

Modes of memory: Early electrophysiological markers of repetition suppression and recognition enhancement predict behavioral performance

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Abstract

Different forms of perceptual memory have opposite physiological effects. Whereas repetition priming often leads to suppression of brain responses, explicit recognition has been found to enhance brain activity. We investigated effects of repetition priming and recognition memory on early gamma-band responses. In a study phase, participants performed a visual discrimination task with task-irrelevant item repetitions. Stimulus repetition suppressed early evoked gamma responses in participants with strong behavioral repetition effects. In a test phase, participants discriminated old from new items. Evoked and induced gamma activity was enhanced for old items. Effects were stronger in participants with better recognition performance. The results demonstrate a modulation of earliest stages of visual information processing by different memory systems, which is dependent on retrieval intention and predicts individual behavioral performance.

Descriptors: Implicit/explicit memory, Direct/indirect memory test, Evoked gamma, Induced gamma, Memory formation, Memory dissociation, Repetition suppression

Visual perceptual memory is revealed when behavior or physiological responses are altered by previous visual experience. Research on the cognitive neuroscience of memory has provided abundant evidence that memory is not a unitary function, but can be subdivided into several functionally and anatomically different subcomponents. A common distinction is made between implicit versus explicit memory processes. Explicit memory is revealed in so-called direct tasks, in which performance on a task requires intentional retrieval of previous experiences. For example, in recognition memory paradigms, participants perform old/new judgments of learned and novel items. In contrast, implicit memory is often inferred from indirect tasks that measure behavioral or physiological effects of previous experiences in a task that does not require conscious or intentional retrieval of those experiences (Schacter & Buckner, 1998; Schacter, Dobbins, & Schnyer, 2004). One widely studied form of implicit memory is repetition priming: the facilitation of behavioral responses caused by stimulus repetition. Repetition priming is

often accompanied by repetition suppression: the reduction of neurophysiological responses to repeated stimuli (Buckner & Koutstaal, 1998; Grill-Spector, Henson, & Martin, 2006). An influential view is that priming and recognition are mediated by functionally independent and neurally distinct memory systems (Donaldson, Petersen, & Buckner, 2001; Groh-Bordin, Zimmer, & Mecklinger, 2005; Mecklinger, 2000; Paller, Hutson, Miller, & Boehm, 2003; Rugg et al., 1998; Voss & Paller, 2006). Repetition suppression has been found in several early visual areas (Buckner & Koutstaal, 1998; Grill-Spector et al., 2006), and under certain circumstances even near striate cortex (Vuilleumier, Schwartz, Duhaux, Dolan, & Driver, 2005), whereas increased neuronal activity in sensory areas has been associated with explicit recognition (Nyberg, 2006; Wheeler, Petersen, & Buckner, 2000). Moreover, double dissociations between priming and recognition memory in different types of amnesic patients have been reported by Keane, Gabrieli, Mapstone, Johnson, and Corkin (1995). In that study, priming was impaired in a patient with bilateral occipital-lobe lesions who had no deficit in visual recognition memory. A patient with bilateral medial temporal lobe lesions showed the reversed pattern of deficits. This dissociation suggests that the processes underlying recognition memory and perceptual priming are functionally and neurally separable. In the study by Schott et al. (2005), response decreases for primed items in the absence of explicit retrieval were found in bilateral occipital and inferior temporal cortex. In contrast, explicit retrieval activated separate areas in parietal, temporal, and prefrontal cortex. It should be noted, however, that other studies

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found partially overlapping networks for priming and explicit memory (for an overview, see Henson, 2003). Hence, depending on task and stimulus material, both implicit and explicit forms of memory may rely on either separate or similar neural structures. As a consequence of the limited temporal resolution of hemodynamic measures, it is unclear whether these memory-related effects in early sensory areas occur temporally early or later as “reentrant” processes after feedback from higher cortical areas (Henson & Rugg, 2003).

Several recent EEG studies, which offer better temporal resolution, have investigated the functions of gamma-band activity, the frequency range from approximately 20 to 100 Hz. Gamma activity has been localized to early sensory cortices (Crone, Sinai, & Korzeniewska, 2006; Gruber, Trujillo-Barreto, Giabbiconi, Valdés-Sosa, & Müller, 2006; Hoogenboom, Schoffelen, Oostenveld, Parkes, & Fries, 2006; Rols, Tallon-Baudry, Girard, Bertrand, & Bullier, 2001) and has been proposed to be involved in processes relevant for memory and object recognition (Başar-Eroglu, Strüber, Schürmann, Stadler, & Başar, 1996; Düzel et al., 2003; Freunberger et al., 2007; Herrmann, Munk, & Engel, 2004; Kaiser & Lutzenberger, 2005; Keil, Gruber, & Müller, 2001; Singer, 1999; Tallon-Baudry & Bertrand, 1999). Recently, Herrmann, Munk, et al. (2004) suggested that gamma activity in early visual cortices is enhanced by early matching of behaviorally relevant visual input with memory representations, which are stored in the form of modified synaptic weights. Other studies reported repetition suppression of gamma responses when stimulus repetition was task irrelevant (Gruber, Malinowski, & Müller, 2004; Gruber & Müller, 2006). In conclusion, both fMRI BOLD responses and EEG gamma activity from early visual areas exhibit memory-related enhancements in explicit memory tasks but show repetition suppression in implicit tasks (cf. Grill-Spector et al., 2006). A possible explanation might be that the effect of previous experience with a given stimulus depends on the type of task a subject has to perform. For instance, Henson, Shallice, Gorno-Tempini, and Dolan (2002) found repetition suppression of the BOLD response only in an implicit but not in an explicit task. It is conceivable that memory effects on gamma-band responses depend on task requirements in a similar manner. To date, the effect of task requirements on recognition enhancement and repetition suppression of early EEG, such as evoked gamma responses, has not been demonstrated within the same experimental paradigm. Moreover, the behavioral relevance of these early effects remains untested.

We analyzed early evoked gamma responses to investigate early effects of repetition priming and recognition memory. Repetition priming was investigated in the study phase of a memory experiment. Participants were instructed to memorize repeatedly presented stimuli in a study phase and to perform a simple discrimination task (Figure 1). Although stimuli were intentionally encoded during the study phase, the discrimination task was an indirect memory task, because it made no reference to the stimulus repetition. Thus, it was not necessary to recall for how often an item had been repeated. Therefore, repetition priming (effects of task-irrelevant stimulus repetitions) was analyzed as a measure of implicit memory processes. Explicit recognition memory was investigated in a subsequent test phase in which old items were to be recognized. The significance of early gamma responses for behavioral performance was investigated by comparing electrophysiological memory effects between participants with strong and weak behavioral effects in the direct and in the indirect task, respectively.

