Subliminal Semantic Priming Changes the Dynamic Causal Influence between the Left Frontal and Temporal Cortex

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Abstract

■ Recent neuroimaging experiments have revealed that subliminal priming of a target stimulus leads to the reduction of neural activity in specific regions concerned with processing the target. Such findings lead to questions about the degree to which the subliminal priming effect is based only on decreased activity in specific local brain regions, as opposed to the influence of neural mechanisms that regulate communication between brain regions. To address this question, this study recorded EEG during performance of a subliminal semantic priming task. We adopted an information-based approach that used independent component analysis and multivariate autoregressive modeling. Results indicated that subliminal semantic priming caused significant modulation of alpha band activity in the left inferior frontal cortex and modulation of gamma band activity in the left inferior temporal regions. The multivariate autoregressive approach confirmed significant increases in information flow from the inferior frontal cortex to inferior temporal regions in the early time window that was induced by subliminal priming. In the later time window, significant enhancement of bidirectional causal flow between these two regions underlying subliminal priming was observed. Results suggest that unconscious processing of words influences not only local activity of individual brain regions but also the dynamics of neural communication between those regions. ■

INTRODUCTION

In the 19th century, Sigmund Freud pointed out the importance of unconscious processes in understanding conscious thoughts and behaviors. Since then, numerous studies have investigated whether or not unconsciously perceived stimuli modulate cognitions and behaviors (Greenwald, Draine, & Abrams, 1996; Kunst-Wilson & Zajonc, 1980). Typically, in such research, an indirect measure is used to show that a stimulus does affect a behavior. The most commonly used indirect approach to studying unconscious processing has been subliminal priming. In this paradigm, a highly visible target stimulus is processed more efficiently, when the same or a semantically related stimulus precedes the target than when the target is preceded by an unrelated prime; all primes are conventionally masked. However, understanding the characteristics of the processes involved in subliminal masked priming remains an issue that has attracted the interest of many researchers.

Recent neuroimaging studies using fMRI have demonstrated that priming induces repetition suppression in various brain regions involved in the processing of target stimuli, particularly in the pFC and temporal cortex (Schacter & Buckner, 1998). Repetition suppression is indicated by reduced neural activity that appears to reflect increased efficiency in stimulus processing and/or improvement in the related decision processes (Henson & Rugg, 2003; Wiggs & Martin, 1998). Specifically, repetition suppression has been hypothesized to induce local neural changes that speed access to relevant object knowledge, thereby facilitating performance. Subliminal presentation of the same or related primes also appears to cause this reduction of neural activity in several brain regions (Dehaene et al., 2001; Naccache & Dehaene, 2001). Such findings suggest that subliminal priming induces efficient neural activity in the regions involved in the processing of target stimuli.

In addition to fMRI studies, electrophysiological recordings, such as EEG or MEG, have also revealed a decrease in specific EEG/MEG components caused by subliminal priming. Several studies have shown that the subliminal priming reduced the amplitude of the N400 component of the ERP (Kiefer & Brendel, 2006; Kiefer, 2002). Furthermore, masked priming has been shown to attenuate high-frequency EEG activity, such as gamma band activity (GBA; Matsumoto & Iidaka, 2008). The neural sources of these activities are not obvious, because of poor special resolution of electrophysiological recordings. However, reductions in electrophysiological indexes appear to correspond to repetition suppression observed in fMRI studies. Gold and Rastle (2007) reported that subliminal

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semantic priming induced the suppression of activity in the left middle temporal gyrus. Furthermore, Bick, Frost, and Goelman (2010) showed suppression in the left insula (with an increase of activities in several regions) caused by subliminal semantic priming. They proposed the hypothesis that reduced neural activities play an important role in the way unconscious processes access the representation of meaning in objects or words.

Recent theoretical and experimental studies have also demonstrated the importance of cortico-cortical interactions, particularly interactions between frontal and temporal or occipital regions (Bar et al., 2006; Bar, 2003) in priming effects. Gotts, Chow, and Martin (2012) proposed a theoretical framework for how enhanced synchrony might relate to priming. Therefore, an important and as yet unanswered question is whether facilitated performance observed in the subliminal priming paradigm is caused only by local changes of neural activity in a certain brain region or whether it is also significantly influenced by changes in the connections (interactions) between distinct local regions, such as the frontal cortex and, for example, the temporal cortex.

In this study, we investigated the role of the cortico-cortical interaction between the occipito-temporal and frontal regions when performing a subliminal semantic priming task. A previous study by Ghuman, Bar, Dobbins, and Schnyer (2008) using MEG has demonstrated the effects of repetition priming on dynamic changes in cortico-cortical interactions; however, no study to our knowledge has provided similar evidence during subliminal priming. Given that recent work has demonstrated the importance of cross-cortical interactions in various types of cognitive processing, we hypothesized that subliminal priming affects the dynamics of change in neural communication between distinct regions in the processing of target stimuli.

