investigated ongoing EEG oscillations in the absence of a cue that could predict the timing of the next stimulus, which had been used by most previous studies. In a first experiment, they found increased ongoing oscillations in the theta band but also in the low beta frequency range (13–17 Hz) for later remembered compared with later forgotten pictures. In a second experiment, a brain computer interface was implemented that allowed for the selective presentation of stimuli in states of increased or decreased power in theta or beta frequencies. Stimulus presentation in dependency to ongoing theta power did not affect encoding performance. Interestingly, however, presenting stimuli in a state of elevated low beta power increased the likelihood of this stimulus being remembered. These results suggest a functional role of ongoing low beta oscillations in encoding. Similar oscillatory states have been found to be related to the encoding of verbal stimuli, both written and spoken (Scholz et al., 2017). Furthermore, it has been shown that low beta oscillations are also related to encoding and can be affected voluntarily if participants are aware of the necessity to encode an upcoming item (Schneider and Rose, 2016), which might suggest a process of encoding-specific preparation for a stimulus.

It is well known that episodic memory performance decreases with increasing age, even during healthy aging (e.g., Koen and

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Yonelinas, 2014; Murre et al., 2013; Salthouse, 2003). However, although older adults constitute a target population when it comes to the investigation of memory processes, it is so far unclear whether similar ongoing oscillatory activities play a role in the encoding abilities of older individuals as they do in young adults. A variety of studies have investigated age-related differences in stimulus-induced effects in relation to later memory using fMRI, most consistently showing age-related under-recruitment of occipital and fusiform cortex but over-recruitment in a set of regions including bilateral middle/superior frontal gyri, anterior medial frontal gyrus, precuneus, and left inferior parietal lobe (for a meta-analysis, see Maillet and Rajah, 2014).

Regarding memory-related neural oscillations, older individuals show altered, mostly reduced, task-related power modulations in frequencies that are associated with successful memory performance in young people, namely in theta (Crespo-Garcia et al., 2012; Lithfous et al., 2015; Rondina et al., 2016; Steiger and Bunzeck, 2017), alpha, and beta (Crespo-Garcia et al., 2012; Lithfous et al., 2015; Sebastián et al., 2011) as well as gamma frequencies (Després et al., 2017; López-Loeza et al., 2016). It was recently demonstrated that for memory recollection, the relation of theta-band activity and memory was reduced for older adults (Strunk et al., 2017). The same study demonstrated also a relation of beta-band desynchronization with memory for older adults. However, both effects were found during stimulus processing. Interestingly, several studies indicate that not only stimulus-induced brain activity is altered in older adults. In addition, for resting state recordings, age-related differences in oscillatory brain activity have widely been reported (e.g., Hashemi et al., 2016). In fact, resting-state theta and alpha activity have been identified as mediators of age-related declines in long-term memory performance (Reichert et al., 2016). Similarly, using fMRI, resting-state functional connectivity within subcortical structures was associated with memory decline in healthy older individuals (Ystad et al., 2010). It is therefore conceivable that alterations in ongoing brain states play an important role in cognitive aging, in particular, in relation to memory processes. However, oscillatory brain states measured during resting states usually reflect a variety of different specific and unspecific processes in contrast to ongoing activity measured in an active task set. In particular, the activity within a prestimulus interval of a memory task can be regarded as an active preparatory brain state with a close relation to the memory process. Therefore, ongoing oscillatory activity in the prestimulus period allows a more direct interpretation of the measured differences and should be differentiated from resting-state measurements. In animal studies, theta-band activity was directly related to synaptic plasticity (Greenstein et al., 1988; Hyman et al., 2003) and is an important mechanism for the theory of rate and temporal coding (Huxter et al., 2003; Buzsáki and Moser, 2013) that was originally introduced to explain spatial memory but was recently extended to associative memory (Terada et al., 2017). In this model, the information within the hippocampus is represented by the firing rate of event or place cells embedded in an ongoing theta rhythm and with respect to the theta phase at stimulus onset. In the extension of the model, the theta rhythm and particular theta band activity at stimulus onset is regarded as essential for the formation of associations between different stimuli or with contextual information while beta band activity is relevant for the encoding of item memory. Therefore, the implementation of distinct oscillatory states in the prestimulus period can be assumed to be important for the encoding of following stimuli.

Neural circuits can be described as nonlinear dynamical systems (Friston, 2000). Even small changes in the initial conditions of a dynamical system can result in profound modulations of the response. This function can be related to the development of specialized dynamic attractor states as outlined in the dynamic field theory (Strub et al., 2017). Here an autonomous adaptation of the dynamic neural field is assumed in particular also for resting levels and gain as represented in ongoing oscillatory activity. This development of specific dynamic attractors that are represented by oscillatory activity during a period without external stimulation can be regarded as the initial conditions for the generation of processing-related states. Thus, modulations of ongoing activity states can affect the establishment of specialized dynamic attractor states during stimulus processing. The distinct prestimulus states can be regarded as top-down influences on local networks and the concept of a dynamic background state is incorporated in computational models of neural dynamics (Srinivasan et al., 2013). Such top-down processes can be related to classical psychological factors such as attention (Gola et al., 2012) or motivation (Steiger and Bunzeck, 2017) or can reflect more specific preparatory processes such as a Bayes prior for the processing state (Miller, 2016). This interplay of different oscillatory states in the pre- and post-stimulus processing period is the result of learning mainly in younger years. The structural changes with age may change in particular the preparatory states that emerge without external stimulation and this change in the top-down preparation process should affect stimulus processing. This assumption is further supported by the neural noise hypothesis of aging that assumes a reduced dynamic of neural communication with aging by an increase in spontaneous, noisy baseline neural activity that prevents the development of an attractor state during the period without external stimulation (Voytek et al., 2015). Therefore, it can be assumed that the dynamic adaption of ongoing activity is reduced with age. In particular the development of spontaneous oscillatory states for memory encoding can be affected by this change of neural activity with age.

