Gamma Band Synchronization and the Formation of Representations in Visual Word Processing: Evidence from Repetition and Homophone Priming

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Abstract

■ The formation of an object's cortical representation seems to rely on synchronized neuronal activity within the gamma band frequency range (gamma band activity [GBA]). In this study, we investigated whether electroencephalogram (EEG) GBA, and its phase synchronization between electrodes, is necessary for the formation of nonobject higher-order cognitive representations, using both repetition and homophone priming tasks. In a repetition priming task, the formation of orthographic, phonological, and semantic representations is promoted by a prime word, whereas in the homophone priming task, the formation of only phonological representations is promoted. In the present study, the lexical processing of a target word induced GBA. In the repetition priming task, induced GBA and phase synchronization were decreased by presentation of the prime word (i.e., a repetition suppression effect) within both 200–300 msec and 400–500 msec time windows. In the homophone priming task, the repetition suppression effect was observed only within the 400–500 msec time window. The fact that repetition suppression effects were found in both priming tasks indicates that GBA and phase synchronization are necessary for the formation of phonological and semantic representations of a word. These results also suggest that formation of orthographic and higher-order cognitive representations occurred over different time courses. ■

INTRODUCTION

When one views an object, different features (e.g., shape, color, location, etc.) of the object are received and processed in the brain. Data from a number of neuroimaging and neuropsychological studies have shown that these different features are processed in anatomically distinct brain regions. Nevertheless, we perceive the presented object as a complete one, presumably by integrating its various features. How does the brain integrate these features? One influential hypothesis is that synchronization of oscillatory neural rhythms provides the communication between brain areas that process different features (Varela, Lachaux, Rodriguez, & Martinerie, 2001; Singer & Gray, 1995).

A number of animal studies have shown that synchrony of oscillatory activities across different brain regions occurs in the visual cortex when different features of objects are integrated (for a review, see Singer & Gray, 1995). This synchrony of activities occurs within the gamma band frequency range (30–80 Hz). Based on these findings, some researchers argue that cortical object representations are activated via synchronized neural activity in cell assemblies that represent various stimulus features distributed across different brain regions (Tallon-Baudry & Bertrand, 1999). Human electroencephalographic (EEG) studies have shown that induced power and phase synchronization of gamma band responses (GBRs) from distinctly different electrodes is enhanced in cases where representations were formed in response to presented stimuli. GBRs of EEG can therefore serve as a signature of synchronized cell assemblies and can, in turn, reveal the mechanics of building object representations (Rodriguez et al., 1999; Tallon-Baudry, Bertrand, Delpuech, & Pernier, 1996).

Several studies have used a priming paradigm to examine this issue. Priming refers to a facilitation of target processing that occurs through prior presentation of a stimulus that is either identical or related in some way to the target. A neural basis of priming has been identified in the form of *repetition suppression*. Repetition suppression manifests as reduced neural activity and is thought to be a by-product of a *sharpening process* of cortical object representation. According to Wiggs and Martin (1998), neurons which code irrelevant features of a repeated stimulus are not activated when the representation of an object is developed. Sharpening of the representation in this fashion yields more efficient stimulus processing, and thus, this mechanism is postulated to account for the behavioral priming effect. According

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to this view, repetition suppression in a priming paradigm would be observed in gamma band activity because elimination of active (but irrelevant) cell assemblies results in an overall reduction of network activity during the coding of a representation. Putatively, this process is mediated by the synchronization of gamma band activity. Consistent with this argument, several studies have reported that reduced spectral power and phase synchronization characterize the gamma band activity caused by repetition priming (Fiebach, Gruber, & Supp, 2005; Gruber & Muller, 2002, 2005; Gruber, Malinowski, & Muller, 2004).

Gruber and Muller (2005) found that when a task involves repetition of familiar objects, repetition suppression occurs in both induced gamma band power and phase synchronization of activity measured at remote electrodes. In contrast, repetition enhancement of these neural activities was reported when unfamiliar objects were repeated. These results suggest that repetition suppression, which involves gamma band activity accompanied by a sharpening process, contributes to representations of familiar objects. Furthermore, it appears that formation of a new cortical network of cell assemblies is achieved through enhancement of GBR with unfamiliar objects. The fact that repetition enhancement was observed in the unfamiliar condition implies that the reduction of gamma band activity is not explained by habituation to the stimuli during testing. Fiebach et al. (2005) replicated the findings of Gruber and Muller using word and pseudoword stimuli.

The previously described research supports the notion that visual object representations are activated by GBR synchrony across various brain regions. However, it is not clear whether the formation of higher-order cognitive representations relies upon these synchronous activities. For example, in visual word recognition, orthographic, phonological, and semantic representations may all be activated and tightly integrated as we read the word (Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001). Indeed, studies of patients with brain lesions and functional imaging research converge to indicate that these different components are stored in distinct brain regions (Giesbrecht, Camblin, & Swaab, 2004; Fujimaki et al., 1999; Caramazza & Hillis, 1991). Nevertheless, it remains unclear how more abstract word representations, such as phonological or semantic, are formed and integrated. A main goal of the present study is to investigate the relationship between gamma band activity and the formation of these higher-order cognitive representations, by examining the repetition suppression effect in a priming paradigm.