We measured neural activity by using high temporal resolution EEG in 22 participants, while they were engaged in a lexical decision task using target words primed by semantically related or unrelated words. The prime words were not identified consciously, because they were presented briefly and masked. To examine the neural activity and networks in the subliminal semantic priming task, we used independent component analysis (ICA) and the frequency domain multivariate autoregressive (MVAR) approach. ICA and ICA clustering analysis have been successfully applied to EEG data to separate mixed signals into temporally independent processes (Makeig et al., 2004; Makeig, Jung, Bell, Ghahremani, & Sejnowski, 1997), thus providing a more functionally relevant analysis of brain dynamics and reducing the spurious cross-cortical interaction originated by the volume conduction of source activity. With this method, we decomposed the scalp electrode EEG into clustered source-space IC activities and examined differences in their oscillatory activity, which was represented as event-related spectral perturbation (ERSP) across related and unrelated conditions.

The MVAR approach enables the determination of causal influences between two independent time series (Bressler & Seth, 2011). According to Granger (1969), at a given point in time, we can say that one stochastic process (Xt) is "causal" to a second stochastic process (Yt) if the autoregressive predictability of Yt is improved by the inclusion of past values of Xt. This method allows us to obtain a sequence of time-varying MVAR coefficient matrices. A time–frequency representation of the information flow can be obtained by computing one or more of the estimators for each coefficient matrix. We examined the change of time–frequency information flow between occipito-temporal and frontal regions, which showed changes of spectral alterations caused by subliminal semantic priming.

METHODS

Participants

Right-handed university students (n = 22, 10 women, age range = 19–27 years, mean age = 21.6 ± 0.8 years) received ¥1000 each for their participation. All participants had normal or corrected-to-normal visual acuity. All experimental procedures were carried out following the Helsinki Declaration. Written informed consent was obtained from each participant before the experiment started.

Materials

Stimuli consisted of 120 prime–target pairs that were either real nouns or pseudowords, consisting of three Japanese Kana script characters. The prime–target combinations included 40 unrelated pairs (e.g., leaf–car) and 40 semantically related pairs (e.g., lemon–orange) that corresponded to the two prime conditions: unrelated and related, respectively. In addition, we included 40 filler items composed of word–pseudoword pairs (e.g., picture–gerba). The semantic relatedness of each word pair and visual complexity, concreteness, familiarity, emotional valence of each prime and target word were investigated from another group of 10 participants by questionnaire. Each participant judged these characteristics of each word and word pair on 1 (*not related, very simple, quite abstract, not familiar, not emotional*) to 7 scale (*strongly related, very complex, quite concrete, very familiar, very emotional*). This indicated that the values of the above variables, with the exception of semantic relatedness, were not different across conditions (Table 1).

Procedure

The experiment involved two separate sessions. Each session consisted of 20 unrelated and 20 related word

Table 1. Mean Values and *SD* for the Characteristics of Semantic Relatedness, Visual Complexity, Concreteness, Familiarity, and the Emotional Valence of Primes and Targets in Each Condition

	Related	*Unrelated*	*t Test*
Target familiarity	5.97 (0.23)	5.98 (0.17)	$t(78) = 0.10$, *ns*
Target concreteness	5.52 (0.2)	5.58 (0.28)	$t(78) = 0.53$, *ns*
Target emotional valence	1.34 (0.23)	1.48 (0.25)	$t(78) = 1.24$, *ns*
Prime familiarity	5.77 (0.29)	5.59 (0.35)	$t(78) = 1.32$, *ns*
Prime concreteness	5.58 (0.38)	5.49 (0.24)	$t(78) = 0.71$, *ns*
Prime emotional valence	1.32 (0.18)	1.24 (0.08)	$t(78) = 0.98$, *ns*
Semantic relatedness	4.23 (0.14)	1.23 (0.08)	$t(78) = 40.05$, $p < .001$

pairs, along with 20 word–nonword pairs. All pairs were presented to participants in a random order. Following a 300-msec first masking period, each prime word was presented for 20 msec between pre- and postprime masking stimuli (30 msec). Immediately following the second mask, the target word was exposed for 2000 msec. After the presentation of a target word, three words including the prime word were presented on the monitor. These three words allowed us to determine whether the prime was perceived subliminally or not (see below). An intertrial interval of 2500 msec was used. Participants were instructed to decide whether the target word was a real word or a pseudoword by pressing the corresponding button. After responding to the target word, participants conducted a forced-choice task for the prime word by choosing from the three words presented on the monitor (visibility test for the prime word). Participants' responses and RTs for target words were recorded. The stimulus was presented on a CRT monitor with a refresh rate of 100 Hz, which was controlled by Presentation software (NeuroBehavioral Systems, Inc., Albany, CA). Vertical and horizontal visual angles of words were 1° and 4°, respectively. The stimuli were presented on a gray background (50 cd/m^2).

The trial scheme is illustrated in Figure 1.