The goal of the present study was therefore to investigate age-dependent differences in memory-related oscillatory brain activity, specifically regarding prestimulus brain activity during encoding. While measuring EEG data, we conducted a subsequent memory paradigm in older and young participants using 2 different previously studied stimulus categories (pictures and words). We hypothesize a general reduction in prestimulus activity irrespective of the subsequently presented stimulus. Therefore, 2 different stimulus categories were used to cover a wider range of memory processes and examine differences and common effects in both groups of participants. We hypothesized that we would replicate previous findings in young participants, which indicated that prestimulus power in the theta and low beta frequency range are associated with later memory for the stimulus (Salari and Rose, 2016). In older adults, we expected to find reduced memory-related modulations of ongoing brain activity compared with young participants, as reported for poststimulus neural processing and resting-state activity (Kardos et al., 2014; Reichert et al., 2016; Rondina et al., 2016; Steiger and Bunzeck, 2017).

2. Materials and methods

2.1. Participants

The total sample consisted of 24 older volunteers (10 males, mean age = 63.1 years, age range 55—75 years) and 29 young volunteers (14 males, mean age = 26.24 years, age range 19—32 years) with no history of psychiatric or neurologic disorders. Volunteers taking psychopharmacological medication or strong pain medication were excluded from the study. All participants were native German speakers and had normal or corrected-to-normal vision. Volunteers participated in return for payment after giving informed consent. The study was approved by the Ethics Committee of the German Psychological Association.

All older volunteers were screened for signs of mild cognitive impairment using the Montreal Cognitive Assessment, which is a highly sensitive mild cognitive impairment screening tool (Nasreddine et al., 2005). Only volunteers with a Montreal Cognitive Assessment score ≥26 were included in the sample (M = 27.75, SD = 1.33). Volunteers from both age groups were screened for depressive symptoms using the revised Beck's Depression Inventory (BDI-II; Hautzinger et al., 2006). Volunteers with a BDI score ≤13 were included in the study. The 2 groups did not differ significantly on their BDI scores, with an average score of 2.58 (SD = 3.56) in older and 3.31 (SD = 3.24) in young participants, Welch's t (47.14) = −0.77, p = 0.44. The total duration of education (school years plus additional higher education) did not differ significantly between young (M = 17.24 years, SD = 2.98) and older volunteers (M = 15.81 years, SD = 4.19; t (40.49) = −1.40, p = 0.17). As a proxy for verbal intelligence, the Mehrfachwahl-Wortschatz-Intelligenztest, a multiple choice vocabulary test, was conducted (Lehrl, 1999), which also revealed no difference in percentile ranks between young (M = 75.58, SD = 18.97), and older (M = 82.37, SD = 21.05; t (46.89) = 1.22, p = 0.23).

2.2. Procedure

After giving informed consent and after completing the neuropsychological testing described previously, participants took part in a subsequent memory task, consisting of 3 phases—encoding, delay, and retrieval—which each lasted about 20 minutes.

In the encoding and retrieval phases, participants were presented with a series of stimuli, namely pictures and words. The pictures (size 336 × 252 pixels; 24 bit color depth) were selected randomly from a pool of 200 pictures. They were photographs of animals, plants or objects which were taken from an internal database, similarly to previous studies (Salari and Rose, 2016; Schneider and Rose, 2016). The words were German nouns selected randomly from a pool of 200 words from the SUBTLEX database, which includes the 10,000 most common words from the subtitles of movies and TV shows translated from English to German (Brysbaert et al., 2011). Words were presented in written form (Helvetica, size 46 pt.)

In the encoding phase, 74 randomly selected pictures and 74 randomly selected words were presented in 4 blocks, each containing 37 items of one stimulus type. Blocks containing words and pictures were alternated with the order being counterbalanced across participants in both groups. All stimuli were presented for 2 seconds and the intertrial interval varied randomly between 3 and 6 seconds so that the timing of the upcoming stimulus was unpredictable for the participants. The task was to judge whether a stimulus represented something living or nonliving. Answers were given by button press using the left and right index fingers, with the mapping between the answers and the buttons being counterbalanced across participants. Participants were instructed that they were participating in a memory task and that they would have to recognize the stimuli afterward. They were asked not to apply any other specific encoding strategies, but to focus on the given task.

Afterward, in the delay phase, participants carried out a working memory task as a distraction from the long-memory task, to avoid rehearsal or retrieval processes. The task comprised numerical series that had to be repeated, which are not expected to interfere with the material from the encoding task.

Finally, in the recognition phase, participants were again presented with the stimuli from the encoding phase, intermixed with 26 new pictures and 26 new words. Again, pictures and words were presented blockwise with 50 stimuli of the same type (words/pictures) within each block. The order of stimuli was randomized. The recognition task followed a 2-step procedure for each trial. In the

first step, participants were presented with a stimulus and had to indicate by button press whether they think it was old or new. After the old/new decision, a visual analog scale was presented, and participants had to indicate how confident they were about their decision on a scale from not confident to highly confident. Then, the next stimulus was presented again with the 2-step procedure to acquire memory and confidence for each trial. Confidence ratings were used to detect possible difference in the strength of memory or as an indicator for the use of different strategies in both groups.

2.3. EEG data acquisition, preprocessing, and time-frequency decomposition

EEG data were collected during the encoding phase from 60 active scalp electrodes (actiCap, Brain Products, Gilching, Germany) in an electrically shielded and sound-attenuated cabin. Data were online-referenced to FCz and later rereferenced offline to the common average. The ground electrode was positioned on the neck. To detect eye movements, EOG data were recorded from above and below the left eye and from the outer canthi of the eyes. Electrode impedances were kept below 20 kΩ. Data were amplified with a low cutoff frequency of 0.53 Hz (=0.3 seconds time constant) and were recorded with a sampling rate of 250 Hz.

EEG data were processed offline using the FieldTrip toolbox (Version 20160124; Oostenveld et al., 2011; http://www.ru.nl/neuroimaging/fieldtrip) implemented in MATLAB (Release 2013a, The MathWorks Inc, Natick, Massachusetts, USA). Epochs from −2000 ms to +1500 ms relative to stimulus onset were extracted and demeaned. Independent component analysis was used to remove blink, eye movement, cardiac, and muscle artifacts based on visual inspection of the time course, spectrum, and topography of each component. Afterward, a semiautomated artifact rejection procedure was applied to eliminate remaining artifacts. For this purpose, amplitudes in all trials from all electrodes were z-transformed across time. Trials in which the maximal z-value was greater than 7 were marked automatically and rejected if considered artifactual by visual inspection. On average, 143.50 trials (SD = 2.66) remained after artifact rejection per participant for young participants and 143.44 (SD = 3.55) for older participants. Time-frequency decomposition was conducted for frequencies between 2 and 30 Hz with a frequency resolution of 1 Hz. A wavelet convolution with a Hanning taper was applied, with the number of cycles linearly increasing from 3 cycles at 2 Hz to 10 cycles at 30 Hz. Because we were interested in activity before stimulus onset, we could not use a prestimulus baseline. To assess the main differences between both groups of participants, the time-frequency spectra of all later remembered trials separately for pictures and words were compared. Data were averaged across trials for each participant. The resulting differences in oscillatory activity were tested for a relation to memory by a correlation of the sensitivity index d′ in each group and separately for pictures and words. For each time point and each frequency between 3 and 17 Hz, the oscillatory power in each participants was calculated and the vector across participants of each group was correlated with the vector of d′ values for all participants of the respective group (in the vector, each participant is represented by the individual d′ value).