It is not possible to selectively examine the amount of repetition suppression that is specific to any one level (i.e., orthographical, phonological, and semantic) in a repetition priming experiment because repetition of the same word should cause repetition suppression at multiple levels. However, Dehaene et al. (2001) have pro-

posed that the priming method becomes a powerful tool for probing the neural code underlying a specific representational level when the physical, phonological, or semantic relationship between the prime and the target is systematically varied. Following this rationale, we used both repetition and homophone priming paradigms to investigate whether the formation of a phonological level of word representation relies on the synchronization of GBR between brain regions. In our repetition priming condition, we presented the same word prior to the target word, assuming that this would preactivate orthographical, phonological, and semantic representations of the target. This preactivation should, in turn, elicit repetition suppression at all three representation levels. In the homophone priming condition, a target word is preceded by a homophone word. In this case, repetition suppression should occur at the phonological and/or semantic level. If these higher-order cognitive representations are based upon synchronization of gamma band activity, we should observe a repression suppression effect on gamma band activity in the homophone priming condition, as well as in the repetition priming condition.

Finally, it is possible that the GBR reflects only the formation of a visual (orthographic) representation during word reading (i.e., plays no role in higher-level word processing). If this is so, then the repetition suppression effect on GBR in our study will be observed only in the repetition priming condition. This is because repetition suppression should not occur at the orthographic level in the homophone priming condition, where the two words have different orthographic features. Furthermore, the present study may reveal functional differences (e.g., on topography or latency) between the orthographic and phonological representation processes via a comparison of the repetition suppression effect in the repetition priming and homophone priming conditions.

Several behavioral and electrophysiological studies have reported that priming effects can be contaminated by various conscious processes, such as expectancies or prime–target matching processes that occur during lengthy presentations of prime words (or long stimulus-onset asynchronies) (Hill, Strube, Roesch-Ely, & Weisbrod, 2002; Spitzer, Braun, Maier, Hermle, & Maher, 1993). To preclude this possibility, we used a relatively short (but not subliminal) prime duration (30 msec) in this experiment.

METHODS

Participants

Eighteen healthy, right-handed university students (10 women, age range = 19 to 30 years, mean age = 22.8 ± 0.8) received 1000 Japanese yen each for their participation. All participants had normal or corrected-to-normal visual acuity. Written informed consent was obtained from each participant before the experiment started.

Materials

Stimuli consisted of 400 prime–target pairs that were divided into two lists (List A and List B). Stimuli were either real nouns or pseudowords that consisted of two Japanese kanji script. The 200 prime–target combinations for each list included 40 nonrelated pairs (e.g., leaf–car), 40 repetition pairs (e.g., lemon–lemon), and 40 homophone pairs (e.g., pair–pear). These corresponded to the three prime conditions: unprimed, repetition, and homophone, respectively. In addition, we included 80 filler items composed of word–pseudoword pairs (e.g., picture–gerba). Word frequency (Amano & Kondo, 2000) was controlled for target words across each condition and list. It should be noted that some Japanese kanji words differentiate between a character and a radical. In order to avoid orthographic overlap between prime and target words in the homophone condition, the kanji words used here all had different characters and radicals.

Procedure

The experiment was conducted across two separate sessions. Nine participants received List A, whereas the remaining participants received List B. Each session consisted of 20 unrelated (unprimed), 20 repetition, and 20 homophone word pairs, along with 40 word–nonword pairs. All pairs were presented to participants in random order. Following a 500-msec fixation period, each prime word was presented for 30 msec between pre- and postmasking stimuli (50 msec). Immediately following the second mask, the target word was exposed for 1000 msec. Intertrial interval was set at 2500 msec. This trial scheme is outlined in Figure 1.

Participants were instructed to decide whether the target word was a real word or a pseudoword by pressing the corresponding button. Participants' responses and reaction times were recorded. After the experiment, participants were asked whether they could identify the various prime words. All participants reported that they were aware that a word was presented before each target but that they were unable to identify the primes.

EEG Recordings and Analysis

The EEG was set to record from 21 International 10–20 system scalp locations (Fp1, Fp2, AFz, Fz, F3, F4, F7, F8, Cz, C3, C4, T7, T8, Pz, P3, P4, P7, P8, Oz, O1, O2) and was referenced to the tip of each participants' nose. Vertical and horizontal eye movements were monitored via an electrode placed on the supra-ridge and canthus of the left eye. Interelectrode impedances were set below 5-kΩ. The EEG and electrooculogram data were filtered using a bandpass of 0.05–60 Hz. The data were digitized with an A–D conversion rate of 500 Hz, and were sampled from the 500 msec preceding the prime words until 2000 msec after the presentation of targets. Trials in which EEG or eye movements exceeded plus or minus 100 were removed from data analysis. The data from five participants were excluded from EEG analysis because of excessive eye movements.

In order to isolate the induced oscillations from the evoked components, event-related potential (ERP) was computed for each participant and this value was subtracted from each trial. This correction was conducted separately for each word condition: unprimed (i.e., unrelated), repetition, and homophone. The time–frequency (TF) energy of each trial was obtained by computing the squared norm of the EEG data convolution with complex Morlet wavelets having a Gaussian shape about its central frequency, both in the time ($SD = \sigma t$) and frequency domains ($SD = \sigma f$). These wavelets had a 7-cycle width, with frequencies ranging from 1 to 60 Hz in 1-Hz increments. For example, at 40 Hz, the wavelet duration ($2\sigma t$) is 58.34 msec with a spectral bandwidth ($2\sigma f$) of 10.92 Hz. TF energy was averaged over trials for each participant, separately for the three conditions. Average power values were expressed as a percentage change relative to the power in a baseline interval from −200 to −50 msec prior to prime word onset, in order to normalize for individual differences in EEG power, and for differences in absolute

