Induced Electroencephalogram Oscillations during Source Memory: Familiarity is Reflected in the Gamma Band, Recollection in the Theta Band

Thomas Gruber[1], Dimitris Tsivilis[2], Claire-Marie Giabbiconi[1], and Matthias M. Müller[1]

Abstract

■ Modulations of oscillatory electroencephalogram (EEG) activity in the induced gamma and theta frequency ranges (induced gamma and theta band responses; iGBRs: >30 Hz; iTBRs: ∼6 Hz) have been associated with retrieval of information from long-term memory. However, the specific functional role of these two forms of oscillatory activity remains unclear. The present study examines theta- and gamma-oscillations within a dual-process framework, which defines "familiarity" and "recollection" as the two component processes of recognition memory. During encoding, participants were instructed to make "bigger/smaller than a shoebox" or "living/nonliving" decisions for different object pictures. During retrieval "old/new" recognition was followed (for items judged old) by a source discrimination task regarding the decision made for each item at encoding. iGBRs (35–80 Hz; 210–330 msec) were higher for correctly identified "old" relative to "new" objects. Importantly, they did not distinguish between successful and unsuccessful source judgments. In contrast, iTBRs (4–7.5 Hz; 600–1200 msec) were sensitive to source discrimination. We propose that iGBRs mirror early associative processes linked to familiarity-related retrieval processes, whereas iTBRs reflect later onsetting, episodic, recollection-related mechanisms. ■

INTRODUCTION

Brain oscillations play an important role during mnemonic functioning (e.g., Axmacher, Mormann, Fernandez, Elger, & Fell, 2006; Düzel et al., 2003; Kaiser, Ripper, Birbaumer, & Lutzenberger, 2003; Sederberg, Kahana, Howard, Donner, & Madsen, 2003; Slotnick, Moo, Kraut, Lesser, & Hart, 2002; Başar, Başar-Eroglu, Karakaş, & Schürmann, 2001; Fell et al., 2001; Keil, Gruber, & Müller, 2001; Klimesch et al., 2001; Klimesch, 1999; Miltner, Braun, Arnold, Witte, & Taub, 1999; Tallon-Baudry, Bertrand, Peronnet, & Pernier, 1998). In particular, the role of oscillations in the gamma (>30 Hz) and theta band (∼6 Hz) have been underlined. In the gamma range, it was suggested that modulations of so-called induced gamma band responses[1] (iGBRs) are key-players during implicit (Gruber & Müller, 2005; Gruber, Malinowski, & Müller, 2004; Gruber, Keil, & Müller, 2002) and explicit memory (e.g., Burgess & Ali, 2002; Gruber, Keil, & Müller, 2001). Furthermore, it was demonstrated that iGBRs mirror early encoding- and retrieval-related processes (Gruber, Tsivilis, Montaldi, & Müller, 2004). Recently, Osipova et al. (2006) replicated these findings and extended the analysis to induced theta band responses (iTBRs). iTBRs showed a similar pattern of results as compared to iGBRs, namely, increased activity for correctly recognized as compared to correctly rejected items ("old/new" effect) during retrieval. However, given recent claims that iGBRs and iTBRs mirror functionally complementary mnemonic mechanisms (Gruber & Müller, 2006), the exact functional role of iGBRs and iTBRs during memory retrieval remains unclear.

According to dual-process accounts (e.g., Jacoby & Dallas, 1981), recognition memory consists of two distinct processes—familiarity and recollection. Recollection is the conscious remembrance of prior events which also includes the retrieval of episodic information, whereas familiarity refers to the subjective feeling that an item has been experienced in the past without reference to episodic details (Curran, DeBuse, Woroch, & Hirshman, 2006; Yonelinas, 2001). To differentiate between familiarity- and recollection-related retrieval processes, we employed a source memory paradigm (e.g., Wilding & Rugg, 1996). During encoding, subjects had to perform a "bigger/smaller than a shoebox" or a "living/nonliving" classification on pictures of everyday objects. During retrieval, an "old/new" judgment was required. For items judged to be old, participants were asked to make a source judgment ("what kind of classification did you make during encoding?"), with correct source memory judgments used as a hallmark of recollection. Incorrect source memory judgments, on the other hand, indicate a failure to

---

[1]University of Leipzig, Germany, [2]University of Manchester, UK

recollect and have been traditionally used as an index of familiarity (Cycowicz, Friedman, & Snodgrass, 2001).

Because familiarity-related processes are thought to reflect the initial activation of a memory trace within representational networks (Schacter, 1990) and the fact that such representational networks are established by means of synchronized iGBRs (Kaiser & Lutzenberger, 2005; Keil et al., 2001; Bertrand & Tallon-Baudry, 2000; Tallon-Baudry & Bertrand, 1999), we expected to find increased iGBRs for correctly recognized old pictures regardless of whether they were accompanied by correct retrieval of source. Based on previous proposals that iTBRs are linked to more elaborate episodic processing (Gruber & Müller, 2006), we hypothesized iTBRs to be sensitive to correct/incorrect source judgments.

To verify that our results are restricted to the hypothesized bands, we have analyzed evoked and induced responses in complementary frequency ranges as well.

METHODS

Participants

Fourteen healthy, right-handed university students (12 women; age = 18 to 24 years, mean = 21.3 ± 2 years) received course credits for their participation. All had normal or corrected-to-normal vision. Informed consent was obtained from each participant. The study conformed to the Code of Ethics of the World Medical Association.

Stimuli and Procedure

Stimuli were 452 colored pictures of concrete objects taken from a standard picture library (Hemera Photo-Objects; Volume 1). The pictures depicted "living" or "nonliving" entities which could be further subdivided into being "bigger" or "smaller" than a shoebox. This choice resulted in four sets of pictures (113 pictures per category) which were matched for luminance and number of pixels. Stimuli were presented on a black background in the center of a 19-in. computer screen placed 1.5 m in front of the participants (frame rate = 70 Hz). The pictures covered an average visual angle of $5.5° \times 5.5°$.

From the stimulus pool of 452 pictures, 432 pictures were randomly chosen for the experiment. The remaining 20 pictures were used for training purposes. The experiment was subdivided into six study–test cycles (with a break of 15 min between study and test) resulting in 720 experimental trials (see below).

Figure 1 depicts an excerpt of the stimulus sequence and a schematic representation of the study and test blocks.

During each study block, 96 items were presented. Each trial started with a cue (400 msec), which instructed the participant as to the upcoming task. The cue was either the word NATUR (German for "nature") or KARTON
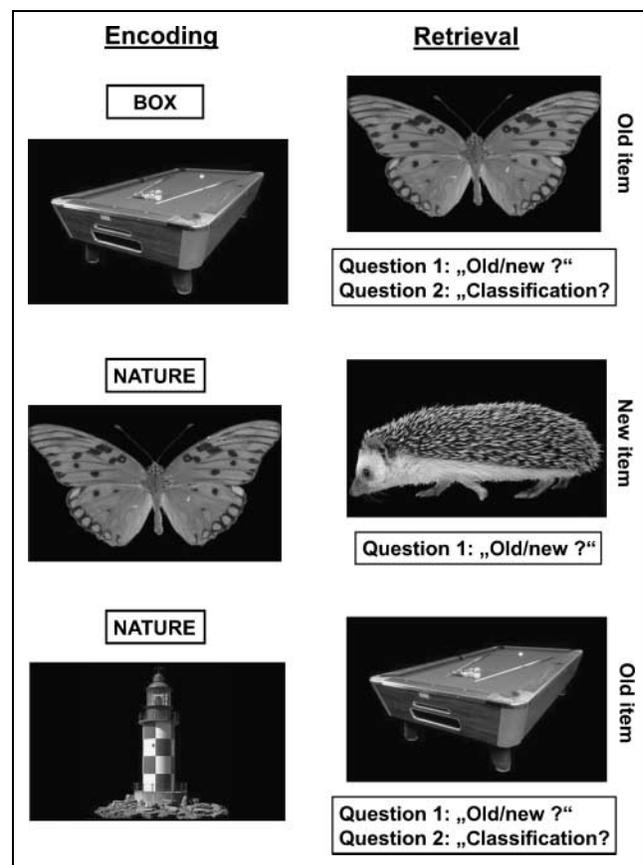

Figure 1. Excerpt of stimulus sequence. During encoding, each stimulus required either a "bigger/smaller than a shoebox" classification indicated by the cue "BOX" or a "living/nonliving" decision indicated by the cue "NATURE." During retrieval, each stimulus was followed by an "old/new" recognition judgment and, in case of correctly classified old items, by an additional judgment regarding the classification made during encoding.