EEG Recording and Analysis

EEG was recorded with the Nihon Koden EEG 1100 (Tokyo, Japan) 33-channel EEG recording unit. EEG signals were recorded with a 120-Hz low-pass filter (12 dB/oct). The sampling rate was 500 Hz and was later downsampled to 250 Hz. The resolution of A/D conversion was 16 bit. Ag/AgCl electrodes were placed on 33 scalp sites according to the international 10–10 system. All electrode impedance was kept below 10 kΩ and typically below 5 kΩ. EEG electrodes were referenced to the nose tip. EEG data analysis was performed using EEGLAB 9.0 (Delorme & Makeig, 2004; www.sccn.ucsd.edu/eeglab) running under Matlab R2010 (MathWorks, Natick, MA). A high-pass FIR filter of 1 Hz (transient bandwidth 0.2 Hz) was applied to continuous EEG data to remove linear trends and to stabilize the results of subsequent ICA. EEG data were segmented into epochs starting 1100 msec

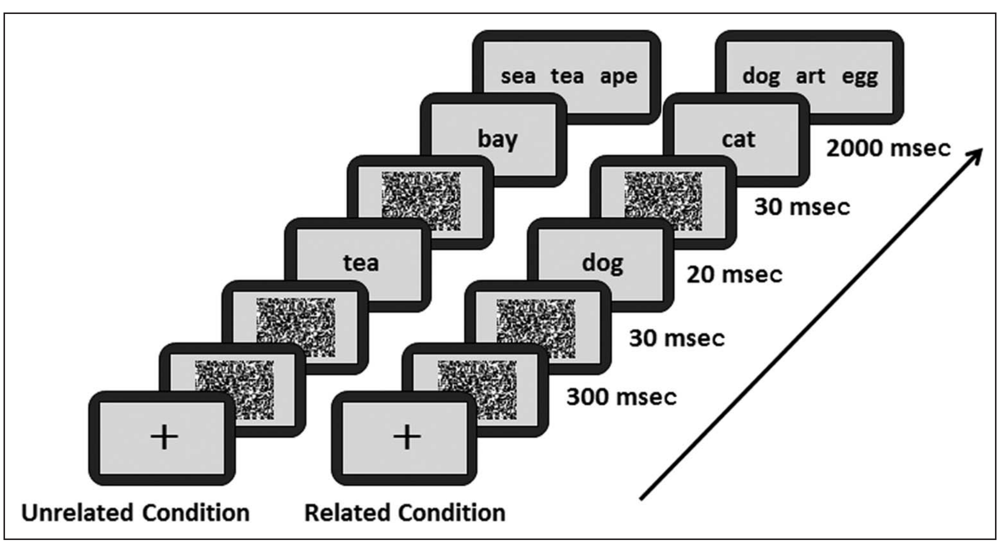


Figure 1. Task scheme: Participants judged whether or not the target word is a real word. In the Unrelated condition, a semantically unrelated word was presented as a prime word. In the Related condition, the prime word was semantically related to the target word. After the lexical decision, participants performed a forced-choice task in which they identified the prime word from three words presented on the monitor.

before and ending 1500 msec after the onset of target words. This relatively long segment epoch was needed to exclude edge effects in wavelet analysis from the critical time window. All epochs were visually inspected to discard trials with irregular noise. The extended Infomax ICA with natural gradient (implemented in EEGLAB) was performed to obtain 33 independent components from each of the 22 participants. We collapsed over experimental conditions when deriving the independent components, so that we could test for condition-specific differences within components (or their clusters). Visual inspection was performed on the data and trials, rather than components, which contained large noise contaminating across plural independent components were discarded. A second ICA was run on pruned data, and an identical rejection procedure was run a second time. The ICA was performed again to obtain the final decomposition. Multiple applications of ICA were conducted to facilitate precise data decomposition. For each IC, an ECD was estimated using DIPFIT 2.2 using the head model with the Montreal Neurological Institute (MNI) standard coordinate system. The purpose of this procedure was mainly to exclude the bad components that were unlikely to have originated from brain regions. Of 726 (22 data sets × 33 ICs) dipoles, according to Miyakoshi, Kanayama, Iidaka, and Ohira (2010), 81 were rejected because of residual variance >30%. Scalp topography, averaged ERSP, was calculated for each IC. For ERSP calculation, the Morlet wavelet was used. Linearly spaced, 100 frequencies ranging from 1 to 120 Hz were calculated every 4 msec starting from 700 msec prior to and ending up to 1300 msec following stimulus (target word) onset. The baseline was set as −700 to −400 msec of target word onset (from −370 to −70 msec of first mask stimuli onset). Wavelet length in cycles was linearly increased with frequencies of 1 at 1 Hz and 20 at 120 Hz (increasing by 0.167 cycles every Hz). This procedure enabled us to obtain a good temporal resolution at lower-frequency bands and a good frequency resolution at higher-frequency bands. The baseline length (300 msec) was sufficient at frequency bands of over 2 Hz in this wavelet cycle. ICA linearly decomposed each participant's EEG data into 33 maximally independent components, each characterized by a different, fixed scalp map, showing the spatial projection of the component to each scalp channel and the time course of activation in each trial. To determine the independent components that were common across participants, we performed cluster analysis on the component maps, ERP, and spectral power. IC clustering was performed using *k*-means with the criteria of scalp topography (normalization weight, 5), ERP (normalization weight, 3), and spectral power (normalization weight, 3) to generate 20 IC clusters. The weights were decided in reference to Makeig et al. (2004) and Miyakoshi et al. (2010). The number of IC clusters was the smallest value, such that all clusters had different characteristics of scalp topography. Cluster membership was then further adjusted by eye for uniformity. Five components that showed EMG characteristics (e.g., constant high, 20–30 Hz activity) gathered in the temporal and frontal areas were removed from these clusters. The IC clusters were visually inspected to determine their physiological significance. We distinguished clusters that represented brain activity from biological noise, such as EMG, eye movements, or blinking. EMG clusters have a high, 20–30 Hz activity and are distributed in the temporal regions. Eye movement clusters were located in the far frontal regions. In the statistical analysis, when plural components from a participant were entered into a cluster, those components were averaged and treated as the data of the participants. A schematic diagram of the data analysis conducted in this study is shown in Figure 2.