Figure 1. Task scheme: Participants were asked to judge whether the target word is a real word. Under the repetition condition, the same word was presented as a prime word. With the homophone condition, the prime word was a homophone of the target word.
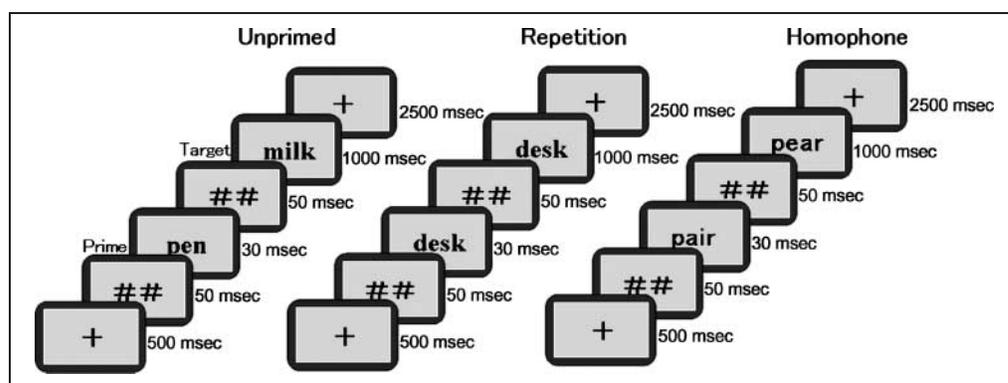
power between different frequency bands. The GBR (average of the 35–60 Hz range) was analyzed in three time windows because visual inspection revealed clear gamma band activity from 200 to 500 msec; the windows were 200–300 msec, 300–400 msec, and 400–500 msec. In addition, to determine whether the observed GBRs were induced or evoked brain activity (Herrmann, Munk, & Engel, 2004; Tallon-Baudry & Bertrand, 1999), the phase-locking factor was computed for each condition, which represents the degree of phase locking across trials in the TF domain (Tallon-Baudry et al., 1996).

Statistical analyses included three repeated measures analyses of variance (ANOVAs). The factors were condition (unprimed, repetition, homophone) and electrode, using data collected from each of the three windows. Phase synchrony of GBR between the recording sites was analyzed according to a procedure suggested by Lachaux, Rodriguez, Martinerie, and Varela (1999). Phase-locking values (PLV) between every electrode pair were computed at each time point and frequency. The average PLVs of GBR (35–60 Hz) were calculated in each condition, for each time window. According to Spencer et al. (2003), statistical analysis of phase synchrony in each condition should entail comparisons of data from each time window, corrected for mean prestimulus baseline. To assess whether the distribution of phase synchronized pairs differed significantly among conditions, we used the chi-square goodness-of-fit test (Spencer et al., 2003). Finally, we averaged the PLV data of all electrode pairs and the corresponding GBR value (35–60 Hz) was entered into the one-way ANOVAs.

There were some ERP amplitude differences between the conditions. These differences were mainly observed at the late time window and at the centro-parietal electrodes (an N400 priming effect). For statistical analysis purposes, the mean amplitude of the 300–500 msec time window was computed in each condition, and a two-way (Condition × Electrode) ANOVA was performed. A Geisser–Greenhouse correction was applied when effects with more than one degree of freedom present in the numerator were evaluated.

RESULTS
Behavioral Data

The mean percent correct response to targets, averaged across all participants, was $94.7 \pm 1.0\%$. A one-way ANOVA performed on the RTs to target words revealed a significant main effect of condition (unprimed vs. repetition vs. homophone) $[F(2, 34) = 15.63, p < .001]$. Post hoc analysis (a Tukey's HSD test) indicated that average RTs for the repetition condition (618.61 msec; $SEM = 13.92$ msec) were significantly shorter than average RTs for both unprimed (664.31 msec; $SEM = 14.03, p < .001$) and for the homophone (639.60 msec; $SEM = 13.68$ msec, $p < .05$) conditions. Furthermore, the mean RT for the homo-

phone condition was significantly shorter than that of the unprimed condition ($p < .01$).

Induced Gamma Band Response

A large power increase was observed in the GBR at centro-parietal regions during the 200–500 msec time window (see Figure 2). For the 200–300 msec time window, a significant Condition by Electrode interaction was observed $[F(40, 480) = 1.78, p < .01]$. Follow-up analyses performed for each electrode site revealed significant main effects of condition for sites Pz $[F(2, 24) = 3.41, p < .05]$, P7 $[F(2, 24) = 3.45, p < .05]$, and P3 $[F(2, 24) = 4.12, p < .05]$. Post hoc analyses showed that, for these electrodes, gamma band power in the repetition condition was significantly weaker than corresponding values for the unprimed and homophone conditions ($p < .05$ in each electrode). In the 300–400 msec time window, we observed neither significant main effects nor a significant Condition by Electrode interaction. Finally, in the later 400–500 msec time window, a significant main effect of condition appeared $[F(2, 24) = 4.23, p < .05]$. Post hoc analyses revealed that the gamma power of unprimed condition was significantly higher than that of the repetition ($p < .01$) and homophone conditions ($p < .05$).