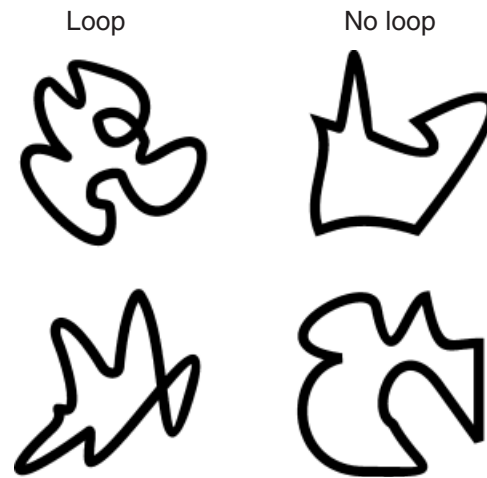


Figure 1. Examples of stimuli with and without a loop in the contour.

Method

Participants

Nineteen people participated in the study (mean age 25; 11 female; all right-handed); all were paid for participation. Participants gave informed consent prior to the start of the experiment. All participants had normal or corrected-to-normal vision and had no recorded history of neurological or psychiatric disorders.

Stimuli and Procedure

The study protocol conformed with local ethics guidelines and the Declaration of Helsinki (Rickham, 1964). Stimulus material consisted of 320 abstract line drawings (see Figure 1). Half of the stimuli had a small loop in the contour. Stimuli were presented centrally with an average diameter of 11° visual angle. The overall stimulus size employed in this study was adopted from Busch, Debener, Kranczioch, Engel, and Herrmann (2004), who reported strong gamma-band responses evoked by stimuli subtending 8° visual angle, but only weak gamma responses evoked by small stimuli. Participants were instructed to maintain central fixation at all times. The experiment comprised eight blocks, each of which consisted of a study phase and a test phase. In each study phase, we presented 20 items, 10 of which were repeated twice and 10 of which were repeated four times, resulting in a sum of 60 trials per study phase of each block. Items were presented for 800 ms followed by a random interstimulus interval ranging from 1700 to 2700 ms. The lag between subsequent repetitions of a given item did not fall below 10 and did not exceed 18 trials. Participants were instructed to indicate with a button press as quickly and as accurately as possible whether or not an item had a loop and to simultaneously memorize the items while disregarding how often an item had been presented. In the test phase, we repeated all items from the preceding study phase intermixed with an equal number of novel items. Participants were instructed to indicate as accurately as possible whether or not they remembered having seen the item in the study phase. Items were presented for 800 ms followed by a blank screen, which was terminated by the participants' response, after which participants received feedback on the correctness of their response. After feedback presentation, a random interstimulus interval ranging from 1700 to 2700 ms was presented. The order in which old items were presented in the test phase corresponded to the order

of presentation in the study phase in order to keep the time lag between study and test of a given item as consistent as possible. A postexperimental interview revealed that none of the participants took note of this regularity. The order in which items were presented, the assignment of stimuli to the group of repeated or new items, and response hands in the test phase were counterbalanced across participants.

Data Acquisition

The experiment was conducted in an electrically shielded and sound-attenuated cabin. A TFT monitor was placed outside this cabin behind an electrically shielded window. All devices inside the cabin were battery operated to avoid interference of the line frequency. EEG was recorded with a BrainAmp amplifier (Brain Products, Munich) using 32 sintered Ag/AgCl electrodes mounted in an elastic cap (Easycap, Falk Minow Services, Munich) and placed according to the 10–10 system, with a nose-tip reference and ground electrode between Fz and Cz. Electrode impedances were below 10 k Ω . Data were sampled at 500 Hz and analog filtered between 0.01 and 250 Hz during recording.

Data Analysis

Analysis of behavioral data. Behavioral performance in the loop versus no-loop discrimination task in the study phase was quantified as the proportion of correct responses and response times (RTs) of correct responses not exceeding the mean response time by two standard deviations after outliers (responses faster than 100 ms or slower than 1500 ms) had been removed. Repetition priming was quantified as the difference between RTs to the first and the fourth presentation of an item in the study phase. Those participants with a behavioral repetition priming effect above the median were included in the “strong-repetition-priming group” whereas those with an effect below the median were included in the “weak-repetition-priming group.” Computation of the ratio between RTs to the first versus the fourth item presentation, rather than absolute differences, resulted in identical group assignments. To confirm that repetition effects differed between groups, RTs and proportion of correct responses were statistically analyzed with a repeated measurements analysis of variance (ANOVA) with the factor repetitions (four levels: first, second, third, and fourth presentation) and group (strong-repetition-priming group vs. weak-repetition-priming group).

Performance in the test phase was quantified as the difference between the percentage of hits (correct recognition of old items) and the percentage of false alarms (false recognition of new items). Separate performance scores were computed for old items that had been presented twice (old-2 items) and those which had been presented four times (old-4 items) in the study phase. Participants with a recognition performance above the median were assigned to the “good-recognition-performance group” whereas those with performance below the median were assigned to the “poor-recognition-performance group.” To confirm that the two groups differed significantly in performance, a two-factors repeated measures ANOVA was computed with the factors recognition (performance for old-2 items vs. performance for old-4 items) and group (good-performance vs. poor-performance group). Response criterion c was computed as the average of the normalized hit rate for all old items and the false alarm rate (Macmillan & Creelman, 2005). Response criterion or bias refers to an observer’s tendency to prefer one response alternative over the other. In the present study, observers with a “conservative”

response bias would tend to judge items as old, whereas observers with a “liberal” response bias would tend to judge items as new.

Analysis of gamma activity. Averaging epochs lasted from 200 ms before to 800 ms after stimulus onset. A baseline interval of 200 ms duration preceding stimulus onset was subtracted before averaging. Automatic artifact rejection excluded trials from averaging if the standard deviation within a moving 200-ms time interval exceeded 40 μ V. All epochs were also visually inspected for artifacts and rejected in the case of eye movements or electrode drifts.