When performing statistical tests on ERSP, mass univariate analysis using cluster level permutation tests (Groppe, Urbach, & Kutas, 2011) for comparing mean values of time–frequency windows of related and unrelated conditions were performed. At first, t scores between conditions were computed for every time–frequency point in all clusters. All t scores that did not exceed threshold ($p < .05$) were ignored. Of the remaining t scores, all t scores without a sufficient number (40) of adjacent above threshold t scores were ignored. Through this method, we identified two time–frequency clusters in the two IC clusters. The MNI coordinates for the centroid of the dipole clusters were (−35, 31, 8) and (−49, −44, −11), which falls within the inferior frontal cortex (IFC) and inferior temporal (IT) cortex. The t scores of each cluster were summed, and the statistical significance of each cluster was tested by permutation test. p Values were controlled by Bonfferoni correction. We will refer to the IC cluster as IFC and IT according to the locations of the centroid. We localized their probable source in MNI template MR image using low-resolution brain electromagnetic tomography (LORETA; Pascual-Marqui, Michel, & Lehmann, 1994).

To measure directional influences between the left IT and left inferior frontal gyrus (IFG), we employed

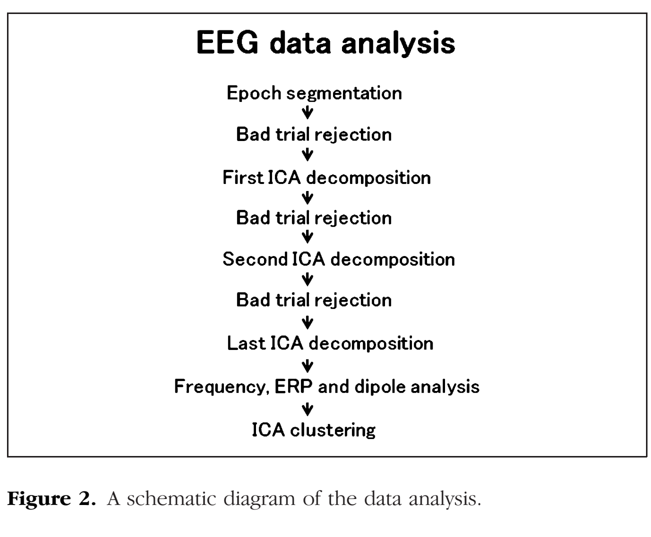
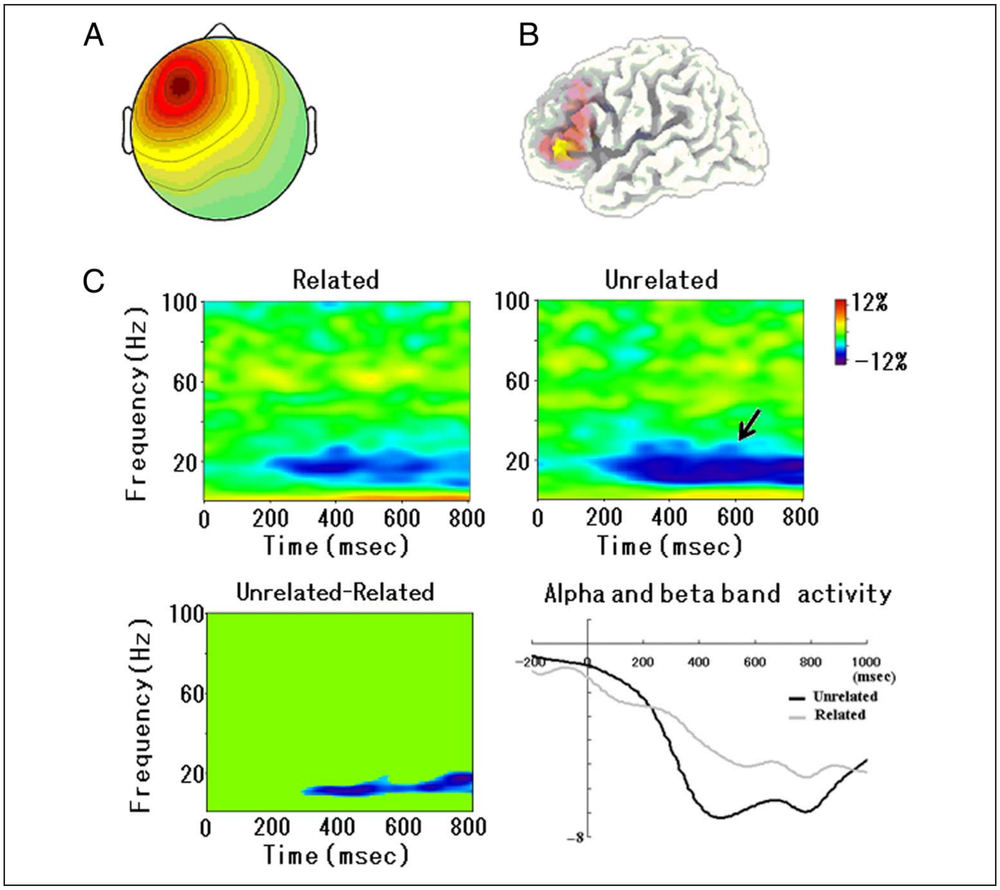


Figure 2. A schematic diagram of the data analysis.