As an additional analysis, the differential effects that compared the remembered trials to the later forgotten trials (subsequent memory effects [SMEs]) were estimated. Here, the main differences in oscillatory activity can affect the comparison of the SMEs in both groups. Therefore, we implemented a normalization across all trials, as described by van den Berg et al. (2016), which involved first the log-transformation of power values at each time point, frequency, and channel, and second the transformation of those values into z-scores across all trials. This procedure allows a direct

comparison of SMEs between groups because the different baseline levels of activity were no longer relevant in the z-scores that were used for the comparison. The data were stratified, that is, the same number of trials per condition (later remembered/later forgotten) was selected randomly in each participant, so that the noise level in both conditions remained equal. Participants with at least 10 artifact-free trials per condition (later remembered/later forgotten) were included in the analyses. For the analyses of SMEs with regard to pictures, 19 young and 17 older participants could be included, and for words, 18 young and 19 older participants were included. Data were averaged across trials for each participant and each condition. For a better comparability, the same participants were used for the analysis of the main differences in oscillatory activity and the relation to memory.

2.4. Statistical analysis

Behavioral data were analyzed in R (Version 3.3.1; R Core Team, 2016; http://www.r-project.org/). From the encoding phase, correctness of the animacy judgments was inspected to check for the compliance of participants. Furthermore, median reaction times were extracted and compared between conditions and groups. The median was chosen because it is not susceptible to outliers than the mean. From the recognition phase, recognition rates and false alarm rates were extracted. Based on signal detection theory, the sensitivity d' in the recognition task was computed (see, e.g., Macmillan, 2002). Median reaction times for the old-new decisions were compared between groups and conditions.

EEG data were analyzed using nonparametric cluster-based permutation tests as implemented in the FieldTrip toolbox (Maris and Oostenveld, 2007). This method controls for the multiple comparison problem using a multistep procedure. In the first step, for every data point, the signal is compared between 2 groups or conditions (e.g., remembered vs. forgotten items) and a t-value is computed. Next, all samples whose t-values are above a specific threshold (in our case, the equivalent of $\alpha < 0.05$) are selected and all samples above the threshold are summarized into clusters of adjacent data points. As a cluster-based test statistic, the sum of t-values of all samples within each cluster is extracted. Afterward the same data set is randomly partitioned into 2 arbitrary conditions. The same steps as aforementioned are repeated, so that a random cluster-based test statistic can be extracted. These random permutation steps are repeated a large number of times (1000 in our case), enabling the formation of a distribution of random cluster-based test statistics. The p-value of the actual empirical clusters is then calculated by computing the

proportion of random permutations that led to a greater cluster statistic than that of the empirical cluster. The advantage of this permutation approach is that it is not dependent on an assumed distribution of the data. In particular for neurobiological systems the measured data are often clustered in the dimensions space, frequency, and time. Therefore, a cluster-based permutation test is optimally suited to sample the distribution of the data and to be used for the correction of multiple comparisons. To assess main differences in oscillatory activity, the correction for multiple comparison was applied to the complete spectra from 3 to 20 Hz. In accordance with our hypotheses, we applied this procedure for the theta (3–7 Hz) and the low beta (13–17 Hz) frequency ranges for the differential contrast regarding the SMEs. SMEs were investigated in each group and for each stimulus type separately and compared between groups if an effect was found.

3. Results

3.1. Behavioral results

An overview of the behavioral outcomes is displayed in Table 1. Accuracy in the encoding task was on average above 90% for both groups in both conditions, indicating high compliance in our participants. Reaction times during encoding were analyzed using a mixed design ANOVA with the within-subject factors memory (later remembered, later forgotten) and stimulus type (pictures, words) and the between-subject factor group (young, older). Significant main effects of stimulus type [$F_{(1,51)} = 8.37$, $p < 0.01$] and memory [$F_{(1,51)} = 21.23$, $p < 0.001$] were revealed because of faster reactions for pictures than words and overall slower reactions for later remembered than later forgotten words (see Table 1). There were no significant interactions (all $p > 0.05$).

As a measure for recognition performance, the sensitivity measure d' was analyzed using a mixed design ANOVA with the within-subject factor stimulus type (pictures, words) and the between-subject factor group (young, older). A main effect of stimulus type was found [$F_{(1,51)} = 12.71$, $p < 0.001$], which represents worse recognition performance for words than for pictures. No other main effect or interaction was found (all $p > 0.05$).

Furthermore, the response bias [according to the signal detection theory (Kantner and Lindsay, 2012)] was estimated separately for picture and word stimuli for the participants that were included in the EEG analysis and was compared between groups. No difference between groups was observed for pictures [$t_{(34)} = 0.98$, n.s.] and words [$t_{(35)} = -0.46$, n.s.].

Table 1
Behavioral results

Value	Young		Older	
	Pictures	Words	Pictures	Words
Encoding				
Categorization hit rate [%]	97.1 (3.4)	93.6 (8.6)	92.7 (9.0)	94.2 (6.1)
RT later remembered [ms]	949.9 (369.2)	1018.6 (239.4)	968.7 (166.4)	1082.1 (184.1)
RT later forgotten [ms]	874.7 (288.8)	936.4 (191.5)	952.2 (223.6)	992.2 (152.2)
Recognition				
Recognition rate [%]	80.2 (11.7)	83.0 (11.7)	79.8 (9.1)	72.9 (16.4)
False alarm rate [%]	11.3 (10.4)	20.2 (10.9)	13.0 (10.9)	20.5 (14.2)
d'	2.06 (0.54)	1.85 (0.56)	1.97 (0.58)	1.50 (0.67)
Response bias	0.41	0.14	0.31	0.19
RT remembered [ms]	1310.3 (352.5)	1321.1 (395.6)	1835.7 (582.1)	1882.2 (712.3)
RT forgotten [ms]	1491.0 (464.4)	1447.8 (429.7)	2158.2 (707.4)	2001.7 (707.4)
Confidence remembered	0.88 (0.07)	0.88 (0.07)	0.88 (0.08)	0.84 (0.11)
Confidence forgotten	0.53 (0.17)	0.44 (0.21)	0.62 (0.15)	0.53 (0.16)

Values in parentheses depict standard deviation.
Confidence values range from 0 (not confident) to 1 (highly confident.)
Key: RT, median reaction time.