A Morlet-based wavelet transform with a “width” of 12 cycles was employed for the analysis of gamma-band activity to provide a continuous measure of the amplitude of a frequency component (for details, refer to Herrmann, Grigutsch, & Busch, 2004). In brief, Morlet wavelets can be thought of as “band-pass filters”, with a Gaussian shape both in the time domain and in the frequency domain around their central frequency. The method thus provides a time-varying magnitude of the signal in each frequency band, leading to a time \times frequency representation of the data. Usually, the characteristics of a wavelet are denoted as $2\sigma_t$ and $2\sigma_f$. The standard deviation σ_t of the Gaussian temporal envelope is reciprocally related to the frequency ($\sigma_t \approx \frac{1}{f}$). The standard deviation in the frequency domain is given by $\sigma_f = \frac{2\pi}{\sigma_t}$. The time resolution of this method thus increases at higher frequencies, whereas the frequency resolution decreases at higher frequencies. Here, we applied wavelets with a constant ratio $\frac{\Delta t}{\sigma_t} = 2\pi$, which corresponds to a temporal wavelet duration ($2\sigma_t = \frac{2}{f_0}$) of two cycles at the wavelet’s center frequency f_0 and a frequency bandwidth of $2\sigma_f \frac{f_0}{\pi} =$. Accordingly, a wavelet with a center frequency of 40 Hz employed in this study had a wavelet duration of $2\sigma_t = 50$ ms and a spectral bandwidth of $2\sigma_f = 12.71$ Hz. To reveal the phase-locked (evoked) fraction of gamma activity, the wavelet transform was performed on the averaged evoked potential. Non-phase-locked (induced) activity was analyzed by performing the wavelet transform for each single trial and averaging the absolute values of the resulting transforms. Because the exact frequency of the gamma-band response varies considerably between participants, the frequency of gamma activity used for statistical analyses was determined individually for each subject. Time-frequency transforms were first computed for every channel and subsequently averaged across electrodes and conditions to increase the signal-to-noise ratio. From these averaged time-frequency scalograms, individual gamma frequencies were obtained as the maximum evoked response in the frequency range between 20 and 100 Hz in a time window from 50 ms to 130 ms (mean = 39 Hz; range: 26–70 Hz) and as the maximum induced response from 200 ms to 400 ms (mean = 51 Hz; range: 30–81 Hz), respectively. Two participants for which no distinct gamma response could be determined were discarded from the analysis of gamma activity.

Statistical analyses of gamma-band activity were performed after selected channels were pooled into an anterior (FP1, FP2, F7, F3, Fz, F4, F8), a central (FC1, FC2, C3, Cz, C4, CP5, CP3, CP2, CP4), and a posterior (P7, P3, Pz, P4, P8, O1, O2) region of interest (ROI). Early gamma-band responses were defined as mean amplitudes of evoked gamma activity in the time window from 50 ms to 130 ms. Late gamma-band responses were defined as the mean amplitude of induced gamma-band activity in the time window from 200 ms to 400 ms. Effects of repetition suppression were analyzed with repeated measures ANOVAs of evoked and induced gamma-band responses in the indirect task

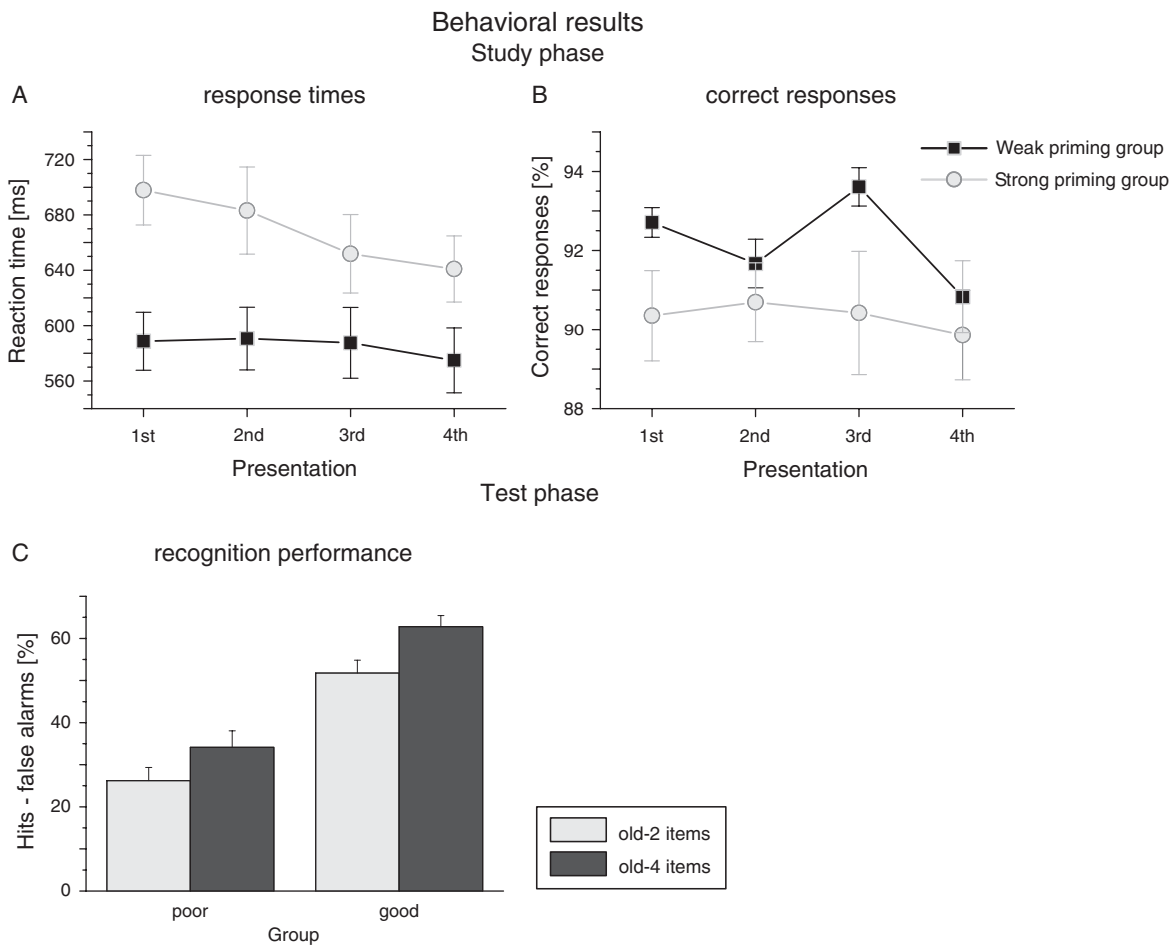


Figure 2. Summary of the behavioral results (mean response times, performance, and standard errors). In the study phase, only the “strong priming group” exhibited faster responses for repeated presentations of an item (A). The proportion of correct responses did not vary significantly between repetitions or groups (B). In the test phase, recognition performance was superior for items that had been presented four times during the study phase (old-4 items) compared to items that were presented only twice (old-2 items). Moreover, performance was considerably better in the “good recognition performance group” (C). Note that participants were assigned to the “repetition-priming groups” according to response times in the study phase, whereas “recognition-performance groups” were defined according to performance in the test phase.