Phase Synchrony

Figure 3 depicts phase synchrony between electrode sites for each condition, as a function of time window. For the 200–300 msec time window, the 102 and 98 electrode pairs showed a significant increase of PLVs with unprimed and homophone conditions, respectively. Fewer electrode pairs (22) exhibited significant phase synchrony in the repetition condition than in both the unprimed and homophone conditions. A chi-square test revealed that the distribution of phase synchronized pairs differed reliably among the conditions ($\chi^2 = 24.99, p < .01$). In contrast, for the 300–400 msec time window, there was no significant distribution difference of the phase synchronized pairs between the conditions (unprimed = 88 pairs, repetition = 75 pairs, homophone = 72 pairs, respectively; $\chi^2 = 0.79, ns$) Finally, in the 400–500 msec time window, synchronized pairs were diminished in the repetition (12 pairs) and in the homophone (40 pairs) conditions, compared to the unprimed (72 pairs) condition ($\chi^2 = 35.52, p < .01$). An ANOVA performed on PLV averaged across all electrode pairs revealed a significant main effect of condition at the 200–300 msec time window $[F(2, 24) = 4.30, p < .05]$. Post hoc analysis showed that the PLV was significantly smaller in the repetition priming condition compared to the unprimed and homophone conditions ($p < .01$). There was also a significant main effect of condition at the 400–500 msec time window $[F(2, 24) = 5.49, p < .05]$. At this time window, the PLV for the

Figure 2. Average time–frequency maps of gamma band power (Pz electrodes) and the comparison of gamma band power (±SEM) between conditions at the 200–300, 300–400, and 400–500 msec time windows. **$p < .01$ and *$p < .05$ versus unprimed condition.
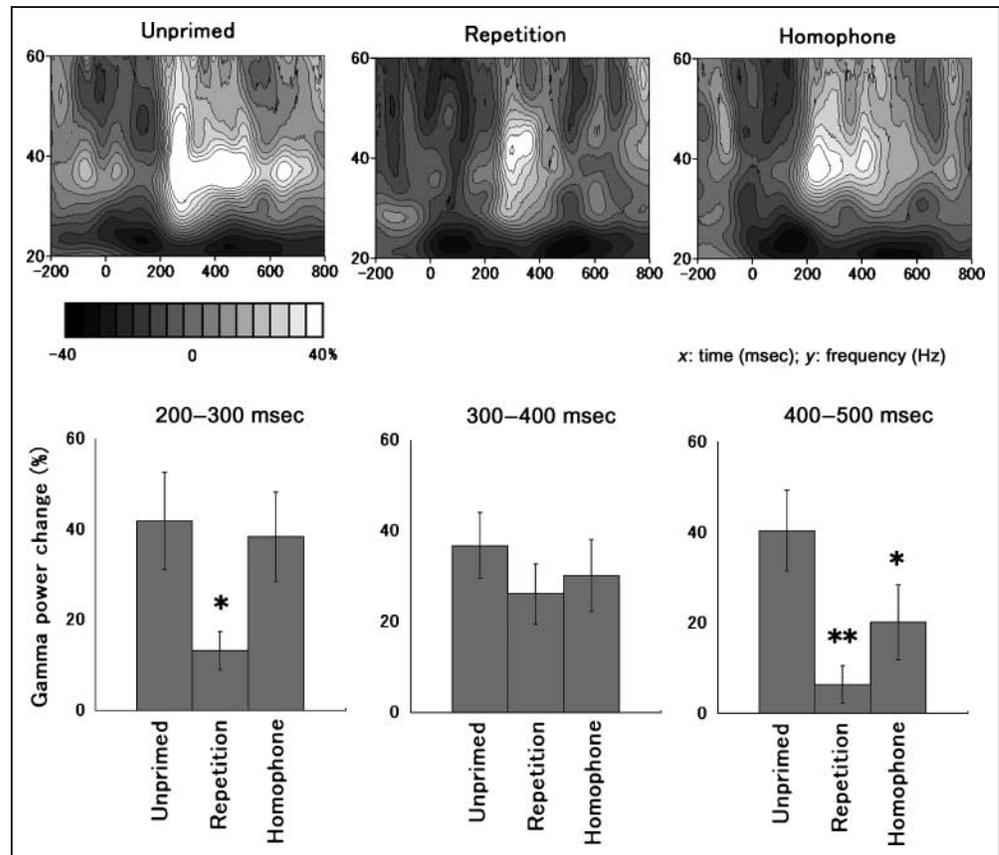
repetition condition was smaller than that for the un-primed condition ($p < .05$). For the homophone condition, there was a trend toward a repetition suppression effect ($p < .07$).

Event-related Potentials

Figure 4 depicts ERP of frontal central and parietal electrode sites for each condition. There was a significant main effect of condition at the 400–500 msec time window [$F(2, 23.8) = 4.40, p < .05$]. Post hoc analyses revealed that the repetition condition was significantly larger than the unprimed condition ($p < .05$). The difference between the unprimed and the homophone condition was not significant. In addition, a significant Condition by Electrode interaction was observed [$F(1.98, 23.81) = 14.957, p < .001$]. Follow-up analyses at each electrode site revealed significant main effects of condition (unprimed, repetition, homophone) for almost all of the sites (Fz, F3, F4, F7, F8, Cz, C3, C4, T7, T8, Pz, P3, P4, P7, P8, O1, O2). Post hoc analyses revealed that, at each site, the amplitude of the repetition condition was significantly larger than that for the unprimed condition, whereas there were no significant differences between the homophone and unprimed conditions. No significant interactions or main effects were found in the other time windows.

DISCUSSION

The goal of the present study was to examine whether gamma band activity, and in particular, its phase synchronization across active brain regions, reflects the formation of phonological representations in word reading. Behavioral priming effects were obtained in both homophone and repetition conditions. Furthermore, we found that both the power of GBR and its synchronization among electrodes were reduced by repetition priming, both within an early time window (200–300 msec) and a relatively later one (400–500 msec). This pattern of findings is suggestive of repetition suppression. In the homophone priming condition, however, a significant repetition suppression effect on gamma band activity was observed only in the 400–500 msec time window.