Figure 3. (A) The mean topography of the components included in IFC cluster. (B) 3-D distribution of a probable component source activity under LORETA decomposition. (C) ERSP and the alpha and beta band activity of this IC cluster. Alpha and beta desynchronization is significantly attenuated by the subliminal priming, indicating that neural activity of this region is reduced by the priming.



MVAR analysis using the Source Information Flow Toolbox (sccn.ucsd.edu/wiki/SIFT). As a preprocessing step in our analysis, we subtracted the ensemble mean from each trial in every IC activities and divided by the standard deviation. In this way, the first-order nonstationarity was removed from the data, and the ensemble of single-trial time series could be considered a stochastic process with zero-mean, as required for the autoregressive modeling method (Gregoriou, Gotts, Zhou, & Desimone, 2009). To test the temporal evolution of the directional influences, we conducted an analysis in successive windows of 500 msec, which were advanced every 12 msec. Using short time windows with high overlap, we could consider the underlying stochastic processes to be locally stationary. For each window segment and for each pair of IC activities, the parameters of the AR model were estimated using the Vieira-Morf algorithm. The model order for each participant was determined based on the Akaike information criteria and Schwarz Bayesian criterion. For the examination of causal influences, we used direct directed transfer function (Korzeniewska, Manczak, Kaminski, Blinowska, & Kasicki, 2003) to measure linear-spaced 100 frequencies ranging from 1 to 100 Hz. In this study, we obtained 23 ICs from 18 participants for the IFC and 22 ICs from 19 participants for the IT cluster. Eighteen participants had components in both the IFC and IT clusters. To perform causality analysis, two ICs of IFC and IT were selected from the same participant. Almost all (15) participants had only one component in each cluster. If a participant had several components in a cluster, we chose a component that made the largest contribution to the data variance in the causality analysis. For statistical analysis of the data, mass univariate analysis was conducted.

RESULTS

Behavioral Data

Participant's hit rates for lexical decisions were generally high (91.7%), and the hit rates were not significantly different between the conditions [90.9% vs. 92%, $t(21) = 1.21$, *ns*]. Only the correct trials in lexical decision task were used for RT analysis. The average RT for lexical decisions in the Related condition (702 msec, $SD = 146$ msec) was significantly shorter than that for comparable responses in the Unrelated condition [715 msec, $SD = 152$ msec; $t(21) = 3.13$, $p < .01$]. This indicated that prime words that were semantically related to target words promoted processing of the targets. The hit rates for the visibility test (34.2%, $SD = 6.4\%$) were not significantly different from chance [33%; $t(21) = 0.65$, $p > .50$], indicating that the prime words were not consciously identified. Furthermore, we reanalyzed the RT data of trials in which participants did not correctly respond to the visibility test. Results of this analysis also indicated that RT in the Related condition (705 msec, *SD* = 142 msec) was significantly shorter than that in the Unrelated condition [713 msec, *SD* = 149 msec; $t(21) = 3.02$, $p < .01$]. The semantic priming effect in trials in which participants correctly responded to the visibility test was also significant [$t(21) = 3.51$, $p < .01$].

EEG Results

Although almost all IC clusters showed no significant priming effect, subliminal semantic priming modulated the activities of two IC clusters. The centroid of dipoles in these clusters fell within the left IFC and left IT cortex. For the left IFG cluster, 23 ICs were contributed from 18 participants. In this cluster, the power of alpha and beta frequencies within the 300–800 msec time window was significantly modulated by semantic priming. The alpha and beta band (8–20 Hz) activity of this cluster was significantly larger for the Related condition than for the Unrelated condition (permutation test, $p < .01$), indicating that alpha suppression was significantly greater in the Unrelated than the Related condition. There was no significant difference in ERP activity in this cluster. Figure 3 represents the topography, probable source estimated by LORETA software and the alpha and beta band activity of this cluster. Furthermore, because the Morlet wavelet is mathematically unstable for widths under 5 without correcting for nonzero mean, we reanalyzed the data using stable wavelet (five cycles) to examine the validity of the results of alpha band activity. Results indicated a significant difference between the conditions for alpha and beta band activity (permutation test, $p < .01$) in the left frontal cluster. In the left IT cluster, which consists of 22 ICs from 19 participants, we observed a significant repetition suppression effect in the GBA (40–70 Hz). The GBA was significantly larger in the Unrelated condition than in the Related condition within the 200–400 msec time window following target onset (permutation test, $p < .05$). Similar to the left IFG cluster, there was no significant difference in ERP activity of this cluster. The topography, probable source as estimated by LORETA software, and the GBA of this cluster are displayed in Figure 4.