of the study phase of the experiment with the factors repetitions (four levels: first, second, third, and fourth presentation) and ROI (anterior, central, posterior). Effects of recognition memory in the direct test of the test phase were analyzed with the ANOVA factors recognition (new items, old-2 items, and old-4 items) and ROI. This analysis comprised responses to old-2, old-4, and new items, irrespective of whether or not they were responded to correctly. Gamma responses were then compared between participants with good and poor recognition performance. The prediction was that if gamma responses were functionally relevant for recognition, those participants with good recognition performance should exhibit stronger differentiation of gamma responses between old and new items than participants with poor performance. Data from both phases were analyzed with an additional factor group, which tested for a relation between gamma-band effects and repetition priming in the study phase (strong-repetition-priming group vs. weak-repetition-priming group) and recognition memory in the test phase, respectively (good-performance vs. poor-performance group). Assignment to one of the two repetition-priming groups was based on RT differences between first and fourth item presentations. Assignment to one of the recognition-memory groups was based on the

difference between percentage of hits to old-4 items and false alarms (see Analysis of behavioral data). Huynh–Feldt corrections were used to adjust for violations of the sphericity assumption for repeated measures factors containing more than two levels (cf. Dien & Santuzzi, 2004). Corrected p values and uncorrected degrees of freedom are reported below along with the ϵ value. Results of post hoc tests were Bonferroni corrected by dividing the criterion alpha level by the number of post hoc comparisons. Only post hoc results that were significant according to this criterion are reported.

Results

Behavioral Results

In the study phase, RTs exhibited a strong repetition priming effect (see Figure 2), that is a reduction of RTs as a function of item repetition: Repetitions, $F(3,48) = 14.13$, $p = .0001$, $\epsilon = .98$. An ANOVA with an additional between-subjects factor confirmed that the repetition priming effect was significantly more pronounced in the strong-repetition-priming group: Repetition \times Group, $F(3,48) = 6.39$, $p = .001$, $\epsilon = .98$. Post hoc

tests revealed that only the strong-repetition-priming group exhibited repetition priming: Repetitions, $F(3,24) = 20.86$, $p = .0001$, $\epsilon = .99$. but not the poor-repetition-priming group: Repetitions, $F(3,24) = 1.29$, $p = .303$, $\epsilon = .92$. This result affirmed that the group assignment, in fact, separated participants with different behavioral patterns. The weak-repetition-priming group was not generally worse in performance. Rather, this group exhibited generally faster RTs than the strong-priming group: Group, $F(1,16) = 5.59$, $p = .031$. The proportion of correct responses (91%) did not vary with repetitions or between groups.

In the test phase, recognition performance was better for old items that had been presented four times (old-4 items) than for those that had been presented only twice (old-2 items) during the study phase: Recognition, $F(1,17) = 44.52$, $p = .0001$, $\epsilon = .99$, in both groups. An ANOVA with an additional between-subjects factor showed that performance was better in the good-performance group than in the poor-performance group: Group, $F(1,17) = 39.98$, $p = .0001$. This result confirmed that the group assignment succeeded in separating participants with differing recognition performance. Response criterion was not correlated with repetition priming or recognition performance.

Furthermore, we tested whether repetition priming in the study phase was correlated with recognition performance in the test phase. However, assignment to the strong- or weak-repetition-priming group was not associated with assignment to the good- or poor-recognition-performance group as indicated by a nonsignificant Pearson's Phi ($\phi = .267$, $p = .245$). Moreover, the repetition priming effect was not correlated with recognition performance ($r = .219$, $p = .367$).

Gamma-Band Responses

Evoked gamma-band activity was observed during both phases of the experiment with a maximum over posterior electrodes and a mean latency of 90 ms (see Figures 3 and 4). Induced gamma activity had a more widespread and more central scalp distribution and was less localized in time and frequency with a mean latency of approximately 300 ms (see Figure 5).

Study Phase

In the study phase, item repetition resulted in suppression of evoked gamma-band responses. Consistent with the posterior topography of evoked gamma activity, this effect was most pronounced over posterior recording sites. Furthermore, the effect was stronger in the strong-repetition-priming group. These findings were statistically confirmed by a significant ANOVA interaction: Repetition \times ROI \times Group, $F(6,90) = 4.01$, $p = .001$, $\epsilon = 1$. A post hoc ANOVA revealed a Repetition \times ROI interaction only in the strong-repetition-priming group, $F(6,42) = 3.48$, $p = .006$, $\epsilon = 1$. Only in this group did item repetition result in a suppression of evoked gamma activity in the posterior ROI, $F(3,24) = 4.58$, $p = .016$, $\epsilon = .85$. No effects of item repetition on induced gamma activity were found.

In addition, we tested for a relationship between repetition suppression of gamma-band responses in the study phase and recognition performance in the test phase. Repetition suppression was compared between groups with good and poor performance in the test phase. This analysis did not yield significant effects of repetition or Repetition \times Group, all $F < 1$, indicating that the degree of repetition suppression in the indirect task was not related to how well items could be remembered in the direct task.

Test Phase

In the test phase, presentation of old items evoked stronger gamma band responses than new items, and the magnitude of this old/new effect differed between groups: Recognition \times Group, $F(2,30) = 4.39$, $p = .021$, $\epsilon = 1$. Post hoc tests revealed that old items evoked more gamma activity than new items only in the good-performance group: Recognition, $F(2,14) = 7.31$, $p = .007$, $\epsilon = .96$. No difference was found between old-2 and old-4 items in this group, $F(1,7) < 1$. Furthermore, the distribution of the recognition effect across the three regions of interest was different between groups: Recognition \times Group \times ROI, $F(4, 60) = 4.36$, $p = .010$, $\epsilon = .72$. Post hoc tests revealed that old items evoked stronger gamma activity than new items in the central, $F(2,14) = 8.99$, $p = .003$, $\epsilon = .99$ and posterior ROI, $F(2,14) = 12.93$, $p = .001$, $\epsilon = .99$, only in the good-performance group. Furthermore, induced gamma activity was stronger for old items compared to new items in all participants: Recognition, $F(2,30) = 4.24$, $p = .030$, $\epsilon = .87$. This effect was more graded than the recognition effect on evoked gamma. A post hoc test revealed a significant effect on induced responses only between old-4 and new items, $F(1,16) = 8.581$, $p = .010$, $\epsilon = .98$.

In addition, we tested for a possible relationship between the old/new effect on evoked gamma-band responses during testing and repetition priming in the study phase. Recognition effects were compared between groups that showed strong and weak behavioral repetition priming in the study phase. A Recognition \times ROI interaction was found, $F(2,30) = 4.24$, $p = .030$, $\epsilon = .87$, but none of the following post hoc analyses testing for recognition effects in the separate ROIs yielded any significant results. In particular, no group effect or interaction was found, indicating old/new effects in the direct task were not related to how strong response times were affected in the indirect task.