When a target word was preceded by a brief exposure of the same word or a homophone, both prime types resulted in decreased target processing time (RT) relative to the unprimed condition. These results suggest that preactivation of a word's representation can facilitate efficient processing of that word. In the present study, a significant priming effect was observed not only in the repetition condition but also in the homophone condition. In principle, the nature of this preactivated representation can be influenced by manipulating the prime–target relationship. Although prior presentation of a repetition prime activates representations of the

Figure 3. Phase synchrony changes in the 35–60 Hz frequency are plotted in space and time dimensions. Black lines indicate significant synchronization between electrode sites. Topographic color represents the power of gamma band response.
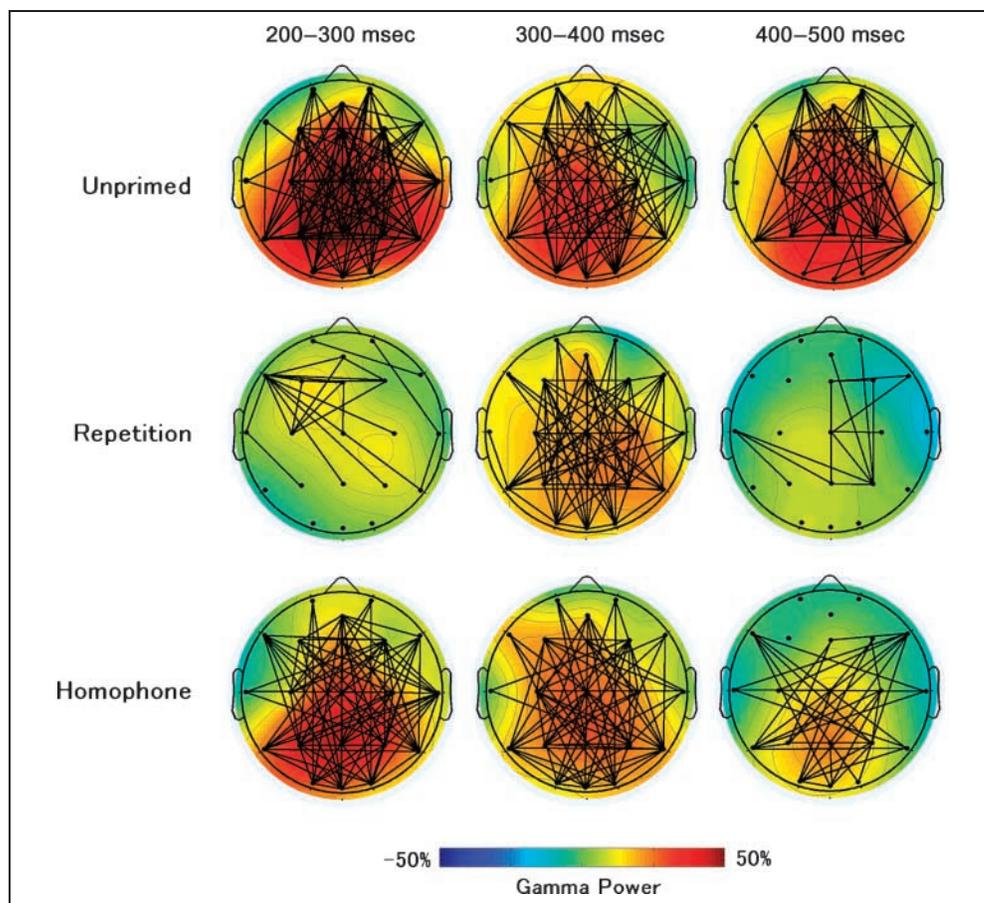
word at multiple levels (orthography, phonology, and semantics), the homophone primes should selectively activate only the phonological representation. Rueckl and Mathew (1999) presented words visually to participants who then performed a word-stem completion task. These researchers reported that visual presentation of a word (e.g., week) enhanced the probability that a word stem was completed with a homophone word (e.g., weak), as well as with the prime word itself (week). This finding implies that a visual presentation of a homophone word can activate the phonological representation of the word and thereby facilitate the word-stem completion task.

In previous studies, it has been reported that words elicit significantly stronger gamma power than nonwords when they are presented in the auditory modality (Krause, Korpilahti, Porn, Jantti, & Lang, 1998; Pulvermuller et al., 1996). It would appear that the GBR can be induced by activation of phonological (auditory) representations of word. Furthermore, the gamma band difference between words and nonwords was observed at relatively late latencies (400 msec) in these studies, indicating that activation of phonological representations developed over this time interval. It seems reasonable to assume that the significant repetition priming effect obtained here results from a preactivation of multiple word representations,

whereas the priming effect in the homophone condition probably results only from preactivation of phonological representations.