3.2. Oscillatory power

For the encoding of the latter remembered picture stimuli, the main differences between younger and older participants showed increased oscillatory power in the group of younger participants in the lower frequency range from 3 to 17 Hz (see Fig. 1A) in the pre- and post-stimulus period. The differences were most pronounced over frontal and parietal-occipital sites (Fig. 1B–E).

A very similar pattern can be observed for the processing of the later remembered word stimuli (see Fig. 2). The group of younger participants showed an increased oscillatory activity in the lower frequency range in the pre- and post-stimulus period. Again, these differences are most pronounced over frontal and parietal-occipital sites (Fig. 2B–E).

Relating the oscillatory activity to the memory performance (d') separately in both groups revealed that mainly in the group of younger participants, prestimulus activity was correlated to memory, whereas in the group of older adults, the oscillatory activity in the poststimulus period was more relevant. For both picture (Fig. 3) and word stimuli (Fig. 4), poststimulus theta-band activity in both groups showed a relation to latter memory. The topographic focus was mainly located at occipital sites (Figs. 3D, F and, 4E). Limited to the group of younger participants, prestimulus beta band was related to latter memory for both kinds of stimuli while this effect was not observed in the group of the older adults. However, the topographic distribution in the group of younger participants was different for both categories of stimuli. While the memory for picture stimuli in the younger group was related to more occipital prestimulus beta-band activity (Fig. 3C), the topographic distribution for the word stimuli showed a more frontal focus (Fig. 4C).

As an additional step, the differential effects between remembered and forgotten stimuli were calculated although the number of forgotten stimuli was quite low in both groups. In the group of young participants, for the SME with respect to pictures, there was a significant cluster in the theta frequency range with greater power for later remembered than later forgotten items, stretching from -20 ms to 850 ms, $p = 0.043$ (one-sided), which was strongest in fronto-central electrodes (see Fig. 5A and B). Furthermore, there was a significant cluster of greater power for remembered than forgotten items in the low beta frequency range between 13 and 17 Hz, which started 400 ms before stimulus onset and lasted until 510 ms after stimulus onset, $p = 0.012$ (one-sided). This effect started out to be focused on central electrodes in the prestimulus time range and spread across most of the scalp after stimulus onset, with strongest effects in fronto-central electrodes (see Fig. 5B). There were no significant SMEs in these time-frequency ranges for words in young participants. In the group of older participants, no significant SMEs in the theta and low beta frequency ranges were detected, neither for words nor pictures. Contrasting the SMEs between the 2 age groups, we detected a stronger difference between remembered and forgotten pictures in young than in older participants in the low beta frequency range. This cluster ranged from -380 to 620 ms after stimulus onset, $p = 0.020$ (one-sided). The effect spanned across a wide range of electrode, with strongest effects on fronto-central channels (see Figs. 5D and 1E).

4. Discussion

In the present study, a clear decrease of oscillatory activity in the low frequency bands (3 to maximal 18 Hz) was detected for picture as well as for word encoding in the group of older adults compared with the younger group. These differences can be observed in the pre- and post-stimulus periods. Interestingly, the relation to the sensitivity index of memory showed an involvement of prestimulus beta-band activity only for the group of younger participants, whereas within the group of older adults the memory-related processing was dominated by poststimulus theta-band oscillatory activity.

The decrease of ongoing oscillatory activity from 3 up to 18 Hz was also reported in previous studies reporting decreased power at lower frequencies in healthy older adults (Babiloni et al., 2006; Cummins and Finnigan, 2007). This finding is in accord with the
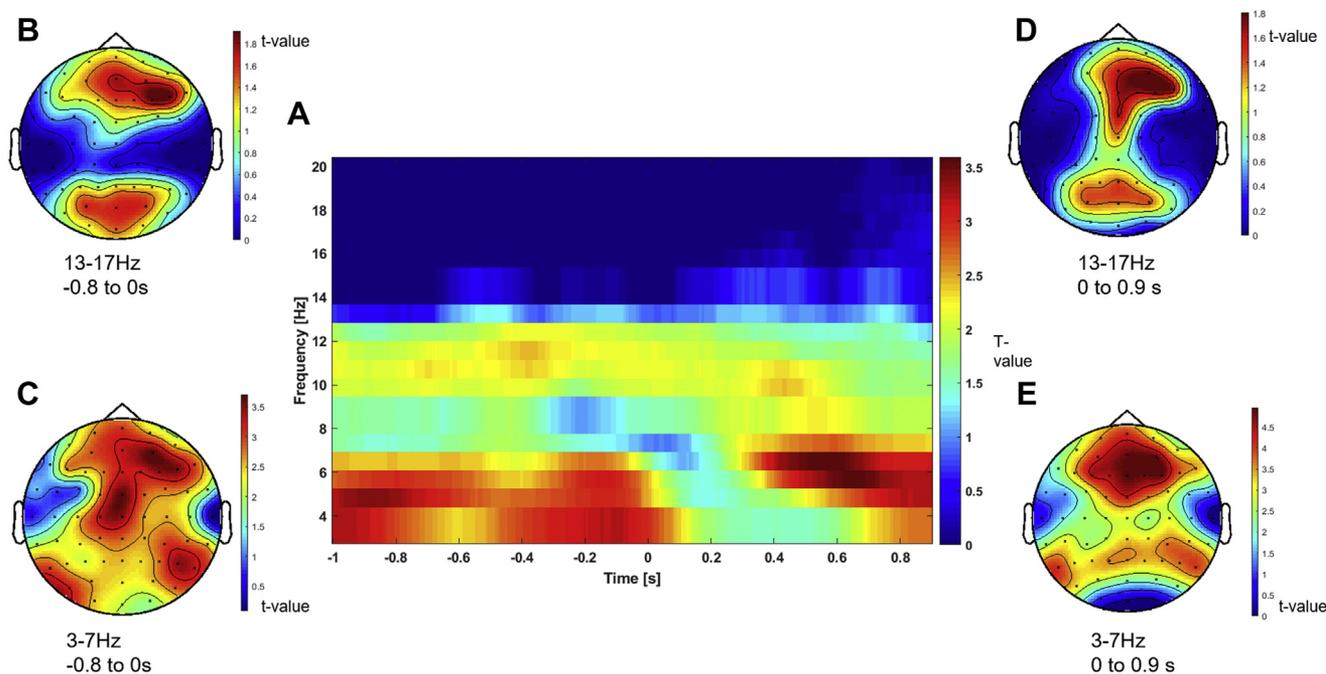