Discussion

The present study investigated early electrophysiological effects of repetition priming and recognition memory and the significance of these effects for behavioral responses. We conducted time-frequency analysis of gamma-band activity, which offers the potential to reveal effects that cannot be obtained from broadband event-related potentials (ERPs). Most previous investigations of gamma-band responses in memory-related tasks did not directly test their relevance for behavioral performance. The majority of these studies employed simple target detection or choice discrimination tasks, which are easy to perform and do not give rise to significant variability in task performance. Therefore, we employed a demanding experimental paradigm and investigated the functional significance of memory-related gamma-band effects by comparing electrophysiological effects between subject groups with strong and weak behavioral effects in the direct and the indirect memory tasks, respectively. Groups were formed based on a median split of behavioral performance. We concur that effects might have been more pronounced in an analysis of participants with particularly strong and weak behavioral effects. However, the median split is an economical use of available data rather than excluding participants near the median to create more distinct groups. Another common criticism of the median split is that dichotomization of a continuous predictor variable into two groups results in loss of statistical power (Irwin & McClelland, 2003; MacCallum, Zhang, Preacher, & Rucker, 2002). Thus, we suggest that

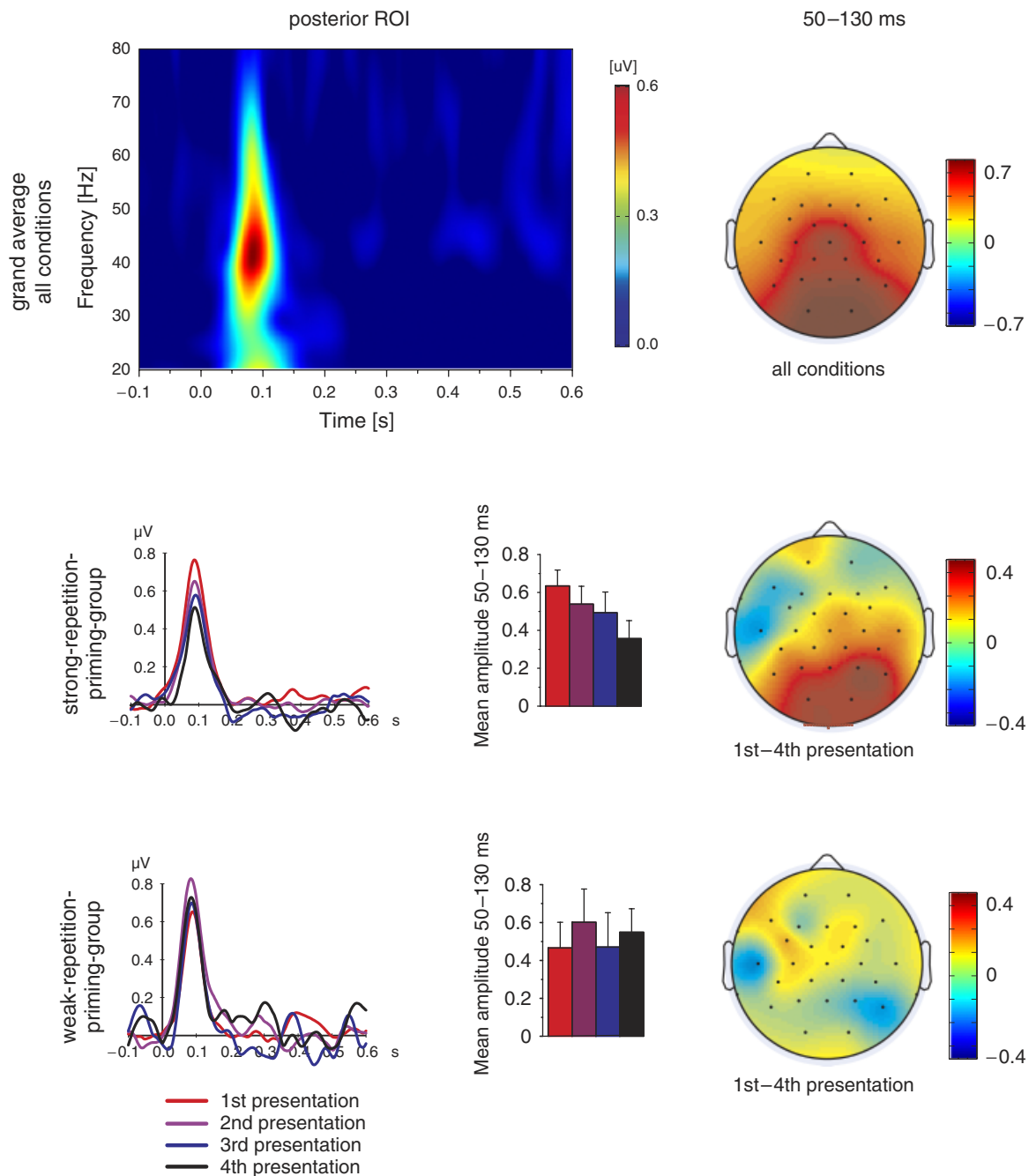


Figure 3. Summary of implicit memory effects on evoked gamma activity in the study phase, averaged across participants. Top row: Time-frequency spectra averaged across conditions and posterior electrodes confirm a distinct signal in the frequency range from 30 Hz to 60 Hz. Note that gamma responses were more circumscribed in frequency in single subject data. The topographic map of amplitudes of individual gamma frequencies averaged across experimental conditions from 50 ms to 130 ms shows an occipital distribution of evoked gamma activity. Second row: Results for the group of participants with strong behavioral repetition priming. Time courses of the averaged individual evoked gamma frequencies in the posterior ROI revealed reduced amplitudes for repeated items. Bar charts represent mean amplitudes in the posterior ROI in the time range from 50 ms to 130 ms. The difference topography (first – fourth presentation) confirms a posterior topography of this effect. Third row: Results for the group of participants with weak behavioral repetition priming. Time courses and topographies of the averaged individual evoked gamma frequencies did not reveal an effect of item repetition.

future studies should acquire a larger sample of participants and use regression analyses or classify groups based on multivariate pattern analysis (Haynes & Rees, 2006). In the study phase of the experiment, abstract line drawings were repeatedly presented while participants performed a simple visual discrimination task.

The indirect task of the study phase tested for effects of item repetitions. These effects can be regarded as a measure of implicit memory processes because the nature of the indirect task did not require participants to recall how often a given item had been presented before and, thus, did not promote retrieval intention.