The MVAR analysis was conducted to evaluate the relative strength of influence between two IC clusters in both directions, that is, IFC to IT and the reverse direction. As a result, top–down processing (IFC → IT) of theta band

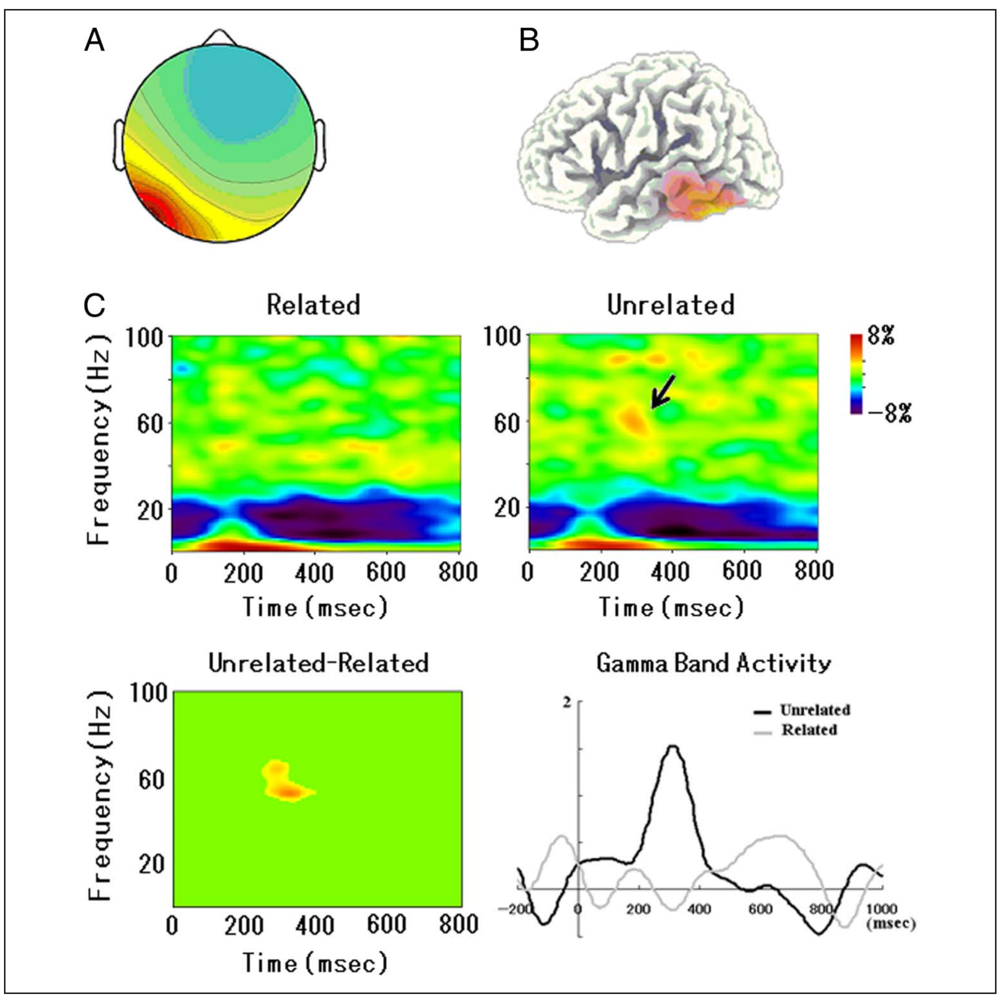


Figure 4. (A) The mean topography of the components included in IT cluster. (B) 3-D distribution of a probable component source activity under LORETA decomposition. (C) ERSP and the GBA of this IC cluster. Gamma band synchronization (in 200–400 msec window) is significantly attenuated by subliminal priming, indicating that neural activity in this region is reduced by the priming.