Fig. 1. Main differences between younger and older participants for the encoding of picture stimuli. Average mean statistical t-values across all electrodes (A) showed increased oscillatory power for the younger participants in pre- and post-stimulus periods and from 3 to 17 Hz ($p < 0.05$, corrected; only significant differences were shown). The topographic plots for the theta and beta band showed that the effects were pronounced over the frontal and parietal-occipital sites during pre- (B and C) and post-stimulus periods (D and E).
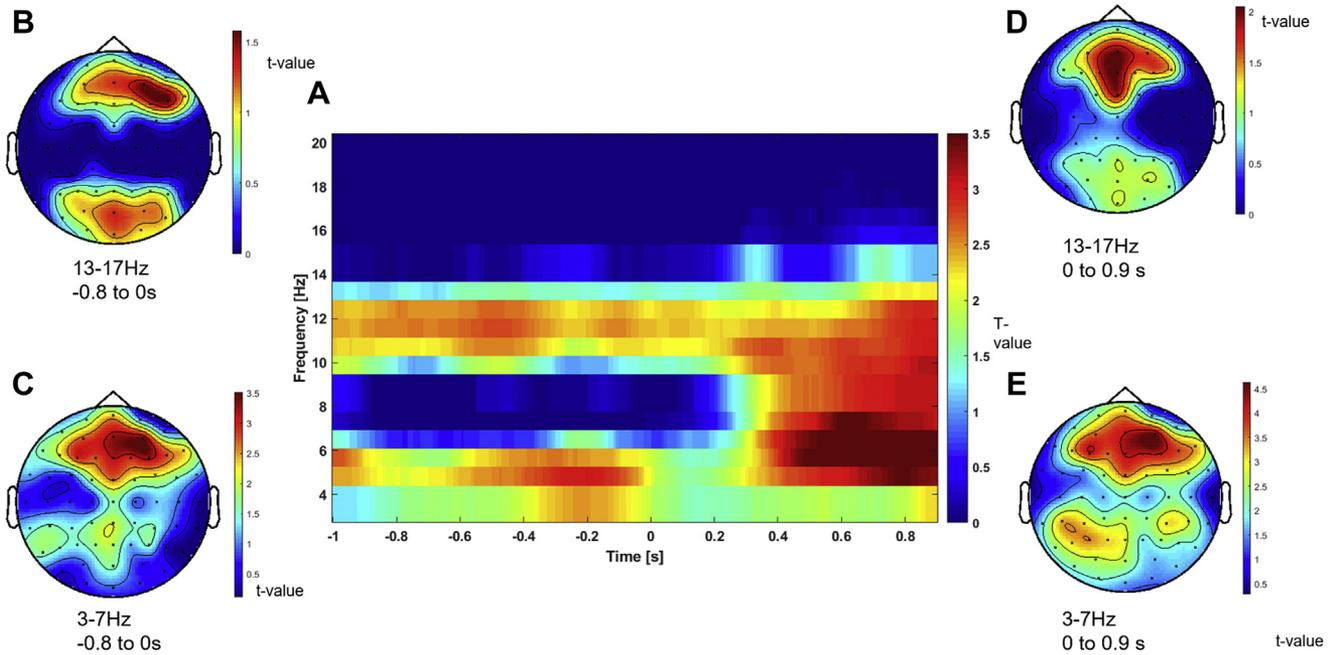
Fig. 2. Main differences between younger and older participants for the encoding of word stimuli. Average mean statistical t-values across all electrodes (A) showed increased oscillatory power for the younger participants in pre- and post-stimulus periods and from 3 to 17 Hz ($p < 0.05$, corrected, only significant differences were shown). The topographic plots for the theta and beta band showed that the effects were pronounced over the frontal and parietal-occipital sites during pre- (B and C) and post-stimulus periods (D and E).

neural noise hypothesis of aging (Voytek et al., 2015) and further indicating that the development of spontaneous oscillatory states or attractors for memory encoding can be affected by this change of neural activity with age. This age-dependent difference can be observed in the prestimulus period but was even pronounced

during stimulus processing, indicating a functional relevance and interaction of poststimulus processing with prestimulus states.