(German for "box"). The "nature" cue indicated that volunteers had to make a "living/nonliving" decision regarding the depicted object; the "box" cue required a "bigger/smaller than a shoebox" evaluation. After the presentation of the cue, the stimulus was presented for 700 msec. Subsequently, participants had to press one key for a "living" or "smaller than a shoebox" object, and another key for a "nonliving" or "bigger than a shoebox" stimulus (depending on the cue). Before the experiment started, participants performed a training session, in order to get used to the key-to-task allocations.

In each test block, the 96 previously presented "old" items were randomly intermixed with 48 "new" stimuli, resulting in 144 trials per block. Each trial started with a fixation cross (600–900 msec, $0.5° \times 0.5°$), which was followed by the presentation of the stimulus (700 msec). Picture onset was synchronized to the vertical retrace of the monitor. The stimulus was then replaced by the fixation cross, which remained on screen for another 800 msec and was followed by a blank screen (900 msec). Subsequently, the participants were required to make an

''old/new'' decision via two response keys. When the presented picture was identified as being ''old,'' participants were prompted to make a memory judgment (''what kind of classification did you make during study?'') via two response keys.

Key-to-task allocations were counterbalanced across participants. Furthermore, the volunteers were instructed to avoid eye movements and blinking during the display of the fixation cross or a stimulus.

The present experimental design results in three relevant experimental conditions: correct rejections (CR), hits with incorrect retrieval of source (H-IS), and hits with correct retrieval of source (H-CS).

Electrophysiological Recordings

Electroencephalogram (EEG) was recorded continuously from 128 Ag–AgCl electrodes with a BioSemi Active-Two amplifier system (BioSemi, Amsterdam, Netherlands). To monitor for eye movements and blinks, the horizontal and vertical electrooculogram (EOG) was recorded. EEG and EOG were sampled at 512 Hz (low-pass filter: 5th order sinc response with a −3 dB point at 128 Hz). Two additional electrodes (Common Mode Sense [CMS] and Driven Right Leg [DRL]) were used as reference and ground (see www.biosemi.com/faq/cms&drl.htm for details). For further off-line analysis, the average reference was used. EEG was segmented to obtain epochs starting 600 msec prior and 1500 msec following picture onset. Artifact correction was performed by means of ''statistical correction of artifacts in dense array studies'' (SCADS; Junghöfer, Elbert, Tucker, & Rockstroh, 2000). This method is widely accepted in the field and was applied and described in several publications (e.g., Müller & Keil, 2004; Gruber, Müller, Keil, & Elbert, 1999; Keil, Müller, Ray, Gruber, & Elbert, 1999). In brief, this procedure uses a combination of trial rejection and channel approximation based on statistical parameters of the data. For each trial, contaminated electrodes are detected based on a threshold criterion derived from the distribution of the amplitude, standard deviation, and gradient of the sensor across all trials. The information of these electrodes is replaced with a spherical interpolation from the full channel set. The limit for the number of approximated channels was set to 20. Epochs containing more than 20 channels with artifacts were rejected. Using this approach, three subjects were excluded due to excessive artifacts (one subject had to be excluded due to poor behavioral performance). For the remaining 10 subjects, the average rejection rate was approximately 20% of the trials.

Data Analysis: Induced Spectral Changes

Spectral changes in oscillatory activity were analyzed by means of Morlet wavelets with a width of 7 cycles per wavelet which is described in detail elsewhere (e.g., Tallon-Baudry & Bertrand, 1999; Bertrand & Pantev, 1994). In brief, the method provides a time-varying magnitude of the signal in each frequency band, leading to a time-by-frequency (TF) representation of the data. Due to fact that induced oscillatory activity occurs with a jitter in latency from one trial to another (Eckhorn et al., 1990), they tend to cancel out in the averaged evoked potential. Thus, TF amplitude is averaged across single-trial frequency transformations, allowing one to analyze non-phase-locked components. Furthermore, because we focused on the non-phase-locked components of the signal, the evoked response (i.e., the ERP) was subtracted from each trial before frequency decomposition (for details, see Busch, Herrmann, Müller, Lenz, & Gruber, 2006).

In order to identify the latency and frequency range of induced spectral peaks, mean baseline-corrected spectral amplitudes (baseline: 500 to 100 msec prior to stimulus onset) across all electrodes and across all experimental conditions was represented in a TF plot separate for the high (30–100 Hz) and low (2–15 Hz) frequency range. For further analysis of iGBR amplitudes, a time window of 210–330 msec after stimulus onset and a frequency range of 35–80 Hz were used (see Results; Figure 2A). Based on a recent finding by Osipova et al. (2006), we have furthermore analyzed a time window from 400 to 1000 msec in a frequency range from 35 to 80 Hz. Regarding iTBRs, a frequency band from 4 to 7.5 Hz in a time window from 600 to 1200 msec after stimulus onset was chosen (see Figure 3A).

Electrodes for further analyses were selected based on spherical spline interpolated topographies (Perrin, Pernier, Bertrand, & Echallier, 1988) of the oscillatory peaks averaged across all conditions (the topographical distributions of the iGBR and iTBR peak and the selected electrodes are indicated in Figures 2B and 3B). Specifically, we applied a repeated measurement design for iGBR and iTBR peaks with a three-level factor of condition (CR/H-IS/H-CS). Due to the fact that there were substantially more CR and H-CS than H-IS trials and, in order to achieve an equal signal-to-noise ratio of electrophysiological activity for all types of items, all induced spectral analyses were based on a randomized subset of CR and H-CS trials matched in number to H-IS trials (for a similar procedure, see Gruber, Tsivilis, et al., 2004).