On the other hand, some studies have found that written homophone words in Japanese or Chinese can, in fact, activate the meaning of their homophone partners (Pollatsek, Tan, & Rayner, 2000; Sakuma, Sasannuma, Tatsumi, & Masaki, 1999; Xu, Pollatsek, & Potter, 1999; Zhou & Marslen-Wilson, 1999; Tan & Perfetti, 1997). For example, Tan and Perfetti (1997) showed that a facilitation effect in target naming is observed when the target is preceded by a homophone. In Japanese kanji words, Sakuma et al. (1999) reported that participants made more false-positive errors on homophone foils than on nonhomophone controls in a semantic decision task. These results indicate that semantic representations can be activated by homophones. In addition, semantic effects on GBR within the context of comprehension were observed at a similar latency range to the time window in the present study, whereas some researchers suggest that phonological activation of words is very fast. Taking into consideration these findings, the repetition suppression effect in the homophone priming condition here might be caused by preactivation of semantic representations, as well as by phonological representations. Given that preactivation of representations is reflected in the
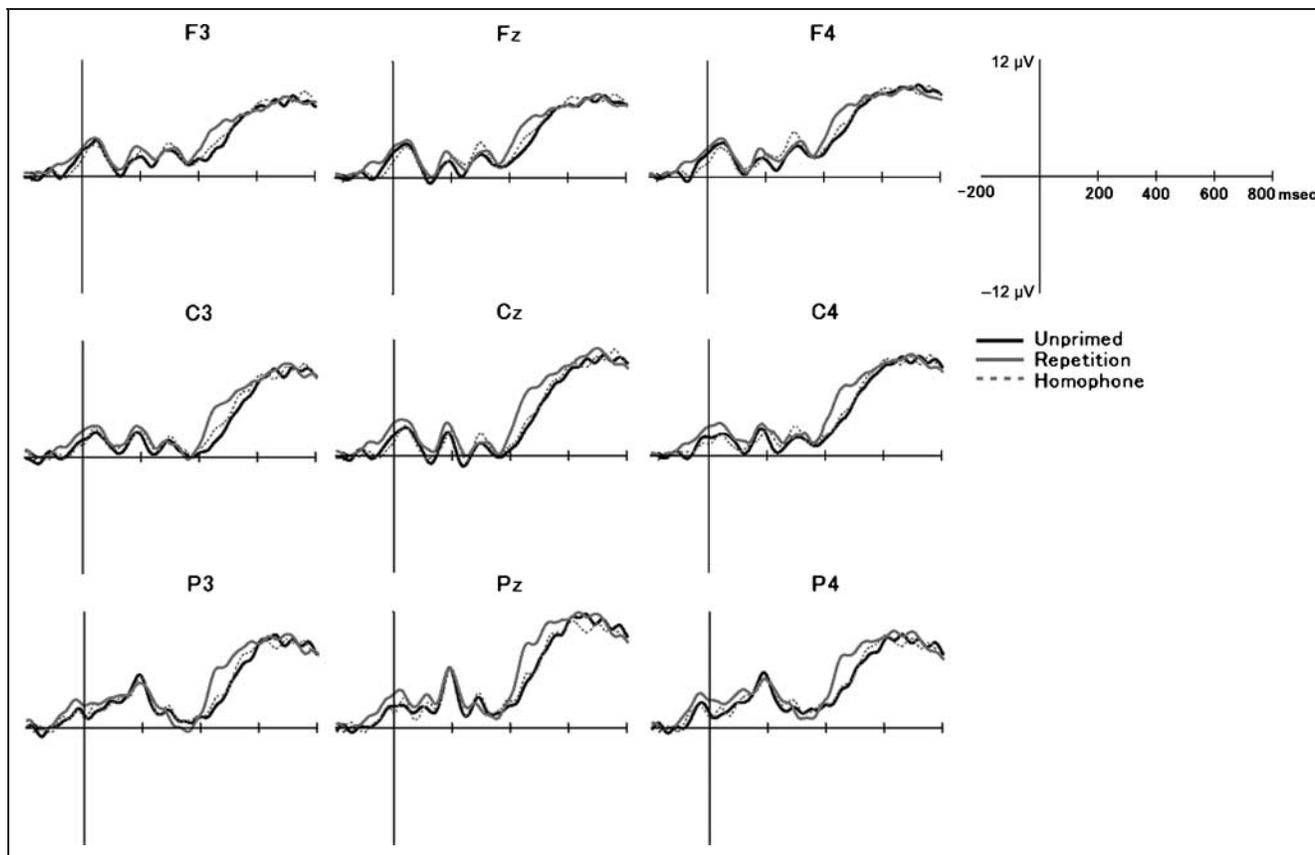
Figure 4. Event-related potentials to the target words at the frontal, central, and parietal regions.

repetition suppression effect, the present gamma band decrease (induced by homophone priming) is evidence that gamma band activity, and its phase synchronization between brain regions, plays an important role in forming phonological and semantic word representations.

The analysis of ERP data provides an implication concerning this issue. The priming task manipulation produced significant ERP change at the 400–500 msec time window, at which the N400 component is elicited. N400 is negative deflection of the ERP signal between 300 and 500 msec, peaking at approximately 400 msec after stimulus presentation. N400 has been shown to be sensitive to semantic deviations, with larger N400 amplitudes for semantically incongruent words compared to congruent words at both sentence and word processing levels (Kutas & Hillyard, 1980). In the repetition or semantic priming paradigms, N400 is reduced when target words are preceded by either semantically related primes or the same word (an N400 priming effect) (Matsumoto, Iidaka, Haneda, Okada, & Sadato, 2005; Van Petten, 1993). N400 is thought to reflect access to the lexical semantic representation of a word (Fischler & Raney, 1989; Van Petten & Kutas, 1987). In this study, the N400 priming effect was observed only in the repetition condition. If N400 reflects access to activated semantic representations, the lack of N400 priming effect in the homophone condition implies the absence of semantic preactivation in the homophone condition. In the homophone condition, semantic representations might not be activated by prime words, resulting in the absence of an N400 priming effect in this condition. If this is the case, it could in fact be argued that the GBR repetition suppression effect is a reflection of preactivation of phonological representations only.