Reliable prestimulus memory-related effects for both stimulus categories were observed in the beta-band activity only for the group of younger participants. This observed memory-related
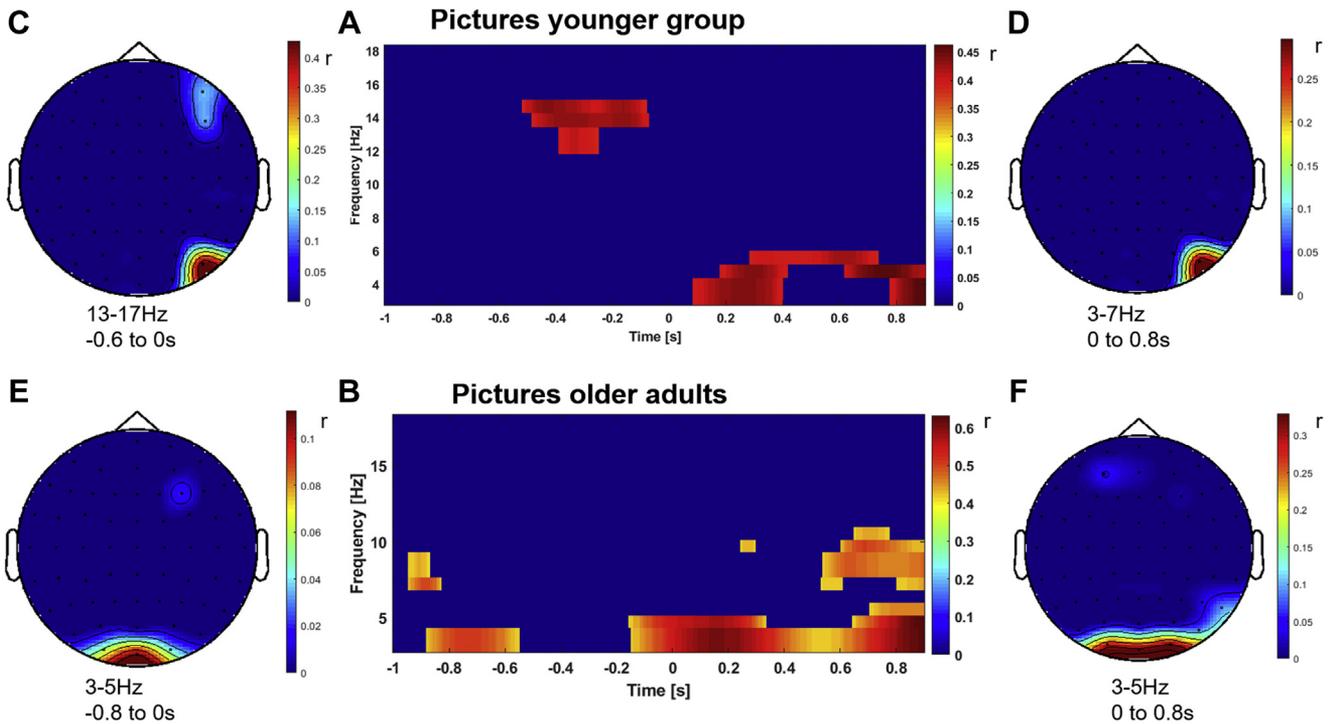

Fig. 3. Relation of oscillatory activity and memory for the encoding of picture stimuli. Correlations of oscillatory power and d'-values separately for each group (A and B; only significant values were presented, $p < 0.05$) showed for both groups a relevance of poststimulus theta-band activity, but only in the younger group prestimulus beta band was related to memory (representative electrode PO8 for the younger group and electrode Oz for the older adults). The topographic plots for the theta and beta band in both groups showed that the effects were pronounced over the occipital sites during pre- (C and E) and post-stimulus periods (D and F).
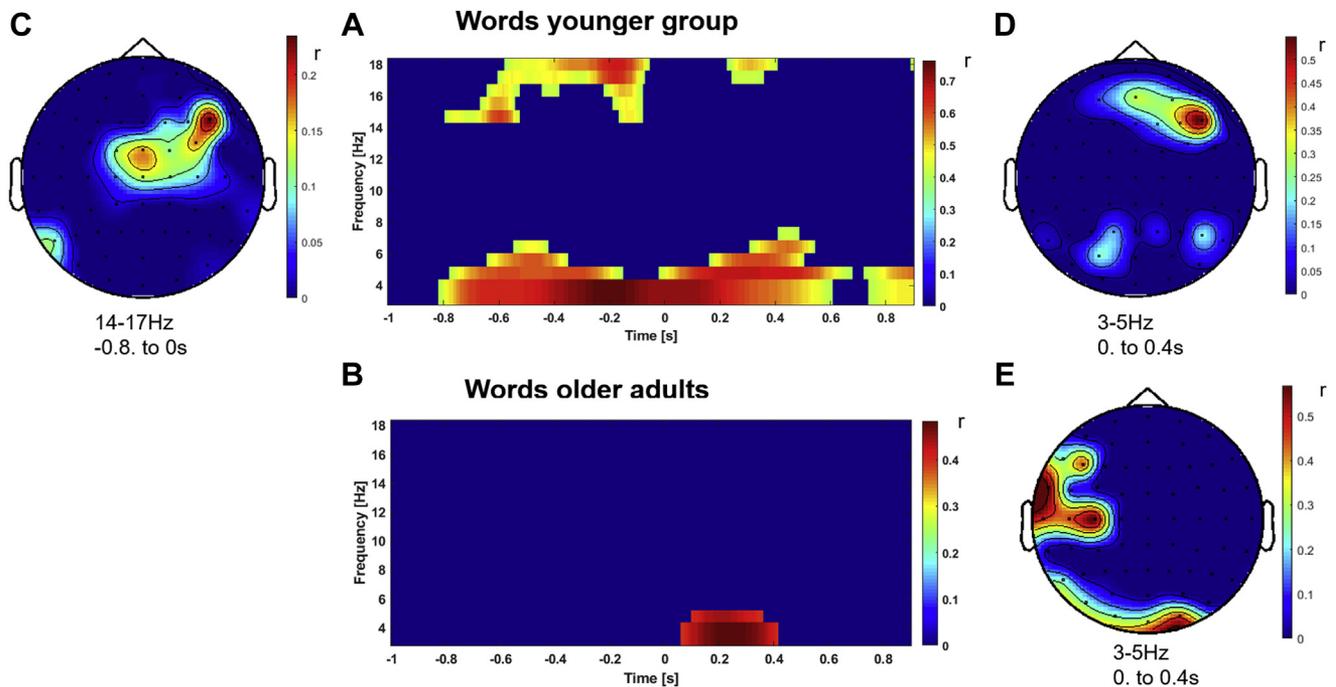
Fig. 4. Relation of oscillatory activity and memory for the encoding of word stimuli. Correlations of oscillatory power and d'-values separately for each group (A and B; only significant values were presented, $p < 0.05$) showed for both groups a relevance of poststimulus theta-band activity, but only in the younger group prestimulus beta and theta band was related to memory (representative electrode F6 for the younger group and electrode Oz for the older adults). The topographic plots for the theta- and beta band in both groups (C–E) showed that the effects were pronounced over the occipital sites in the group of older adults, but the main focus of relation of memory for the words and activity in the younger group was located more over frontal areas.

effects in the low beta band replicates previous findings from our laboratory that have also shown associations between ongoing activity in the low beta frequency range and memory formation for an upcoming item for identical stimulus categories (Salari and Rose, 2016; Schneider and Rose, 2016; Scholz et al., 2017). Using an adaptive stimulation approach, it has been revealed that stimuli that were specifically presented during states of elevated beta power were more likely to be remembered later on (Salari and Rose, 2016). In line with these findings, other studies have used intracranial recordings from medial temporal lobe areas and found prestimulus effects in the theta and alpha frequency range that also extended into the low beta frequency band (Fell et al., 2011; Merkow et al., 2014). The fact that no reliable prestimulus activity in relation to memory formation was observed in the group of older adults is in line with the hypothesis that the changes with age particularly affect the development of oscillatory states in the absence of external stimulation. In contrast to studies using resting-state measures the here observed reduced oscillatory activity in the prestimulus period is indicative for the reduction of a memory-specific preparatory process as shown in previous studies (Salari and Rose, 2016; Schneider and Rose, 2016; Scholz et al., 2017).