Note that the present approach, namely, to average all experimental conditions to define the relevant peaks, seems favorable to avoid biasing the choice of the time and frequency windows, and thus, the comparisons between conditions in the subsequent analysis of variance (ANOVA; for a similar approach, see Gruber, Giabbiconi, Trujillo-Barreto, & Müller, 2006; Gruber, Trujillo-Barreto, Giabbiconi, Valdés-Sosa, & Müller, 2006; Fiebach, Gruber, & Supp, 2005). The selected time and frequency ranges are in line with previous studies on oscillatory brain

Figure 2. (A) Grand mean baseline-corrected TF plot across all experimental conditions, and across all electrodes for the induced high-frequency range (the box indicates the induced gamma peak). (B) Grand mean spherical–spline interpolated amplitude map (averaged across all conditions) for the induced gamma peak at 210–330 msec and 35–80 Hz. (C) Mean induced gamma peak amplitudes (±SE) at parieto-occipital electrodes (as indicated in B) subdivided according to the experimental conditions (*p < .05; ns = not significant). CR = correct rejections; H-IS = hits followed by incorrect source judgments; H-CS = hits associated with correct source judgments.
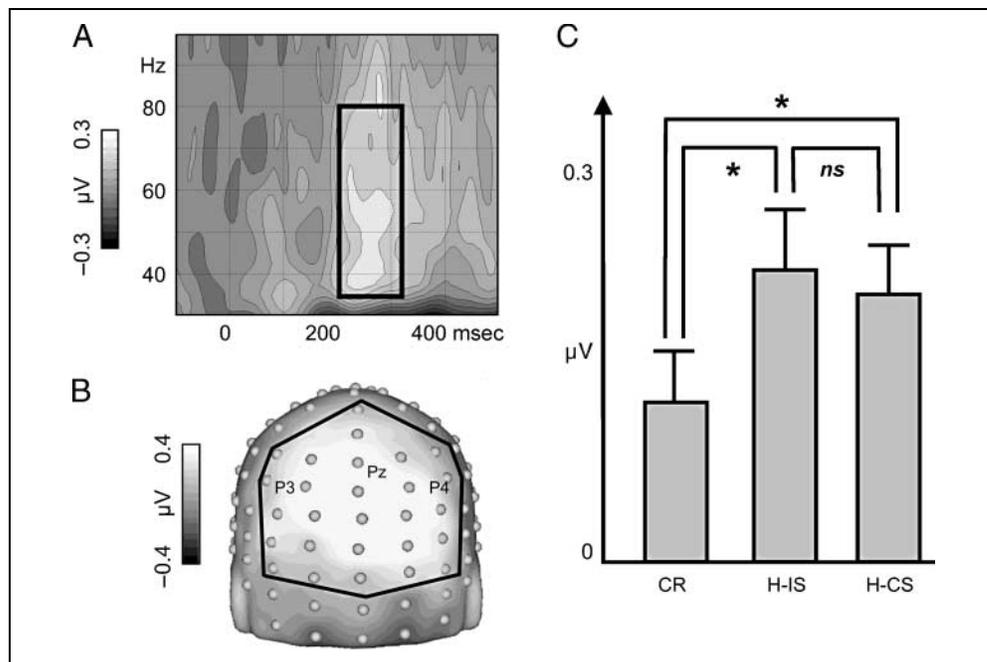
activity (e.g., Deiber et al., 2007; Gruber & Müller, 2006; Guderian & Düzel, 2005; Gruber, Malinowski, et al., 2004; Jensen & Tesche, 2002; Klimesch, 1999).

Importantly, all relevant spectral peaks (as defined above) were tested against zero by means of one-group t test in order to examine if the observed signal is significantly different from the general background noise.

To draw a complete picture of induced oscillatory activity, we applied the above ANOVA model to the induced alpha and beta band. The time–frequency range and electrodes for these analyses were chosen based on

a previous publication (Gruber & Müller, 2006): alpha (9–12 Hz, 200–800 msec, parietal electrodes) and beta (14–20 Hz, 50–350 msec, posterior electrodes).

Data Analysis: Evoked Spectral Changes

Evoked oscillatory activity was analyzed by means of spectral decompositions of the averaged and unfiltered evoked response. To define the latency and frequency range of evoked spectral peaks, mean baseline-corrected spectral

Figure 3. (A) Grand mean baseline-corrected TF plot across all experimental conditions, and across all electrodes for the induced low-frequency range (the box indicates the induced theta peak). (B) Grand mean spherical–spline interpolated amplitude map (averaged across all conditions) for the induced theta peak at 600–1200 msec and 4–7.5 Hz. (C) Mean induced theta peak amplitudes (±SE) at fronto-central electrodes (as indicated in B) subdivided according to the experimental conditions (*p < .05; ns = not significant). CR = correct rejections; H-IS = hits followed by incorrect source judgments; H-CS = hits associated with correct source judgments.
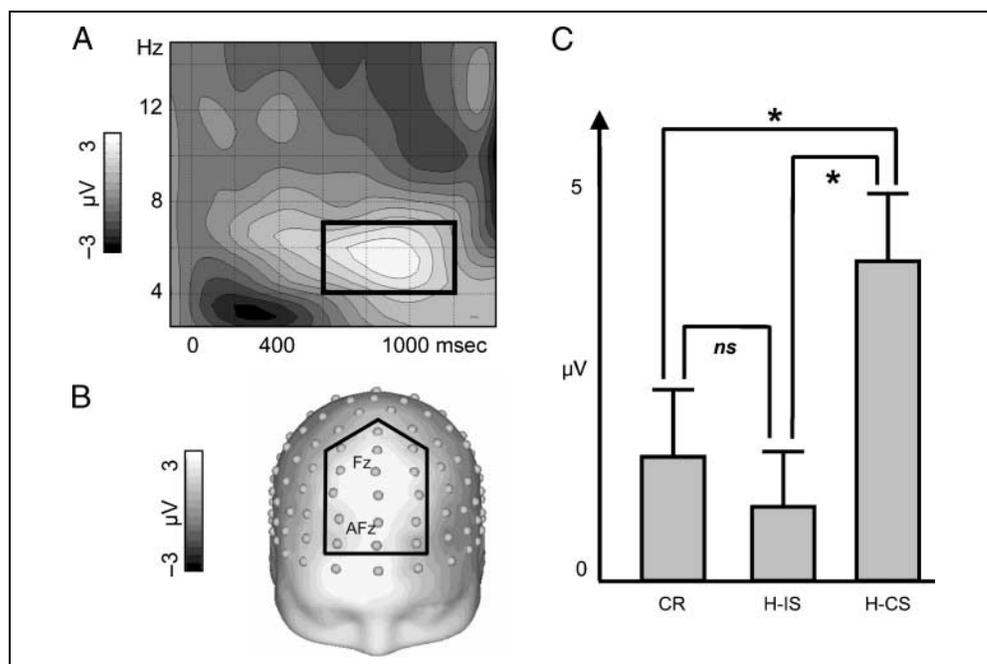
amplitudes (baseline: 500 to 100 msec prior to stimulus onset) across posterior electrodes and across all experimental conditions were represented in a TF plot for the high (22–70 Hz) and low (3–20 Hz) frequency range. The electrodes for these plots were chosen based on previous publications (Gruber & Müller, 2006; Herrmann, Munk, & Engel, 2004). For statistical analysis of the evoked gamma band response, a time window from 70 to 120 msec after stimulus onset and a frequency range from 25 to 45 Hz were analyzed by means of the ANOVA models described above (the same posterior electrodes as for the TF plot were used; see Figure 4B). For statistical analysis of evoked low-frequency response, a time window from 50 to 350 msec and a frequency range from 6 to 14 Hz were analyzed at posterior electrodes sites indicated in Figure 4E. Furthermore, we have analyzed the evoked beta response from 14 to 20 Hz (50–350 msec) at posterior electrodes (see Gruber & Müller, 2006).

To exclude baseline differences between conditions as an alternative explanation for our results, we have tested the baseline-uncorrected evoked and induced frequency range with the identical ANOVA model described above, in a time window from 500 to 100 msec prior to stimulus onset.

Wherever appropriate, p values were adjusted by Greenhouse–Geisser corrections in all ANOVAs. Planned comparisons were conducted in order to analyze relevant differences by means of paired t tests. Means and standard errors (SE) are presented throughout the manuscript.