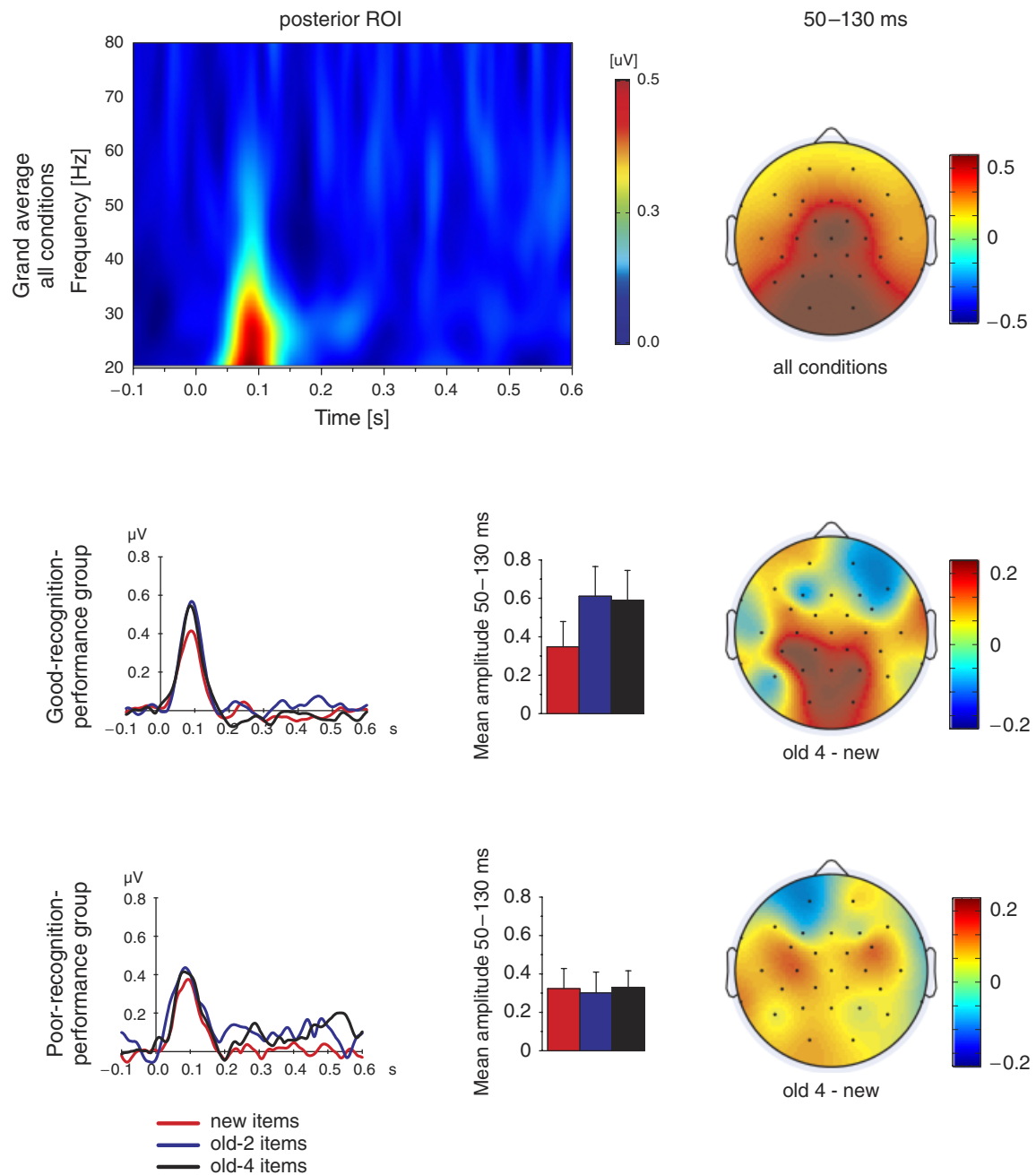


Figure 4. Summary of explicit memory effects on evoked gamma activity in the test phase, averaged across participants. Top row: Time-frequency spectra averaged across conditions and posterior electrodes confirm a distinct signal in the frequency range from 30 Hz to 60 Hz. Note that gamma responses were more circumscribed in frequency in single subject data. The topographic map of amplitudes of individual gamma frequencies averaged across experimental conditions from 50 ms to 130 ms shows an occipital distribution of evoked gamma activity. Second row: Results for the group of participants with good behavioral recognition performance. Time courses of the averaged individual evoked gamma frequencies in the posterior ROI revealed larger amplitudes for old items as compared to new items. Old-2 items had been presented twice and old-4 items had been presented four times during the study phase. Bar charts represent mean amplitudes in the posterior ROI in the time range from 50 ms to 130 ms. The difference topography (old4 – new items) confirms a posterior topography of this effect. Third row: Results for the group of participants with poor behavioral recognition performance. Time courses and topographies of the averaged individual evoked gamma frequencies did not reveal an old/new effect.

The notion that this represents an indirect memory test is supported by the participants’ reports in the postexperimental interviews. Participants consistently reported that they were generally aware of the fact that items were repeated, but that they did not pay particular attention to or even count the rep-

etitions of the items in the study phase. Most participants also reported that they were not aware of how often old items presented in the test phase had been presented previously during the study phase. Moreover, if the indirect task in the study phase were confounded by participants’ explicit retrieval attempts,