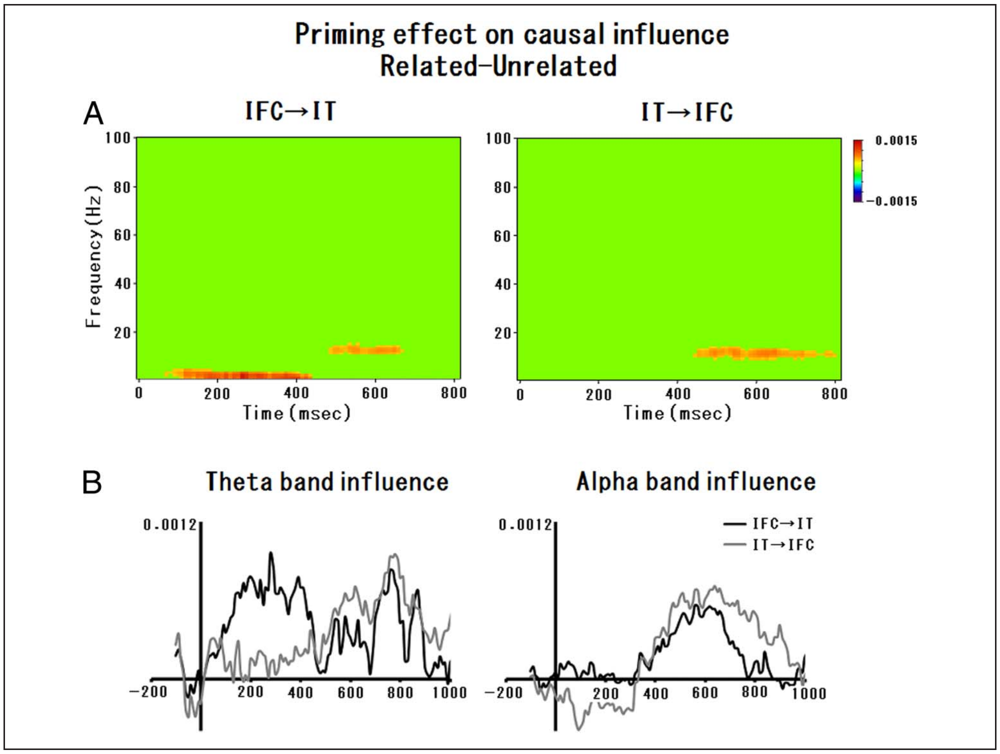


Figure 5. (A) Time–frequency plot of differences in the causal influence between the Related and the Unrelated condition. These plots indicate significant differences between the conditions. (B) Time course of causality value difference (Related vs. Unrelated) for theta and alpha band activity. In the theta frequency band, greater causality value from the IFC to the IT was observed at the earlier time window (200–400 msec) in the Related, compared with the Unrelated condition. In alpha band activity, enhancement of causality value at the later time window (400–800 msec) was bidirectional.

activity (2–7 Hz) identified a significant difference in the causality value between conditions within the 200–400 msec time window. In this window, the causal influence was unidirectional in that the causal value directed from IFC to IT was significantly larger in the Related condition than in the Unrelated condition (permutation test, $p < .01$). However, in the 400–800 msec time window, the causal influence value of alpha band activity was bidirectional, in that subliminal priming was enhanced in both directions. That is, both when a causal flow was directed from IFC to IT (permutation test, $p < .05$) and when it was directed in the reverse direction, that is, from IT to IFC (permutation test, $p < .01$), we found the causal influence value to be significantly greater in the Related condition compared with the Unrelated condition. The differences of causal influence value between the two conditions are displayed in Figure 5.

DISCUSSION

We examined electrophysiological responses of brain regions to clarify interregional connectivity between specific brain regions in response to subliminal semantic priming. We observed a significant semantic priming effect, indicating that subliminally presented prime words changed the semantic processing of target words. We applied the ICA and ICA clustering techniques to the electrophysiological data to identify and maximally isolate independent brain processes. The resulting two IC clusters (left IT and IFC) showed a significant modulation of activities that resulted from unconscious semantic priming, indicating that these clusters were involved in unconscious, semantic, or lexical processing of words. Moreover, we identified modulations of the information flow between these two brain regions. Furthermore, the modulation of causal influence differed for different time windows. At the early time window, the enhancement of a unidirectional causal influence was observed, which was suggestive of top–down (IFC → IT) causality, whereas in the later time window, the enhancement caused by subliminal priming was bidirectional, which is suggestive of both bottom–up and top–down effects.

A number of neuroimaging studies have revealed the important contribution of the IT and IFC of the left hemisphere in the semantic processing of words (Lau, Phillips, & Poeppel, 2008). For example, the performance of semantic decision tasks and semantic generation tasks is consistently associated with robust activation in IFC (Pugh et al., 1996; Price et al., 1994). It is hypothesized that the left IFC mediates controlled semantic retrieval or semantic working memory processes (Lau et al., 2008). Furthermore, it is evident that subliminal presentation of words evokes IFC activity, confirming the involvement of this region in the unconscious processing of words (Diaz & McCarthy, 2007). We also observed a significant modulation of alpha and beta band activity caused by unconscious semantic priming. A number of previous EEG studies have found that alpha band activity reflects neuronal inhibitory processing and that the enhancement of neuronal activity is indexed by a decrease of power in the alpha band, known as alpha-desynchronization (Pfurtscheller, 2001; Pfurtscheller

& Aranibar, 1977). Several studies have also reported that alpha-desyncronization was attenuated by repetition priming. Alpha-desynchronization for visual processing was observed not only in occipital regions but, in the case of semantic processing, also in the pFC (Klimesch, Doppelmayr, Pachinger, & Russegger, 1997). The decrease of alpha-desynchronization in the Related condition is suggestive of reduced neuronal activity caused by unconscious semantic priming. It has been reported that semantic priming reduces LIFC activity (Gold et al., 2006; Matsumoto, Iidaka, Haneda, Okada, & Sadato, 2005). Given the involvement of the LIFC in the control of semantic or lexical information, the reduced activity of the LIFG observed in this study might reflect a decrease in cognitive effort associated with the evaluation and/or decision-making related to words induced by unconscious semantic priming. The recent finding that alpha band activity is a signature of access to stored information (Klimesch, 2012) is also compatible with the above interpretation.

We did not find a significant semantic priming effect for lower-frequency bands (delta and theta band) activity. This might be because of the characteristics of the wavelet used in this study. It is difficult to obtain data having sufficient temporal resolution at lower-frequency bands; therefore, we used wavelets having low cycles to obtain good temporal resolution at lower-frequency bands. However, the Morlet wavelet is mathematically unstable for widths under 5, and as a result, priming effect at lower-frequency bands might have superficially disappeared. It is suggested that the priming effect at lower frequencies should be examined in detail in future studies.