RESULTS

Behavioral Data

Analyses of encoding and retrieval performance were restricted to data from subjects included in the EEG analyses. Participants performed well during the study phase, classifying correctly $92 \pm 4\%$ of the items. At test, $85 \pm 2\%$ of the studied items were correctly recognized (hits; $15 \pm 2\%$ misses), whereas only $13 \pm 2\%$ of new items were incorrectly classified as old (false alarms). Importantly, the two encoding tasks resulted in equivalent levels of memory performance, that is, we found no significant differences between the ''living/nonliving'' and the ''shoebox'' task (all t values < 1).

The source discrimination rate was in line with previous studies of source memory (e.g., Cansino, Maquet,

Figure 4. (A) Grand mean baseline-corrected TF plot across all experimental conditions, and across posterior electrodes of the evoked high-frequency response. The box indicates the evoked gamma peak. (B) Grand mean spherical–spline interpolated amplitude map (averaged across all conditions) of this peak (25–45 Hz, 70–120 msec). Electrodes used for statistical analysis are indicated. (C) Mean evoked gamma peak amplitudes (±SE) at posterior electrodes (as indicated in B) subdivided according to the experimental conditions (no significant differences were found). CR = correct rejections; H-IS = hits followed by incorrect source judgments; H-CS = hits associated with correct source judgments. D, E, F: Same for the evoked low-frequency response (6–14 Hz; 50–350 msec; no significant differences were found).
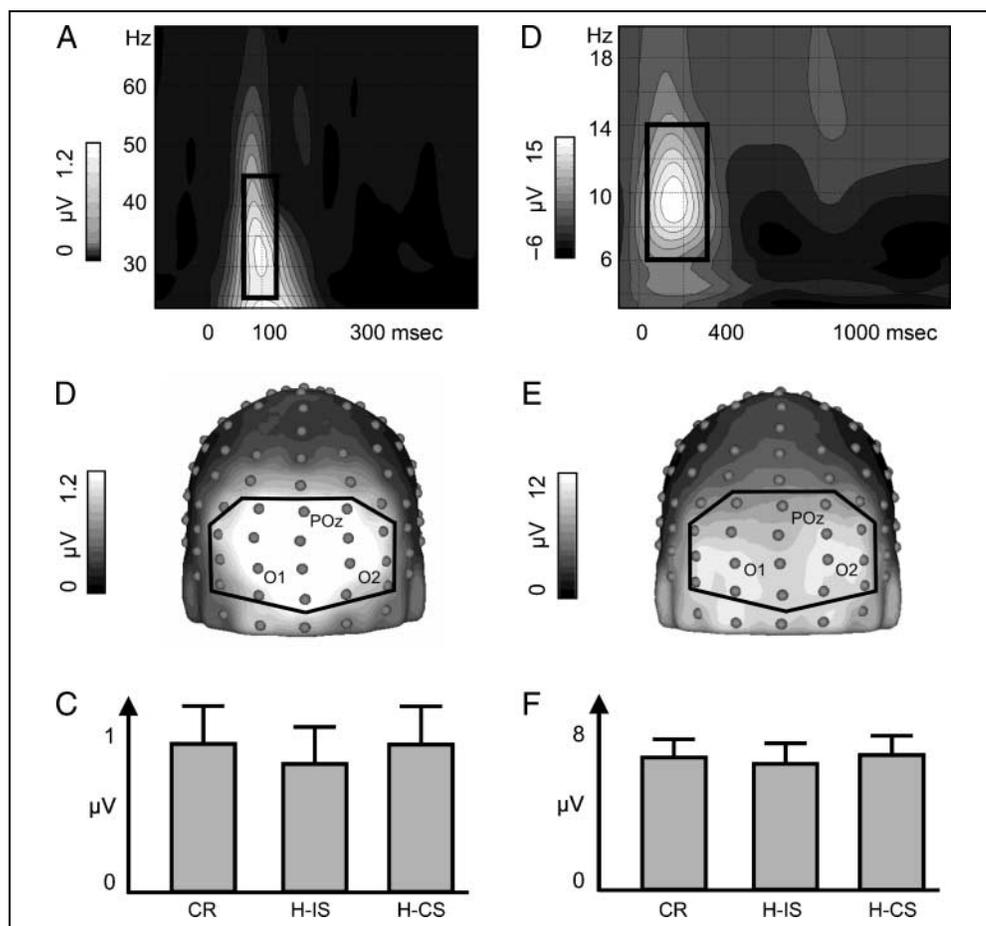
Dolan, & Rugg, 2002; Wilding, 1999, 2000) with 65 ± 3% of the recognized items receiving a correct source judgment. Note that due to the low number of false alarms and misses, the brain responses related to these items were not analyzed.

Induced Spectral Changes during Retrieval

Figure 2A depicts the baseline-corrected TF plot averaged across all experimental conditions, all 128 electrodes and 10 subjects. Spectral amplitudes in the induced gamma range show a clear peak in a time window from 210 to 330 msec after stimulus onset in a frequency range between approximately 35 and 80 Hz (indicated by the box in Figure 2A). The spherical–spline interpolated topography of this peak revealed a broad distribution with a maximum at parieto-occipital electrode sites. For further analyses, a regional mean centered on this maximum was used (for topography and utilized electrodes, see Figure 2B). The spectral amplitudes at theses electrodes subdivided according to the experimental conditions are depicted in Figure 2C. The repeated measures ANOVA of these values revealed a significant main effect condition [$F(2, 18) = 3.92$, $p < .05$], which is depicted in Figure 2C. Most interestingly, we found significantly greater iGBRs for hits associated with a correct retrieval of source information [H-CS; $t(9) = 3.25$, $p < .01$] *and* hits accompanied by incorrect source memory [H-IS; $t(9) = 2.28$, $p < .05$] as opposed to correct rejections (CR). No significant difference between H-IS and H-CS items was found. Thus, iGBRs were not modulated by correct retrieval of source. The examination of the time window from 400 to 1000 msec revealed no significant effects.

The analysis of induced theta amplitudes followed the same logic as the iGBR analysis. The results are depicted in Figure 3A–C. In contrast to the induced gamma burst, iTBRs were found to be modulated by correct source memory. In particular, spectral amplitudes in the lower frequency range revealed a clear peak in a time window from 600 to 1200 msec after stimulus onset in a frequency range between approximately 4 and 7.5 Hz (see Figure 3A) with a maximum at fronto-central electrode sites (see Figure 3B). Statistical analysis of the spectral amplitudes in this time window and the indicated electrodes resulted in a significant main effect of condition [$F(2, 18) = 4.66$, $p < .05$], which is depicted in Figure 3C. Planned comparisons revealed a significant difference between correct rejections (CR) and hits associated with correct source memory [H-CS; $t(9) = -2.46$, $p < .05$] but not between CR and H-IS items. Furthermore, hits related to correct source memory (H-CS) were accompanied by greater iTBR amplitudes as opposed to hits with incorrect retrieval of additional episodic information [H-IS; $t(9) = 2.53$, $p < .05$].

Tests against background noise (i.e., against zero) revealed significant signal increase for all iGBRs and the H-CS induced theta peak [all $t(9) > 3$, $p < .05$]. The iTBR peaks related to CR and H-IS items were not significantly different from zero, that is, their amplitudes did not differ from the general background noise level. No significant results were found in the induced alpha and beta band.