The topography of the beta-band effects in the group of younger participants suggested the involvement of different processes for the preparatory processing of the 2 stimulus categories. For the word stimuli, the topography for the prestimulus beta band showed that the memory-related effects were pronounced over frontal areas with additional involvement of occipital sites. The focus for the beta-band effect of the picture stimuli was over occipital areas with some effects over frontal areas. No effects for the beta-band in the prestimulus period were observed in the group of older adults.

Besides or in addition to a memory-specific preparatory process, possible other underlying functions could explain the association between ongoing low beta oscillations and successful encoding that

we showed here for young participants. Using resting-state EEG in young participants, a correlation has been found recently between the amount of ongoing beta power before vocabulary learning and the amount of recalled items afterward (Küssner et al., 2016). The authors interpreted beta power in this context as a measure of arousal or alertness. Similarly, modulation of activity in the low beta range (15–18 Hz) and of the sensory motor rhythm (SMR; 12–15 Hz) by means of neurofeedback training both led to enhancements in specific behavioral and neurophysiological measures of attention (Egner and Gruzelier, 2001, 2004). For the SMR, these effects have been interpreted as potentially resulting from decreased sensorimotor interference during cognitive tasks, whereas low beta activity was associated with rather general arousal due to alterations in a noradrenergic vigilance and alertness network (Egner and Gruzelier, 2004; Sterman, 1996). Indeed, in line with these interpretations and our findings, it has recently been shown that the encoding of an item is impeded if it is presented in a state of reduced sustained attention (deBettencourt et al., 2018). Interestingly, anticipatory attention has been related to increased beta power in young participants (Kamiński et al., 2012). Furthermore, corresponding to our findings, but in the domain of attention, decreased activity in the beta band in older individuals have been associated with impaired performance in a visual attention task (Gola et al., 2012, 2013). Reduced sustained attention or arousal might therefore be one mechanism explaining the results of the present study.

Another related concept is the association of beta oscillations with the inhibition of unwanted interference. In a series of studies, it has been shown that successful encoding of verbal information is related to a poststimulus power decrease, that is, desynchronization, in alpha and beta frequencies, which is hypothesized to reflect the representation of the semantic content of the encoded information (Hanslmayr et al., 2009, 2012, 2016). Successful inhibition of
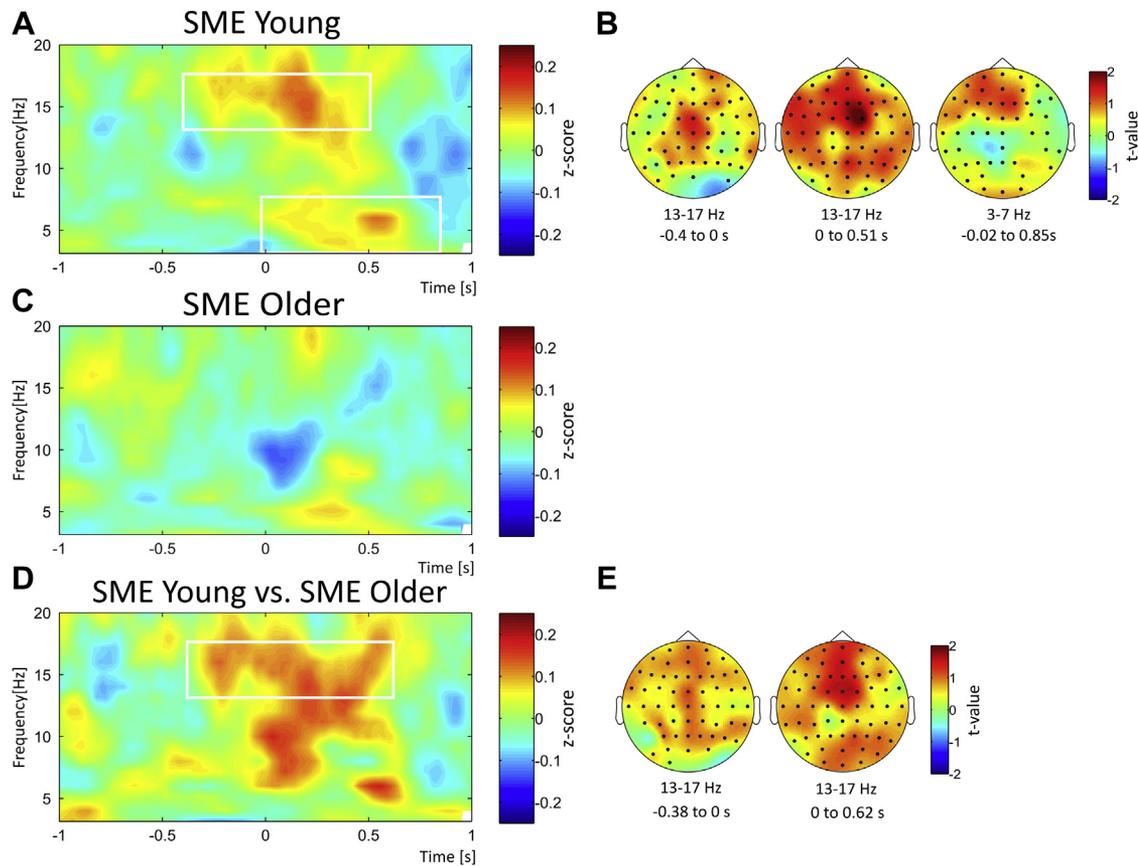
Fig. 5. Subsequent memory effects (SMEs; later remembered - later forgotten) for pictures in young (A and B) and older (C) participants and the group difference (D and E) in these SMEs. The time-frequency plots on the left (A, C, and D) display grand averages of the differences in normalized activity, averaged across all electrodes. White rectangles mark time-frequency bins that comprised significant clusters in the respective contrast. The topographic plots on the right (B and E) depict t-values averaged across significant time-frequency clusters. For the beta clusters, these were split into pre- and post-stimulus time ranges. Black dots represent electrodes that contain at least one significant data point within the cluster.

interfering information on the other hand was shown to be associated with increased beta activity (Waldhauser et al., 2014). In the light of these findings, it seems plausible to assume that long-term memory encoding is facilitated for items presented during ongoing states of increased beta power (synchronization), when the semantic processing of interfering thoughts is inhibited. Indeed, in accordance with our findings, older individuals show impairments in the suppression of task-irrelevant information (Chao and Knight, 1997; Gazzaley et al., 2005).