Whether N400 does, indeed, reflect access to semantic representations is still controversial, as N400 is also highly sensitive to the use of strategic mechanisms, such as expectancy or semantic integration of a word (Matsumoto, Iidaka, Nomura, & Ohira, 2005; Kiefer, 2002; Brown & Hagoort, 1993). The N400 priming effect observed here was likely caused by these strategic components, as the presentation of prime words in the present study was not subliminal. Alternatively, the ERP difference at the 300–500 msec time window might have been generated by the delay of the peak of late positive component in the unprimed or homophone conditions, rather than by the N400 amplitude change. The issue of whether the GBR repetition suppression effect is due to preactivation of semantic representations or phonological representations should be clarified in future research by comparing homophone and semantic priming conditions.

Dehaene et al. (2001) conducted a functional magnetic resonance imaging study of repetition priming that was intended to identify the neural basis of unconscious word processing. They manipulated the relationship between prime and target word. In one condition, they presented prime and target words in the same case (car–car), and in another condition, the prime and target words differed according to case (car–CAR). These researchers found a case-specific repetition suppression effect that was mediated by the right extrastriate cortex, and a corresponding case-independent effect that was mediated by the left fusiform and precentral gyri. They hypothesized that the right extrastriate cortex is involved in feature-specific visual coding, whereas the left fusiform region processes letter strings at a shape-invariant level. The present study also manipulated prime–target relationships in a repetition priming paradigm and, in addition, attempted to identify their respective time courses.

Gamma band activity at around a 200–300 msec latency has been reported when participants perceive meaningful visual objects. This activity has been interpreted as a signature of the formation of visual object representations (Gruber & Muller, 2002, 2005; Gruber et al., 2004). In the present study of visual word presentations, repetition suppression on gamma band power and phase synchronization among electrodes were both observed within this time window only in the repetition priming condition. Accordingly, we infer that this early latency window reflects the time interval in which a visual representation is preactivated by a prime. We assume that orthographic representations are formed during this interval via integrative activity among different brain regions. On the other hand, both homophone and repetition priming produced suppression within a later time window (400–500 msec). As described above, previous studies have also reported gamma band activity within a relatively late time window (Krause et al., 1998; Pulvermuller et al., 1996). Taken together, the present findings and those of earlier studies suggest that the formation of phonological and semantic representations occurs during this later time window (400–500 msec). In addition, the present data also suggest that the time course for development of phonological/semantic representations is later than that required for the formation of orthographic word representations. Although we also observed a clear increase of gamma band power at the 300–400 msec time window, there were no significant differences in this activity as a function of condition. We suspect that gamma band activity within this time window reflects other cognitive processes, such as the processing of mask stimuli.

Finally, we should note one possible limitation of this study. The present results can be explained by the representation activation theory of induced gamma band activity, but the GBR might also reflect top–down access to the activated representations. Recent researchers emphasize the relationship between top–down processing and the concept of the oscillatory neuronal network (e.g., Engel, Fries, & Singer, 2001). If the top–down theory is correct, the reduction of GBR found here can be explained by the decrease of load in the top–down access to the representations, as well as reduced neuronal network activation. Priming reduces the load for the access of (or search for) activated representations. GBR reduction is a reflection of the load reduction for top–down access, and not the representation activation per se. The 400–500 msec time window does seem relatively late for activation of phonological representation, according to the theory that fast and obligatory phonological processing occurs in reading, although this theory is based mainly on languages with alphabetic script (e.g., Farrar, Van Orden, & Hamouz, 2001). According to this view, top–down access can explain reduced GBR at the 400–500 msec time window. Alternatively, the present data can be explained by assuming that repetition suppression is due to activation of semantic representations. These issues should be clarified in a future experiment.

In summary, our results implicate several important roles for gamma band activity in word processing. The repetition/homophone priming paradigm revealed that both the formation of visual orthographic representations and the more abstract phonological/semantic word representations rely on gamma band activity and phase synchronization among brain regions. This process may reflect the integrative activity of several brain regions, which appears to be an important factor in the formation of all types of cortical word representations. We also discovered different time courses for formation of these various types of representations. A visual or orthographic representation of a word is formed after about 200–300 msec following its presentation, whereas a phonological or a semantic representation appears to be formed after about 400–500 msec.

REFERENCES

Amano, S., & Kondo, T. (2000). *Lexical properties of Japanese*. Tokyo: NTT Database, Sanseido.

Brown, C. M., & Hagoort, P. (1993). The processing nature of the N400: Evidence from masked priming. *Journal of Cognitive Neuroscience, 5,* 34–44.

Caramazza, A., & Hillis, A. E. (1991). Lexical organization of nouns and verbs in the brain. *Nature, 349,* 788–790.

Coltheart, M., Rastle, K., Perry, C., Langdon, R., & Ziegler, J. (2001). DRC: A dual route cascaded model of visual word recognition and reading aloud. *Psychological Review, 108,* 204–256.

Dehaene, S., Naccache, L., Cohen, L., Bihan, D. L., Mangin, J. F., Poline, J. B., et al. (2001). Cerebral mechanisms of word masking and unconscious repetition priming. *Nature Neuroscience, 4,* 752–758.

Engel, A. K., Fries, P., & Singer, W. (2001). Dynamic predictions: Oscillations and synchrony in top–down processing. *Nature Reviews Neuroscience, 2,* 704–716.