Evoked Spectral Changes during Retrieval

Spectral amplitudes in the evoked gamma range were characterized by a peak in a time window from approximately 70 to 120 msec and a frequency range between 25 and 45 Hz (see Figure 4A), which is characterized by a focused posterior topographical distribution (see Figure 4B). However, the analysis of these peaks revealed no significant effects (see Figure 4C). Spectral amplitudes in the evoked low-frequency range (6–14 Hz) were analyzed in a latency range from 50 to 350 msec (see Figure 4D) and an average of the signals at the posterior region indicated in Figure 4E. This analysis revealed no significant effects (see Figure 4F). Furthermore, the analysis of the evoked beta response revealed no significant effects.

Importantly, tests for baseline differences (500 to 100 msec prior to stimulus onset) between conditions revealed no significant effects for the evoked and the induced high- and low-frequency band responses (all F values < 1).

DISCUSSION

Using a source discrimination task, we investigated the involvement of induced oscillatory brain activity in the gamma and theta frequency bands in recollection and familiarity, the two processes believed to underlie recognition memory judgments. Behaviorally, participants showed good levels of recognition performance and, more importantly, were able to distinguish between sources with a sufficiently high accuracy, indicating that our choice of encoding tasks was effective.

Induced Gamma Band Responses

Regarding the iGBR, a significant "old/new" effect was observed in a frequency range from 35 to 80 Hz at approximately 210–320 msec after stimulus onset. Old items were associated with higher iGBRs relative to new items, a finding which replicates previous reports (Gruber, Tsivilis, et al., 2004; Düzel et al., 2003; Gruber et al., 2002).

Traditionally, iGBRs have been linked to processes involved in the activation of a "cortical representation" of an object (Tallon-Baudry & Bertrand, 1999). These representations involve perceptual, semantic, and task-related features and are dispersed in many and distant cortical areas (Gruber & Müller, 2005, 2006; Gruber,

Giabbiconi, et al., 2006). It has been suggested that the integration of activity at these sites is achieved by means of synchronized oscillations in the gamma frequency range (Singer & Gray, 1995; Engel, Konig, Kreiter, Schillen, & Singer, 1992; von der Malsburg & Schneider, 1986). The present findings are in agreement with the cortical representation theory. In terms of cortical distribution, the broad scalp topography of iGBRs is consistent with synchronous activity in multiple cortical areas. This interpretation is underpinned by a recent finding suggesting that the generators of object-related iGBRs involve an extensive network of parieto-occipital, inferior–temporal, and frontal areas (Gruber, Trujillo-Barreto, et al., 2006).

The "old/new" iGBR effects further suggest that memory can modulate this representational activity. Although the mechanism responsible for this difference remains unclear, it is possible that it results from (1) a facilitation of the activation of the constituent components of old relative to new stimuli (Osipova et al., 2006; Summerfield & Mangels, 2005) and (2) the additional activation of areas related to explicit mnemonic processes (Gruber & Müller, 2006).

Importantly, the present findings offer a more precise characterization of the induced gamma network role in memory retrieval. The fact that successful source retrieval did not modulate the "old/new" gamma effects (iGBRs elicited by correct source judgments did not differ from those elicited by incorrect source judgments) suggests that induced gamma activity is elicited by neuronal modules, which determine an item's overall familiarity status. These networks support recognition judgments of previous occurrence but are not sensitive to contextual or episodic information.

Noteworthy, we found no evidence of a sustained gamma effect similar to that reported by Osipova et al. (2006). It is possible that differences in retrieval requirements of the two studies may be responsible for this different finding. Osipova et al. used a yes/no recognition task, whereas in the present study, a source discrimination task was added. Furthermore, Osipova et al. asked participants to respond only when confident and withhold responding if uncertain. This could have also affected the hit rate, which at 60% is substantially lower than the recognition hit rate in the present study. One might speculate that either one or both of these factors (response demands and the difficulty of the recognition test) could have required the "induced gamma networks" to work for a longer period of time in Osipova et al.'s study.

It is important to stress that the observed "old/new" effects in the iGBR are specific to explicit or declarative tasks and not simply due to item repetition. Repetition priming effects are associated with a decrease in iGBR amplitudes relative to new items (Gruber & Müller, 2002, 2005; Gruber, Malinowski, et al., 2004), the exact opposite pattern to that observed with the explicit memory tasks used in the present and previous studies. Thus, repetition-related decreases of neuronal activity, which

are discussed as a neuronal marker of a "sharpened" (i.e., more efficient) cortical representation (Grill-Spector, Henson, & Martin, 2006), seem to play no major role during explicit mnemonic functioning. This interpretation is in concordance with a recent study in which we demonstrated repetition-related decreases of iGBRs during implicit, but not explicit, memory (Gruber & Müller, 2006). Similar findings have been reported for the hemodynamic response as well (Henson, Shallice, Gorno-Tempini, & Dolan, 2002).

It could be argued that, by adopting retrieval of source as our recollection criterion, we were only able to capture a portion of the episodic experience, and thus, ignored task-irrelevant recollections. For example, remembering a sound heard when studying a particular item is a form of recollection, although it would not assist source discrimination. These so called "noncriterial" recollections (Yonelinas & Jacoby, 1996) could have been present in both correct and incorrect source trials and could have diluted any potential differences. There are three points that refute this argument. First, "noncriterial" recollection tends to function in a way that resembles familiarity memory when the types of processing required by the encoding tasks are sufficiently dissimilar to allow easy discrimination (Yonelinas & Levy, 2002; Yonelinas & Jacoby, 1996). Under this condition, "noncriterial" recollection is expected to be minimal. The behavioral results clearly indicate that this requirement has been satisfied. Second, if source incorrect trials were driven primarily by recollection, then the neural activity elicited by source correct and source incorrect trials should not differ. The evidence, however, contradict this prediction. A number of EEG studies have shown that, in contrast to source correct trials, source incorrect trials do not elicit the parietal old/new effect (e.g., Wilding, 1999; Senkfor & Van Petten, 1998; Wilding & Rugg, 1996). This effect has been associated with recollection-based retrieval and was also observed for "remember" judgments (Duarte, Ranganath, Winward, Hayward, & Knight, 2004; Klimesch et al., 2001), and word-pair recognition (Weyerts, Tendolkar, Smid, & Heinze, 1997), but was not present in a patient with selective hippocampal damage (Duzel, Vargha-Khadem, Heinze, & Mishkin, 2001). Furthermore, a direct comparison between recollection indices derived from two different behavioral paradigms (remember/know vs. source correct/incorrect) revealed equivalent parietal old/new effects (Rugg, Schloerscheidt, & Mark, 1998). Taken together, these findings clearly show that a source discrimination task is a valid method to assess the neural correlates of recollection-related processes. Third, and more importantly, source discrimination was found to modulate induced theta band activity.

Induced Theta Band Responses

In contrast to iGBRs, induced theta activity (4–7.5 Hz, 600–1200 msec after stimulus onset) clearly discriminated

between correct and incorrect source trials, suggesting that our manipulation of recollection was effective in producing reliable differences. This finding extends previous reports revealing close links between induced theta activity and recollection (Klimesch et al., 2001). For example, it was demonstrated that pictures of previously encountered faces elicited higher iTBRs when additional episodic information regarding the background context in which these faces were presented during study could be remembered (Guderian & Düzel, 2005). Furthermore, in a recent study, enhanced iTBRs were observed when recollection-related strategies were used for the retrieval of previously presented pictures of familiar objects (Gruber & Müller, 2006). Additionally, our findings are in agreement with ERP studies, in which similar manipulations modulated the parietal ''old/new'' effect (e.g., Wilding & Rugg, 1996; Wilding, Doyle, & Rugg, 1995).

An alternative explanation for our late effect in the theta band is that it represents the influence of postdecisional evaluation processes. However, this interpretation seems unlikely because postretrieval responses (>800 msec) are known to be unaffected by recollection success (for details, see Mecklinger, 2000).