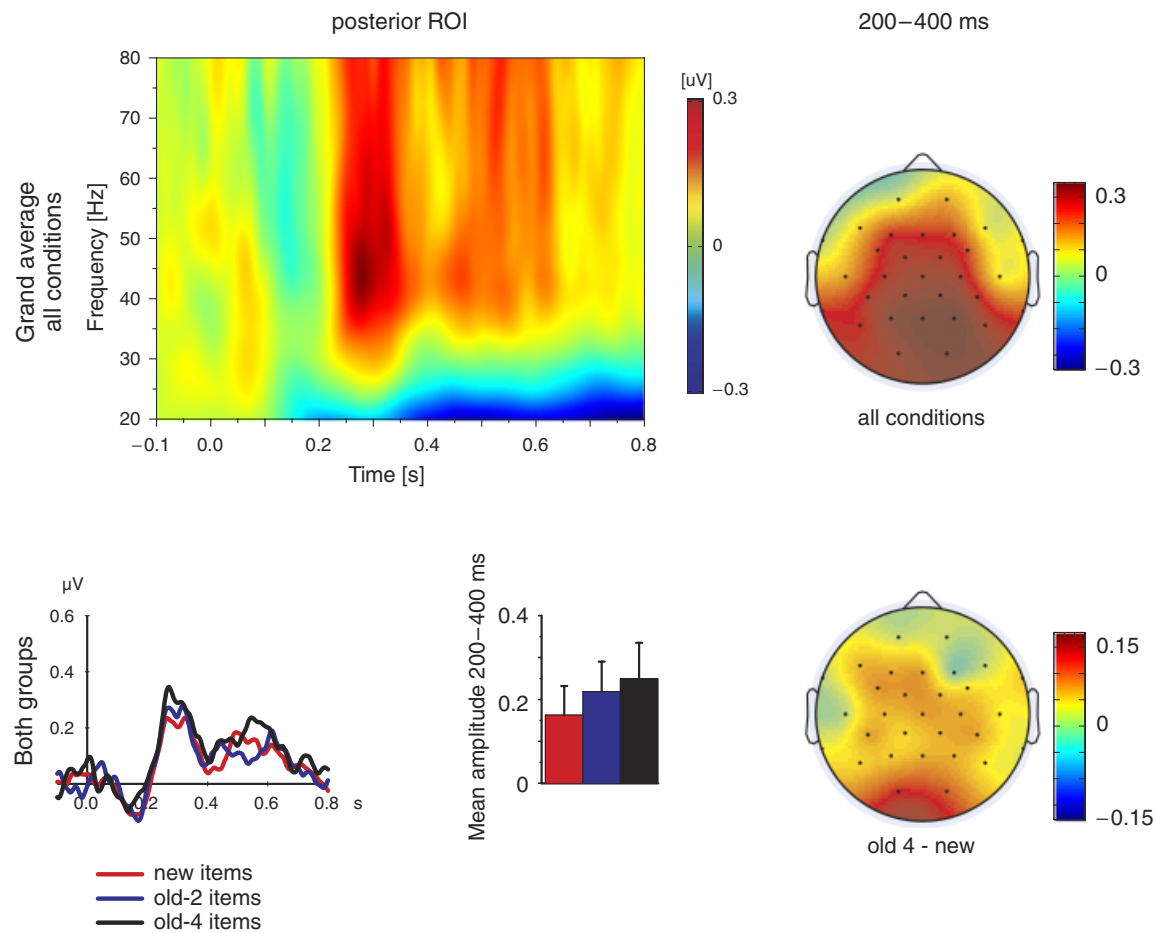


Figure 5. Summary of explicit memory effects on induced gamma activity in the test phase, averaged across participants. Top row: Time-frequency spectra averaged across conditions and posterior electrodes confirm a distinct signal in the frequency range from 30 Hz to 100 Hz. Topographic maps of amplitudes of individual gamma frequencies averaged across experimental conditions from 200 ms to 400 ms show a parieto-occipital distribution of induced gamma activity. Second row: Time courses of the grand averaged individual gamma frequencies in the posterior ROI revealed larger amplitudes of induced gamma-band activity for old as compared to new items in all participants. Old-2 items had been presented twice and old-4 items had been presented four times during the study phase. Bar charts represent mean amplitudes in the posterior ROI in the time range from 200 ms to 400 ms. The difference topography (old4 – new items) confirms a parieto-occipital topography of this effect.

repetition effects should resemble old/new effects in the test phase. As will be detailed below, this was not the case. Rather, effects in the indirect and direct tasks were diametrically opposed. In the test phase, participants were to discriminate old from new items. Old/new effects in the direct task of the test phase served as an index of explicit recognition memory. This type of paradigm has been widely used in previous investigations of priming effects on behavioral and physiological responses (Grill-Spector et al., 2006; Gruber & Müller, 2005; Penney, Maess, Busch, Derrfuss, & Mecklinger, 2003) and of physiological correlates of recognition memory (Groh-Bordin, Zimmer, & Ecker, 2006; Gruber, Tsivilis, Montaldi, & Müller, 2004; Paller, 2004).

Response times in the study phase were accelerated by item repetition. Behavioral repetition priming was associated with a decrease of evoked gamma activity. This repetition suppression is regarded as a correlate of implicit memory processes (Tulving & Schacter, 1990) and has been interpreted as a “sharpening” of cortical object representations (Wiggs & Martin, 1998). In this context, sharpening is understood as the sparser neuronal representation of stimuli, whereby neurons that code features

irrelevant for identification of a stimulus are no longer activated. As a result, less resources are required for identification when the stimulus is presented anew.

Repetition suppression has been reported in previous fMRI, ERP, and gamma activity studies (Grill-Spector et al., 2006; Groh-Bordin et al., 2005; Gruber, Malinowski, et al., 2004; Henson & Rugg, 2003). Repetition suppression of early evoked gamma-band responses, which have been localized to early visual cortices (Gruber et al., 2006; Hoogenboom et al., 2006; Lachaux et al., 2000; Narici, Carozzo, Lopez, Ogliastro, & Sannita, 2003; Rols et al., 2001), is in line with fMRI studies that reported repetition suppression in several early visual areas. These areas include the occipito-temporal cortex, the occipital cortex, and even the striate cortex under certain conditions (Henson et al., 2002; Vuilleumier et al., 2005; Wig, Grafton, Demos, & Kelley, 2005). The fact that the electrophysiological effects of the present study occurred at a latency of approximately 90 ms argues against a temporally late reentrant mechanism that modulates activity in anatomically early visual areas after feedback from higher cortical areas (Henson & Rugg, 2003). Instead, perceptual processes appear to be modulated by visual experience even at

earliest stages. The results also demonstrate the utility of time-frequency analysis of electrophysiological responses, as the effects observed in the present analysis considerably preceded repetition effects reported in event-related potential studies. ERP correlates of repetition priming are usually observed after 200 ms (Groh-Bordin et al., 2005; Paller et al., 2003), suggesting that some repetition effects might arise relatively late, perhaps after interactions with frontal cortex. The suppression of evoked gamma activity by item repetition might also be related to differential attentional demands. Several authors have, in fact, reported that repetition suppression depends on attentional stimulus processing (Eger et al., 2004; Yi & Chun, 2005). It should be noted, however, that initial and repeated item presentations were intermixed throughout the study phase. Thus, repetition suppression in this experiment is unlikely to result from a general change in attentional involvement, expectations, or strategies in the course of the experiment. It also appears unlikely that participants noticed each item repetition and, as a result, devoted less effort to processing the items. In this case, effects of item repetition should not have manifested as repetition suppression but should instead have resembled the enhancement effects for old items in the direct task of the test phase, which was not the case. Moreover, if repetition effects resulted from participants' explicit memory strategies, these effects should have been associated with recognition performance in the direct memory test. That is to say, participants with stronger repetition suppression in the test phase should have exhibited better recognition performance in the test phase, which was also not the case.

In this study, we were unable to replicate previous reports of repetition effects on later induced gamma-band responses (Gruber, Malinowski, et al., 2004). This may be due to the large number of intervening stimuli in the present study (10 to 18 items). Several studies have demonstrated a reduction of repetition effects as a function of the number of intervening stimuli (e.g., Henson, Rylands, Ross, & Rugg, 2004). Alternatively, induced gamma activity may have been reduced due to the lack of semantic associations with the abstract line drawings (Gruber & Müller, 2006).