The left IT region, including the fusiform gyrus, has been considered to be a key region associated with the processing of lexical information. Functional MRI studies using semantic tasks, such as semantic categorization, or judgment of semantic properties of words, frequently result in activity in the left IT region (Price, Winterburn, Giraud, Moore, & Noppeney, 2003; Buchel, Price, & Friston, 1998). Several studies have reported observing semantic priming effects in this region, such as reduced activity in the Related condition compared with the Unrelated condition (Gold et al., 2006; Wheatley, Weisberg, Beauchamp, & Martin, 2005). Interestingly, semantic priming effects have also been observed in this region, when the SOA between the prime and the target word was relatively short, indicating that this region was sensitive to automatic semantic priming effects, rather than to controlled conscious effects. As described in the Introduction, fMRI studies of subliminal semantic priming have shown a significant suppression in the left temporal region. These findings suggest that this region might be involved in the storage of lexical or semantic representation of words.

The present results show that unconscious semantic priming significantly attenuated the GBA in this region. This result is compatible with previous reports that semantic priming (picture–word priming or visual–audio priming) attenuated the GBA in the left temporal region (Friese, Supp, Hipp, Engel, & Gruber, 2012; Travis et al., in press). Human EEG studies have shown that induced power of GBA is enhanced in cases where representations are formed in response to stimuli that are presented (Tallon-Baudry & Bertrand, 1999). According to the sharpening model of neurons (Wiggs & Martin, 1998), a reduction in GBA implies that subliminal semantic priming causes more efficient formation of semantic representations. Given that the GBA is correlated with the BOLD effect (Niessing et al., 2005), this interpretation is quite consistent with the findings of fMRI studies.

The important and novel finding of this study concerns enhanced neural communication, accompanied by reduced local activity between the IFC and IT. Previous findings gave rise to hypotheses regarding neural mechanisms that are related to the reduction of neural responses in subliminal priming in terms of processing efficiency enhanced by local changes in neural bundles. Our results bring a new insight to this topic by demonstrating that subliminal priming results in more efficient transmission of information at the neural network level, as well as reduced computational demands at the level of local neuronal assemblies, which in turn, facilitate behavior. This view is in line with recent studies investigating the cortico-cortical interaction during normal (supraliminal) priming tasks (Kujala, Vartiainen, Laaksonen, & Salmelin, 2012; Ghuman et al., 2008). However, the enhanced cortico-cortical interaction reported in previous priming studies could be because of explicit memory or working memory processes. That is, given the task constraints of these studies, it was possible that participants consciously retrieved the prime stimuli and compared them with test stimuli. The latter processes possible require an interaction between various brain regions; therefore, it was difficult to conclude from such prior research that the efficiency of the cortico-cortical network was induced only by the priming effect. The present design rules out such a possibility, because we used a subliminal priming paradigm, and therefore, participants could not consciously use the information in the prime words for the task. Consequently, the present results provide stronger evidence for the relationship between enhanced cortico-cortical networks and the priming effect.

An enhanced cortico-cortical interaction was observed in the theta frequency and the alpha band. Previous studies have revealed that these frequency band activities play an important role in the formation of neural networks in various brain regions (Benchenane, Tiesinga, & Battaglia, 2011; Colgin, 2011; Freunberger, Klimesch, Griesmayr, Sauseng, & Gruber, 2008; Klimesch, Sauseng, & Hanslmayr, 2007). Recent studies have also confirmed that supraliminal semantic priming enhances the theta band activity and intertrial coherency in language regions, indicating that semantic priming has an effect on the synchronized activity between distinct regions (Salisbury & Taylor, 2012). The results of the MVAR analysis suggest that the unconscious priming effect is accomplished through the influence that flows from the IFC to the IT region. The hypothesis that subliminal priming depends heavily on feedback from pFC processing is supported by MEG findings demonstrating that the activity of pFC for processing words is very fast, being in the region of <130 msec (Cornelissen et al., 2009; Bar et al., 2006) and that repetition-induced neural response changes generally occur earlier in pFC than in the temporal cortex regions (Marinkovic et al., 2003). Furthermore, previous priming studies have reported an enhanced top–down influence from higher regions to IT regions (Ghuman et al., 2008). Given that this modulation was observed within a relatively early time window in this study is suggestive that the enhancement of a top–down influence might be related to efficient access to the semantic representation of words. Prior unconscious exposure to a word may activate a system in the pFC accessing lexical information. This preactivated system could subsequently be used to access lexical information regarding the target word within the temporal cortex, if the activated systems were (semantically) related.

Combining this top–down effect with the bottom–up systematic analysis facilitates the recognition of a target word. This interpretation is in line with the view of Bar et al. (2006) that the early interaction between pFC and temporal cortex plays an important role in object recognition. As opposed to the early modulation of causal influence from theta band activity, a subliminal priming effect on the causal influence of alpha band activity was observed for a relatively slow time window, which was bidirectional. Possibly, the enhancement of bidirectional information flow reflects fluent evaluation, or the selection of semantic information. Efficient interactions between the frontal and temporal cortices could lead to faster evaluation, or selection of semantic or lexical information. We speculate that the observed enhancement of information flow between the IFC and IT reduces the computational demands for the lexical decision task in these two regions, thereby attenuating activations in local regions. However, this study did not identify the directional relationship between the reduced local activity and the enhanced interaction. Therefore, it is suggested that future studies should be designed to examine the "causal" relationship between these two phenomena.

Our results indicated that subliminally presented words could unconsciously change not only the activity of local regions but also the neural communication between the regions. These results emphasize the critical role of the dynamics of interactions across large-scale brain networks in the unconscious processing of various aspects of information.

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