General Remarks on the Relation of iGBRs to iTBRs

As pointed out above, we found a functional dissociation between iGBRs and iTBRs in our source memory experiment. This dissociation is further supported by possible differences in their cerebral origins. Animal studies focussing on the hippocampus have demonstrated the important role of low-frequency responses for mnemonic processing (e.g., Holscher, Anwyl, & Rowan, 1997). Furthermore, numerous studies have pointed out that the theta rhythm reflects dynamic interactions between the hippocampal system and the neocortex (for a review, see Bastiaansen & Hagoort, 2003). In particular, it was suggested that the firing of prefrontal neocortical cells is phase-locked, and thus, clocked by the hippocampal theta rhythm (Jensen, 2005). Although it is unlikely that hippocampal oscillations are directly detectable in the EEG, theta oscillations might thus allow drawing indirect conclusion regarding hippocampal functioning (Burgess & Gruzelier, 2000). In contrast, iGBRs are most believed to reflect cortico-cortical connections within perceptual and higher associative areas (Gruber, Trujillo-Barreto, et al., 2006; Lachaux et al., 2005; Varela, Lachaux, Rodriguez, & Martinerie, 2001).

The proposed functional dissociation between induced gamma and theta effects is further underlined by the difference in their respective latencies, with iGBRs occurring before the iTBR peak reached its maximum. This pattern is consistent with behavioral response-signal studies, which show that familiarity-based judgments can support successful recognition from about 100 msec earlier than recollection-based judgments (Hintzman, Caulton,

& Levitin, 1998; Hintzman & Curran, 1994), suggesting that familiarity processes are completed before recollection processes. Similarly, a number of ERP studies have identified a familiarity sensitive, ''old/new'' effect which onsets earlier (at around 300 msec following stimulus presentation) than the parietal ''old/new'' effects which onset from about 500 msec poststimulus and has been linked to recollection (for a review, see Mecklinger, 2000). It is also noteworthy that induced gamma oscillations usually show an effect before a corresponding ERP effect is evident (Gruber, Tsivilis, et al., 2004). Thus, although oscillatory brain activity reveals a similar temporal order pattern of effects to the ERP studies, the exact latency of these effects may differ.

A previous study, however, came to different conclusions regarding the functional role of gamma activity. Using the ''remember/know'' paradigm (e.g., Gardiner & Java, 1990), Burgess and Ali (2002) associated recollection (but not familiarity) with higher gamma activity. Furthermore, the topographical and temporal distribution of gamma activity differed markedly from our findings. They found a maximum of the gamma effect at electrode site F3 in a latency range of 300–500 msec after stimulus onset. One possible explanation for the discrepant findings is that at least some of the participants in the Burgess and Ali study may have interpreted the distinction between ''remember/know'' as one of memory strength or confidence rather than of episodic experience strength (cf. Dunn, 2004; Gardiner, 2001; Donaldson, 1996). If so, Burgess and Ali's results could reflect differences in gamma band activity between strong and weak memories, rather than the presence or absence of contextual information. Alternatively, gamma activity may be sensitive to the method used to measure recollection. The possibility that gamma activity could both index recollection in the ''remember/know'' paradigm but fail to discriminate between sources is not as unlikely as it seems at first. A comparison of induced theta activity between the present study and that of Klimesch et al. (2001) illustrates this point. Using different indices—source correct versus incorrect in the present study and remember versus know in Klimesch et al.—both studies report a recollection-related increase in theta band activity. However, whereas Klimesch et al. also found an earlier effect (300–450 msec poststimulus), which was specific to ''know'' (i.e., familiarity-based) judgments, no such familiarity component (indexed by the contrast between source incorrect and new trials) was found in the present study (see also Guderian & Düzel, 2005). Thus, gamma and theta band effects may be sensitive to subtle task differences between different estimates of recollection and familiarity, which would, in turn, reflect the operation of both anatomically and functionally distinct neuronal populations. Although ERP and behavioral studies offer little support for this view (Yonelinas, 2001; Rugg et al., 1998), more frequency analyses studies using different paradigms and statistically powerful

designs are needed before any firm conclusions are drawn.

Evoked Oscillatory Activity

Despite previous notions that evoked gamma oscillations play a crucial role during mnemonic functioning (Herrmann et al., 2004), we found no modulation of the early evoked high-frequency response (25–45 Hz, 70–120 msec) in our experiment. The present findings are rather in line with the claim that the evoked gamma burst is linked to the perceptual processing of low-level features which can be regarded as prerequisite for the activation of a memory trace as reflected in the iGBR (e.g., Eckhorn et al., 1990). Regarding the reported evoked low-frequency responses, it is highly likely that they reflect the P1 and N1 ERP complex in the frequency domain (Gruber, Klimesch, Sauseng, & Doppelmayr, 2005), which is usually not linked to memory processes.

Conclusion

We have demonstrated that iGBRs and iTBRs have functionally complementary roles during the retrieval of information from long-term memory. It is likely that their relationship is one of independence in the sense that an increase in iGBRs is not always accompanied by an increase in theta. Thus, our finding extends existing models of simultaneous gamma and theta oscillations during memory processes (e.g., Demiralp et al., 2007; Axmacher et al., 2006; Jensen, 2006; Lisman, 2005), which propose a mechanism of nested gamma and theta oscillations.

With respect to dual-process theories of recognition memory, the present findings add their support to electrophysiological, hemodynamic, and neuropsychological evidence suggesting that familiarity and recollection are supported by distinct neuronal networks (for reviews, see Aggleton & Brown, 2006; Rugg & Yonelinas, 2003; Mayes & Roberts, 2001). Although there is corroborating evidence relating late onsetting theta activity to recollection, more studies are needed to examine the sensitivity of induced gamma band activity to manipulations of familiarity and recollection. In particular, such studies should use (A) different designs tapping into the two processes underlying recognition memory and (B) paradigms which provide a larger number of trials (as, e.g., needed for source analysis).

Acknowledgments

Note

1. Induced gamma-band responses refer to transient oscillatory bursts of activity at around 270 msec after stimulus onset (depending on the time point of object identification; Martinovic, Gruber, & Müller, 2007), which are not precisely phase-locked to the onset of a stimulus (Eckhorn, Reitboeck, Arndt, & Dicke, 1990).

REFERENCES

Aggleton, J. P., & Brown, M. W. (2006). Interleaving brain systems for episodic and recognition memory. *Trends in Cognitive Sciences, 10,* 455–463.

Axmacher, N., Mormann, F., Fernandez, G., Elger, C. E., & Fell, J. (2006). Memory formation by neuronal synchronization. *Brain Research, Brain Research Reviews, 52,* 170–182.

Başar, E., Başar-Eroglu, C., Karakaş, S., & Schürmann, M. (2001). Gamma, alpha, delta, and theta oscillations govern cognitive processes. *International Journal of Psychophysiology, 39,* 241–248.

Bastiaansen, M., & Hagoort, P. (2003). Event-induced theta responses as a window on the dynamics of memory. *Cortex, 39,* 967–992.

Bertrand, O., & Pantev, C. (1994). Stimulus frequency dependence of the transient oscillatory auditory evoked response (40 Hz) studied by electric and magnetic recordings in humans. In C. Pantev, T. Elbert, & B. Lütkenhöner (Eds.), *Oscillatory event-related brain dynamics* (pp. 231–242). New York: Plenum Press.

Bertrand, O., & Tallon-Baudry, C. (2000). Oscillatory gamma activity in humans: A possible role for object representation. *International Journal of Psychophysiology, 38,* 211–223.