Farrar, W. T., IV, Van Orden, G. C., & Hamouz, V. (2001). When SOFA primes TOUCH: Interdependence of spelling, sound, and meaning in "semantically mediated" phonological priming. *Memory & Cognition, 29,* 530–539.

Fiebach, C. J., Gruber, T., & Supp, G. G. (2005). Neuronal mechanisms of repetition priming in occipitotemporal cortex: Spatiotemporal evidence from functional magnetic resonance imaging and electroencephalography. *Journal of Neuroscience, 30,* 3414–3422.

Fischler, I., & Raney, G. E. (1989). Language by eye: Behavioral, autonomic and cortical approaches to reading. In J. R. Jennings & M. G. H. Coles (Eds.), *Handbook of cognitive psychology: Central and autonomic nervous system* (pp. 511–574). New York: Wiley.

Fujimaki, N., Miyauchi, S., Putz, B., Sasaki, Y., Takino, R., Sakai, K., et al. (1999). Functional magnetic resonance imaging of neural activity related to orthographic, phonological, and lexico-semantic judgments of visually presented characters and words. *Human Brain Mapping, 8,* 44–59.

Giesbrecht, B., Camblin, C. C., & Swaab, T. Y. (2004). Separable effects of semantic priming and imageability on word processing in human cortex. *Cerebral Cortex, 14,* 521–529.

Gruber, T., Malinowski, P., & Muller, 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., & Muller, 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., & Muller, 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.

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

Hill, H., Strube, M., Roesch-Ely, D., & Weisbrod, M. (2002). Automatic vs. controlled processes in semantic priming-differentiation by event-related potentials. *International Journal of Psychophysiology, 44,* 197–218.

Kiefer, M. (2002). The N400 is modulated by unconsciously perceived masked words: Further evidence for an automatic spreading activation account of N400 priming effects. *Cognitive Brain Research, 13,* 27–39.

Krause, C. M., Korpilahti, P., Porn, B., Jantti, J., & Lang, H. A. (1998). Automatic auditory word perception as measured by 40 Hz EEG responses. *Electroencephalography and Clinical Neurophysiology, 107,* 84–87.

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

Lachaux, J. P., Rodriguez, E., Martinerie, J., & Varela, F. J. (1999). Measuring phase synchrony in brain signals. *Human Brain Mapping, 8,* 194–208.

Matsumoto, A., Iidaka, T., Haneda, K., Okada, T., & Sadato, N. (2005). Linking semantic priming effect in functional MRI and event-related potentials. *Neuroimage, 24,* 624–634.

Matsumoto, A., Iidaka, T., Nomura, M., & Ohira, H. (2005). Dissociation of conscious and unconscious repetition priming effect on event-related potentials. *Neuropsychologia, 43,* 1168–1176.

Pollatsek, A., Tan, L. H., & Rayner, K. (2000). The role of phonological codes in integrating information across saccadic eye movements in Chinese character identification. *Journal of Experimental Psychology: Human Perception & Performance, 26,* 607–633.

Pulvermuller, F., Eulitz, C., Pantev, C., Mohr, B., Feige, B., Lutzenberger, W., et al. (1996). High-frequency cortical responses reflect lexical processing: An MEG study. *Electroencephalography and Clinical Neurophysiology, 98,* 76–85.

Rodriguez, E., George, N., Lachaux, J. P., Martinerie, J., Renault, B., & Varela, F. J. (1999). Perception's shadow: Long-distance synchronization of human brain activity. *Nature, 397,* 430–433.

Rueckl, J. G., & Mathew, S. (1999). Implicit memory for phonological processes in visual stem completion. *Memory & Cognition, 27,* 1–11.

Sakuma, N., Sasannuma, S., Tatsumi, I. F., & Masaki, S. (1999). Orthography and phonology in reading Japanese kanji words: Evidence from the semantic decision task with homophones. *Memory & Cognition, 26,* 75–87.

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

Spencer, K. M., Nestor, P. G., Niznikiewicz, M. A., Salisbury, D. F., Shenton, M. E., & McCarley, R. W. (2003). Abnormal neural synchrony in schizophrenia. *Journal of Neuroscience, 23,* 7407–7411.

Spitzer, M., Braun, U., Maier, S., Hermle, L., & Maher, B. A. (1993). Indirect semantic priming in schizophrenic patients. *Schizophrenia Research, 11,* 71–80.

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., Delpuech, C., & Pernier, J. (1996). Stimulus specificity of phase-locked and non-phase-locked 40 Hz visual responses in human. *Journal of Neuroscience, 16,* 4240–4249.

Tan, L. H., & Perfetti, C. A. (1997). Visual Chinese character recognition: Does phonological information mediate access to meaning? *Journal of Memory and Language, 37,* 41–57.

Van Petten, C. A. (1993). A comparison of lexical and sentence-level context effects in event-related potentials. *Cognitive Processes, 8,* 485–531.

Van Petten, C. A., & Kutas, M. (1987). Ambiguous words in context: An event-related potential analysis of the time course of meaning activation. *Journal of Memory and Language, 26,* 188–208.

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

Wiggs, C. L., & Martin, A. (1998). Properties and mechanisms of perceptual priming. *Current Opinion in Neurobiology, 8,* 227–233.

Xu, Y., Pollatsek, A., & Potter, M. C. (1999). The activation of phonology during silent Chinese word reading. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 25,* 838–857.

Zhou, X., & Marslen-Wilson, W. (1999). Phonology, orthography, and semantic activation in reading Chinese. *Journal of Memory and Language, 41,* 579–606.