A further central finding of the present study is that repetition suppression of early evoked gamma activity was observed only in participants who exhibited a behavioral effect of repetition priming. Interestingly, the individual degree of behavioral repetition priming in the study phase was not predictive of subsequent recognition performance in the test phase. Similarly, the degree of repetition suppression of early gamma responses was also unrelated to recognition performance. This result is consistent with the assumption that implicit and explicit memory processes are supported by dissociable memory systems with different neural substrates (Donaldson et al., 2001; Groh-Bordin et al., 2005; Rugg et al., 1998; Tulving & Schacter, 1990). It should be noted that the present results do not speak against a role of enhanced gamma activity for the formation of explicit memory traces (Fell et al., 2001; Osipova et al., 2006; Sederberg, Kahana, Howard, Donner, & Madsen, 2003). This effect was found in explicit memory tasks when subsequently remembered items were compared to subsequently forgotten items (for a review, see Axmacher, Mormann, Fernández, Elger, & Fell, 2006), whereas we investigated reduced gamma activity with item repetition in an implicit memory task, which is assumed to involve different neural mechanisms.

We also found that response times in participants with weak repetition priming were significantly faster from the outset compared to participants with strong repetition priming, but their RTs were not reduced as a function of item repetition. It is con-

ceivable that these participants adopted a more efficient strategy for solving the "loop/no-loop" task, leading to a floor effect where RTs could not be facilitated any further by repetition priming. A candidate for such a strategy might be the selective processing of the items' global (the shape with or without a loop) or local (a junction on the shapes outline) dimension. In fact, Kim, Ivry, and Robertson (1999) and Koivisto and Revonsuo (2004) have reported that priming of hierarchical stimuli is more pronounced for the global dimension. Although we cannot substantiate this assumption, it is conceivable that in the present experiment, some participants (later classified as strong primers) adopted a global strategy that gave rise to stronger repetition priming effects, whereas others (later classified as weak primers) used a more efficient local strategy, which was not prone to priming effects. Future studies should systematically investigate repetition effects for local and global information on response times and gamma-band activity.

The results also show that repetition suppression is not a necessary or automatic consequence of stimulus repetition. In line with previous fMRI and EEG studies (Donaldson et al., 2001; Gruber & Müller, 2006; Henson et al., 2002), we found that gamma activity in the direct task was not suppressed by repetitions of old items. Instead, recognition of old items enhanced both early evoked and later induced gamma-band responses. This finding is in line with an fMRI study by Henson et al. (2002), who found repetition suppression of the blood-oxygenation-level dependent response only in an implicit but not in an explicit task. Recognition enhancement of early evoked gamma activity was well pronounced in participants with good behavioral recognition performance, but this effect was absent in participants with poor performance. In fact, in participants who could not well discriminate old from new (and to which, presumably, most items appeared new), early evoked gamma responses to all items did not exceed the magnitude of responses to new items in participants with good performance.

Effects of explicit memory on evoked gamma-band responses were not associated with the level of repetition priming in the study phase. The results are in line with the suggestion that early gamma-band responses are a correlate of an early matching of visual input with memory representations. For instance, Herrmann, Lenz, Junge, Busch, and Maess (2004) found that early evoked gamma activity elicited by line drawings of familiar objects is stronger than gamma responses evoked by unknown nonsense figures. Furthermore, Herrmann, Mecklinger, and Pfeifer (1999) and Herrmann and Mecklinger (2001, 2000) investigated gamma activity in the oddball paradigm, in which participants had to maintain a template of the task-relevant target stimulus in short-term memory and to match each presented stimulus with that template. The authors revealed that target stimuli evoked larger gamma-band responses than nontargets and that the amplitude of responses evoked by nontargets depends on the similarity (the match) between stimulus and target. According to the "match-and-utilization model" (MUM; Herrmann, Munk, et al., 2004), visual input into early extrastriate cortex leads to rapid activation of higher visual areas in occipito-temporal cortex (e.g., V4), where perceptual memory representations are stored in the form of enhanced synaptic connections between and within visual areas. Mnemonic properties of V4 neurons have been demonstrated by Rainer, Lee, and Logothetis (2004). In this study, monkeys learned to recognize objects in noisy displays, and this learning was reflected in a modification of response properties of V4 neurons. Gamma-

band activity has been frequently found in intracranial recordings from V4 and occipito-temporal cortex in monkeys (Bichot, Rossi, & Desimone, 2005; Rols et al., 2001) and humans (Lachaux et al., 2000). According to the MUM model, input that matches such memory representations results in a rapid local feedback signal, which in turn leads to enhanced gamma activity in the network. In the instance of missing memory representations, local feedback does not occur, leading to weaker gamma responses.

The importance of rapid feedback signals in early vision has also been highlighted in other recent models of visual processing (Bullier, 2001; Körner, Gewaltig, Körner, Richter, & Rodemann, 1999; Lamme & Roelfsema, 2000). The present results extend previous reports by demonstrating that effects of memory matching on early gamma-band activity are dependent on the current task and retrieval intention and are strongly associated with behavioral recognition performance. The fact that the same signal was found to be differentially modulated by implicit and explicit memory processes indicates that evoked gamma activity in itself is not a genuine signature of these memory systems. Rather, evoked gamma activity appears to reflect an early perceptual process, which is under the modulatory control of top-down influences which act in a task-dependent manner (Başar, Başar-Eroglu, Karakaş, & Schürmann, 2000; Busch, Schadow, Fründ, & Herrmann, 2006). In other words, the old/new effect found for evoked gamma activity is not a direct correlate of an explicit memory system, but it is a correlate of the effect that this memory system exerts on early visual processing. Moreover, the

association of evoked gamma effects and behavioral effects suggest that these top-down modulations of perceptual processes are directly related to the facilitation of behavioral responses by implicit and explicit memory.

Later induced gamma activity exhibited an old/new effect only for items that had been presented four times during the study phase. It has been proposed that induced gamma activity is a signature of the activation of a cortical object representation integrating perceptual as well as semantic object features (Gruber & Müller, 2006). It is conceivable that, for the abstract stimuli employed in the present study, the buildup of a semantic association requires a minimum number of repetitions. In the present study, participants frequently reported that they sometimes learned to associate the abstract patterns with meaningful interpretations (such as an animal). Hence, the old/new effect might have been observed only for old-4 items because memory traces with semantic associations might have been too weak after only two presentations.

In conclusion, we were able to demonstrate that the effect of a repeated encounter with a stimulus can be observed on earliest visual responses. These early effects are dependent on the nature of the task and the participants' retrieval mode (the intention to retrieve information from visual memory). Evidence for repetition suppression was found in an indirect memory task, and evidence for response enhancement by memory matching was found in a direct recognition memory task. Furthermore, we demonstrated that these electrophysiological effects parallel behavioral performance.

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