Burgess, A. P., & Ali, L. (2002). Functional connectivity of gamma EEG activity is modulated at low frequency during conscious recollection. *International Journal of Psychophysiology, 46,* 91–100.

Burgess, A. P., & Gruzelier, J. H. (2000). Short duration power changes in the EEG during recognition memory for words and faces. *Psychophysiology, 37,* 596–606.

Busch, N., Herrmann, C. S., Müller, M. M., Lenz, D., & Gruber, T. (2006). A cross-lab study of event-related gamma activity in a standard object-recognition paradigm. *Neuroimage, 33,* 1169–1177.

Cansino, S., Maquet, P., Dolan, R. J., & Rugg, M. D. (2002). Brain activity underlying encoding and retrieval of source memory. *Cerebral Cortex, 12,* 1048–1056.

Curran, T., DeBuse, C., Woroch, B., & Hirshman, E. (2006). Combined pharmacological and electrophysiological dissociation of familiarity and recollection. *Journal of Neuroscience, 26,* 1979–1985.

Cycowicz, Y. M., Friedman, D., & Snodgrass, J. G. (2001). Remembering the color of objects: An ERP investigation of source memory. *Cerebral Cortex, 11,* 322–334.

Deiber, M. P., Missonnier, P., Bertrand, O., Gold, G., Fazio-Costa, L., Ibanez, V., et al. (2007). Distinction between perceptual and attentional processing in working memory tasks: A study of phase-locked and induced oscillatory brain dynamics. *Journal of Cognitive Neuroscience, 19,* 158–172.

Demiralp, T., Bayraktaroglu, Z., Lenz, D., Junge, S., Busch, N. A., Maess, B., et al. (2007). Gamma amplitudes are coupled to theta phase in human EEG during visual perception. *International Journal of Psychophysiology, 64,* 24–30.

Donaldson, W. (1996). The role of decision processes in remembering and knowing. *Memory & Cognition, 24,* 523–533.

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. *Brain Research, Cognitive Brain Research, 18,* 255–272.

Dunn, J. C. (2004). Remember–know: A matter of confidence. *Psychological Review, 111,* 524–542.

Düzel, E., Habib, R., Schott, B., Schoenfeld, A., Lobaugh, N., McIntosh, A. R., et al. (2003). A multivariate, spatiotemporal analysis of electromagnetic time–frequency data of recognition memory. *Neuroimage, 18,* 185–197.

Duzel, E., Vargha-Khadem, F., Heinze, H. J., & Mishkin, M. (2001). Brain activity evidence for recognition without recollection after early hippocampal damage. *Proceedings of the National Academy of Sciences, U.S.A., 98,* 8101–8106.

Eckhorn, R., Reitboeck, H. J., Arndt, M., & Dicke, P. (1990). Feature linking via synchronization among distributed assemblies: Simulations of results from cat visual cortex. *Neural Computation, 2,* 293–307.

Engel, A. K., Konig, P., Kreiter, A. K., Schillen, T. B., & Singer, W. (1992). Temporal coding in the visual cortex: New vistas on integration in the nervous system. *Trends in Neurosciences, 15,* 218–226.

Fell, J., Klaver, P., Lehnertz, K., Grunwald, T., Schaller, C., Elger, C. E., et al. (2001). Human memory formation is accompanied by rhinal–hippocampal coupling and decoupling. *Nature Neuroscience, 4,* 1259–1264.

Fiebach, C. J., Gruber, T., & Supp, G. (2005). Neuronal mechanisms of repetition priming in occipitotemporal cortex: Spatiotemporal evidence from functional magnetic resonance imaging and electroencephalography. *Journal of Neuroscience, 25,* 3414–3422.

Gardiner, J. M. (2001). Episodic memory and autonoetic consciousness: A first-person approach. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences, 356,* 1351–1361.

Gardiner, J. M., & Java, R. I. (1990). Recollective experience in word and non word recognition. *Memory & Cognition, 18,* 23–30.

Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: Neural models of stimulus-specific effects. *Trends in Cognitive Sciences, 10,* 14–23.

Gruber, T., Giabbiconi, C. M., Trujillo-Barreto, N., & Müller, M. M. (2006). Repetition suppression of induced gamma band responses is eliminated by task switching. *European Journal of Neuroscience, 24,* 2654–2660.

Gruber, T., Keil, A., & Müller, M. M. (2001). Modulation of induced gamma band responses and phase synchrony in a paired associate learning task in the human EEG. *Neuroscience Letters, 316,* 29–32.

Gruber, T., Keil, A., & Müller, M. M. (2002). Modulation of induced gamma band responses in a perceptual learning task in the human EEG. *Journal of Cognitive Neuroscience, 14,* 732–744.

Gruber, T., Malinowski, P., & Müller, M. M. (2004). Modulation of oscillatory brain activity and evoked potentials in a repetition priming task in the human EEG. *European Journal of Neuroscience, 19,* 1073–1082.

Gruber, T., & Müller, M. M. (2002). Effects of picture repetition on induced gamma band responses, evoked potentials, and phase synchrony in the human EEG. *Cognitive Brain Research, 13,* 377–392.

Gruber, T., & Müller, M. M. (2005). Oscillatory brain activity dissociates between associative stimulus content in a repetition priming task in the human EEG. *Cerebral Cortex, 15,* 109–116.

Gruber, T., & Müller, M. M. (2006). Oscillatory brain activity in the human EEG during indirect and direct memory tasks. *Brain Research, 1097,* 194–204.

Gruber, T., Müller, M. M., Keil, A., & Elbert, T. (1999). Selective visual–spatial attention alters induced gamma band responses in the human EEG. *Clinical Neurophysiology, 110,* 2074–2085.

Gruber, T., Trujillo-Barreto, J. N., Giabbiconi, C. M., Valdés-Sosa, P. A., & Müller, M. M. (2006). Brain electrical tomography (BET) analysis of induced gamma band responses during a simple object recognition task. *Neuroimage, 29,* 888–900.

Gruber, T., Tsivilis, D., Montaldi, D., & Müller, M. M. (2004). Induced gamma band responses: An early marker of memory encoding and retrieval. *NeuroReport, 15,* 1837–1841.

Gruber, W. R., Klimesch, W., Sauseng, P., & Doppelmayr, M. (2005). Alpha phase synchronization predicts P1 and N1 latency and amplitude size. *Cerebral Cortex, 15,* 371–377.

Guderian, S., & Düzel, E. (2005). Induced theta oscillations mediate large-scale synchrony with mediotemporal areas during recollection in humans. *Hippocampus, 15,* 901–912.

Henson, R. N., Shallice, T., Gorno-Tempini, M. L., & Dolan, R. J. (2002). Face repetition effects in implicit and explicit memory tests as measured by fMRI. *Cerebral Cortex, 12,* 178–186.

Herrmann, C. S., Munk, M. H. J., & Engel, A. K. (2004). Cognitive functions of gamma-band activity: Memory match and utilization. *Trends in Cognitive Sciences, 8,* 347–355.

Hintzman, D. L., Caulton, D. A., & Levitin, D. J. (1998). Retrieval dynamics in recognition and list discrimination: Further evidence of separate processes of familiarity and recall. *Memory & Cognition, 26,* 449–462.

Hintzman, D. L., & Curran, T. (1994). Retrieval dynamics of recognition and familiarity judgments: Evidence for separate processes of familiarity and recall. *Journal of Memory and Language, 33,* 1–18.