These 2 processes, that is, sustained attention and inhibition of interference, do not necessarily occur exclusively but could rather go hand in hand. Recently, integrative views on beta oscillations related these oscillations to the maintenance of an ongoing state, also referred to as the "status quo" (Engel and Fries, 2010), or, taking it one step further, to the reactivation of task-specific states and contents (Spitzer and Haegens, 2017). In the case of the present study, the reactivation of the task instruction to encode items in a deep, semantic way as well as the maintenance of an attentive, anticipatory state could well lead to the inhibition of interference, resulting in enhanced memory formation.

The relevance of prestimulus beta-band activity for memory encoding was supported by the analysis of the SME effect for picture processing. We found SMEs for pictures in young participants, with stronger EEG activity in the theta (3–7 Hz) and low beta (13–17 Hz) frequency range for later remembered than later forgotten pictures. The effect in the low beta frequency range

started 400 ms before stimulus onset, suggesting that it is associated with a beneficial state for the successful formation of a memory of an upcoming item. The effect in the theta frequency range occurred mainly after stimulus onset, with the short prestimulus difference probably being due to temporal smoothing as part of the time-frequency transformation. Crucially, in the present study, we could show that in older individuals, SMEs in ongoing low beta oscillations were significantly reduced.

From a theoretical perspective as outlined in the dynamic field theory (Strub et al., 2017) or the neural noise hypothesis of aging (Voytek et al., 2015), the dynamic adaption of ongoing activity seems to be reduced with age. Therefore, the dynamic preparatory process for memory encoding that is reflected in the prestimulus beta-band activity is affected by age-related differences. The interpretation of the development of prestimulus oscillatory states as top-down processes (Miller, 2016) suggests that the differences that emerge with age resulted in a decreased ability to develop stable states in the absence of external stimulation. The interpretation of a reduced top-down preparation process in older adults is in accord with evidence for decreased ability to suppress irrelevant stimuli (perceptual noise) with age (Layton, 1975).

In contrast to the reduced prestimulus beta-band activity, in particular for picture processing, the poststimulus theta-band activity is more pronounced (more extended over time) in the group of older adults which may reflect a compensatory process during the processing of the actual stimulus that resulted in comparable

memory formation. These results are indicative for a possibly stronger poststimulus processing in the absence of preparatory prestimulus processes in the group of older adults.

Regarding the missing SME for word processing in both groups, it should be noted that the power for the calculation of both SMEs was very low because of the fact that the amount of forgotten trials was low in both groups. The relational approach with only the remembered trials showed reliable effects for both categories of stimuli, and in another study, reliable SMEs also for words were reported (Scholz et al., 2017).

The poststimulus theta effect with regard to the encoding of pictures and words in the present study is in accordance with previous studies that also related theta oscillations to memory formation (e.g., Hanslmayr et al., 2011; Klimesch et al., 1996; Lega et al., 2012; Osipova et al., 2006). Note, however, that there have also been studies showing opposite effects with decreased power for later remembered than later forgotten stimuli (e.g., Burke et al., 2013; Sederberg et al., 2007). Theta oscillations have often been observed to be generated in medial temporal lobe areas and have been associated with the role of binding information (Hanslmayr et al., 2016; Staudigl and Hanslmayr, 2013).

Previous studies have, however, reported age-related alterations in theta activity (Crespo-Garcia et al., 2012; Lithfous et al., 2015; Rondina et al., 2016; Steiger and Bunzeck, 2017), which have also been linked to memory performance (Reichert et al., 2016). In a previous study in young participants, it was shown that elevated ongoing theta power was positively related to successful associative encoding of an item and its context (Scholz et al., 2017), a function which is known to be strongly affected by aging (Old and Naveh-Benjamin, 2008). A recent study further demonstrated that a decrease in memory-related theta-band activity with age can be detected already in middle-aged women (Kober et al., 2016).

It is noteworthy that we found alterations in neural activity between the 2 age groups even though older participants did not show significantly reduced memory performance or differences in the confidence ratings during recognition.

Indeed, the identification of functional indicators of cognitive aging that arise before a noticeable decline in cognitive performance is crucial because beginning slight cognitive impairments are known to be compensated for and are therefore often not easily detected by behavioral tests alone (Reuter-Lorenz and Campbell, 2008).

This finding is noteworthy, as it has been shown previously for other cognitive domains that ongoing activity can be modulated via noninvasive neuromodulatory approaches (Enriquez-Geppert et al., 2017; Herrmann et al., 2013). Such neuromodulatory interventions can in turn lead to sensory or cognitive enhancements (Enriquez-Geppert et al., 2014; Salari et al., 2014; Vosskuhl et al., 2015). The identification of a neural state that is beneficial for the encoding of new information is therefore an important step toward a potential oscillation-based noninvasive neuromodulatory intervention for the enhancement or at least the preservation of episodic memory functions in healthy aging. Neuromodulatory approaches are also necessary to clarify the causality in the relationship between ongoing oscillations in the low beta band and memory encoding in older adults because the present results are purely correlative.

5. Conclusions

The present study demonstrated a reduction of oscillatory activity for lower frequencies in older adults in pre- and post-stimulus periods. Furthermore, it confirmed the association between ongoing power in the low beta band and successful memory formation for pictures and words in young participants. It also revealed an age-related reduction in this memory-related modulation of ongoing low beta oscillations, despite the fact that older participants still showed similar recognition performance to young participants. These results indicate that age-related differences in neural processing may be detected before behavioral impairments can be observed, as early neural changes are perhaps being compensated for by other mechanisms. Beta activity seems to have a potentially positive impact on memory, making it an interesting and promising target for neuromodulatory approaches in future research.

Disclosure

The authors declare that this research was conducted in the absence of any actual or potential conflicts of interest.

Acknowledgements

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