Holscher, C., Anwyl, R., & Rowan, M. J. (1997). Stimulation on the positive phase of hippocampal theta rhythm induces long-term potentiation that can Be depotentiated by stimulation on the negative phase in area CA1 in vivo. *Journal of Neuroscience, 17,* 6470–6477.

Jacoby, L. L., & Dallas, M. (1981). On the relationship between autobiographical memory and perceptual learning. *Journal of Experimental Psychology: General, 3,* 306–340.

Jensen, O. (2005). Reading the hippocampal code by theta phase-locking. *Trends in Cognitive Sciences, 9,* 551–553.

Jensen, O. (2006). Maintenance of multiple working memory items by temporal segmentation. *Neuroscience, 139,* 237–249.

Jensen, O., & Tesche, C. D. (2002). Frontal theta activity in humans increases with memory load in a working memory task. *European Journal of Neuroscience, 15,* 1395–1399.

Junghöfer, M., Elbert, T., Tucker, D. M., & Rockstroh, B. (2000). Statistical control of artifacts in dense array EEG/MEG studies. *Psychophysiology, 37,* 523–532.

Kaiser, J., & Lutzenberger, W. (2005). Human gamma-band activity: A window to cognitive processing. *NeuroReport, 16,* 207–211.

Kaiser, J., Ripper, B., Birbaumer, N., & Lutzenberger, W. (2003). Dynamics of gamma-band activity in human magnetoencephalogram during auditory pattern working memory. *Neuroimage, 20,* 816–827.

Keil, A., Gruber, T., & Müller, M. M. (2001). Functional correlates of macroscopic high-frequency brain activity in the human visual system. *Neuroscience and Biobehavioral Reviews, 25,* 527–534.

Keil, A., Müller, M. M., Ray, W. J., Gruber, T., & Elbert, T. (1999). Human gamma band activity and perception of a gestalt. *Journal of Neuroscience, 19,* 7152–7161.

Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: A review and analysis. *Brain Research, Brain Research Reviews, 29,* 169–195.

Klimesch, W., Doppelmayr, M., Yonelinas, A., Kroll, N. E., Lazzara, M., Rohm, D., et al. (2001). Theta synchronization during episodic retrieval: Neural correlates of conscious awareness. *Brain Research, Cognitive Brain Research, 12,* 33–38.

Lachaux, J. P., George, N., Tallon-Baudry, C., Martinerie, J., Hugueville, L., Minotti, L., et al. (2005). The many faces of the gamma band response to complex visual stimuli. *Neuroimage, 25,* 491–501.

Lisman, J. (2005). The theta/gamma discrete phase code occurring during the hippocampal phase precession may be a more general brain coding scheme. *Hippocampus, 15,* 913–922.

Martinovic, J., Gruber, T., & Müller, M. M. (2007). Induced gamma-band responses predict recognition delays during object identification. *Journal of Cognitive Neuroscience, 19,* 921–934.

Mayes, A. R., & Roberts, N. (2001). Theories of episodic memory. *Philosophical Transactions of the Royal Society of London, Series B, 356,* 1395–1408.

Mecklinger, A. (2000). Interfacing mind and brain: A neurocognitive model of recognition memory. *Psychophysiology, 37,* 565–582.

Miltner, W. H. R., Braun, C., Arnold, M., Witte, H., & Taub, E. (1999). Coherence of gamma-band activity as a basis for associative learning. *Nature, 397,* 434–436.

Müller, M. M., & Keil, A. (2004). Neuronal synchronization and selective color processing in the human brain. *Journal of Cognitive Neuroscience, 16,* 503–522.

Osipova, D., Takashima, A., Oostenveld, R., Fernandez, G., Maris, E., & Jensen, O. (2006). Theta and gamma oscillations predict encoding and retrieval of declarative memory. *Journal of Neuroscience, 26,* 7523–7531.

Perrin, F., Pernier, J., Bertrand, O., & Echallier, J. F. (1988). Spherical splines for scalp potential and current source density mapping. *Electroencephalography and Clinical Neurophysiology, 72,* 184–187.

Rugg, M. D., Schloerscheidt, A. M., & Mark, R. E. (1998). An electrophysiological comparison of two indices of recollection. *Journal of Memory and Language, 39,* 47–69.

Rugg, M. D., & Yonelinas, A. P. (2003). Human recognition memory: A cognitive neuroscience perspective. *Trends in Cognitive Sciences, 7,* 313–319.

Schacter, D. L. (1990). Perceptual representation system and implicit memory: Toward a resolution of the multiple memory system debate. *Annals of the New York Academy of Sciences, 608,* 543–571.

Sederberg, P. B., Kahana, M. J., Howard, M. W., Donner, E. J., & Madsen, J. R. (2003). Theta and gamma oscillations during encoding predict subsequent recall. *Journal of Neuroscience, 23,* 10809–10814.

Senkfor, A. J., & Van Petten, C. (1998). Who said what? An event-related potential investigation of source and item memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 24,* 1005–1025.

Singer, W., & Gray, C. M. (1995). Visual feature integration and the temporal correlation hypothesis. *Annual Review of Neuroscience, 18,* 555–586.

Slotnick, S. D., Moo, L. R., Kraut, M. A., Lesser, R. P., & Hart, J. J. (2002). Interactions between thalamic and cortical rhythms during semantic memory recall in human. *Proceedings of the National Academy of Sciences, 99,* 6440–6443.

Summerfield, C., & Mangels, J. A. (2005). Functional coupling between frontal and parietal lobes during recognition memory. *NeuroReport, 16,* 117–122.

Tallon-Baudry, C., & Bertrand, O. (1999). Oscillatory gamma activity in humans and its role in object representation. *Trends in Cognitive Sciences, 3,* 151–162.

Tallon-Baudry, C., Bertrand, O., Peronnet, F., & Pernier, J. (1998). Induced gamma-band activity during the delay of a visual short-term memory task in humans. *Journal of Neuroscience, 18,* 4244–4254.

Varela, F., Lachaux, J. P., Rodriguez, E., & Martinerie, J. (2001). The brainweb: Phase synchronization and large-scale integration. *Nature Reviews Neuroscience, 2,* 229–239.

von der Malsburg, C., & Schneider, W. (1986). A neural cocktail-party processor. *Biological Cybernetics, 54,* 29–40.

Weyerts, H., Tendolkar, I., Smid, H. G. O. M., & Heinze, J. J. (1997). ERPs to encoding and recognition memory with and without retrieval of source. *NeuroReport, 8,* 1583–1588.

Wilding, E. L. (1999). Separating retrieval strategies from retrieval success: An event-related potential study of source memory. *Neuropsychologia, 37,* 441–454.

Wilding, E. L. (2000). In what way does the parietal ERP old/new effect index recollection? *International Journal of Psychophysiology, 35,* 81–87.

Wilding, E. L., Doyle, M. C., & Rugg, M. D. (1995). Recognition memory with and without retrieval of study context: An event-related potential study. *Neuropsychologia, 33,* 743–767.

Wilding, E. L., & Rugg, M. D. (1996). An event-related potential study of recognition memory with and without retrieval of source. *Brain, 119,* 889–905.

Yonelinas, A. P. (2001). Components of episodic memory: The contribution of recollection and familiarity. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences, 356,* 1363–1374.

Yonelinas, A. P., & Jacoby, L. L. (1996). Noncriterial recollection: Familiarity as automatic, irrelevant recollection. *Consciousness and Cognition, 5,* 131–141.

Yonelinas, A. P., & Levy, B. J. (2002). Dissociating familiarity from recollection in human recognition memory: Different rates of forgetting over short retention intervals. *Psychonomic Bulletin & Review, 9,* 575–582.