

Language comprehension dependent on emotional context: A magnetoencephalography study

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ABSTRACT

In communication, language can be interpreted differently depending upon the emotional context. To clarify the effect of emotional context on language processing, we performed experiments using a cross-modal priming paradigm with an auditorily presented prime and a visually presented target. The primes were the names of people that were spoken with a happy, sad, or neutral intonation; the targets were interrogative one-word sentences with emotionally neutral content. Using magnetoencephalography, we measured neural activities during silent reading of the targets presented in a happy, sad, or neutral context. We identified two conditional differences: the happy and sad conditions produced less activity than the neutral condition in the right posterior inferior and middle frontal cortices in the latency window from 300 to 400 ms; the happy and neutral conditions produced greater activity than the sad condition in the left posterior inferior frontal cortex in the latency window from 400 to 500 ms. These results suggest that the use of emotional context stored in the right frontal cortex starts at ~300 ms, that integration of linguistic information with emotional context starts at ~400 ms in the left frontal cortex, and that language comprehension dependent on emotional context is achieved by ~500 ms.

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1. Introduction

In communication, language can be interpreted differently depending upon the context, as determined by different types of linguistic and paralinguistic information. For example, the same sentence may be interpreted differently depending on the emotional context, which is often derived from prosody, i.e., whether words are spoken in a happy, sad, or angry tone. Language comprehension that is dependent on the emotional context plays an important role in the establishment of smooth communication and good personal relationships.

It is well known that the right hemisphere damage impairs comprehension of emotional content conveyed by prosody, a condition referred to as “aprosodia” (Heilman et al., 1975; Tucker et al., 1977; Ross and Rush, 1981; Tompkins and Flowers, 1985; Bowers et al., 1987; Borod et al., 1990; Cancelliere and Kertesz, 1990; Blonder et al., 1991; Van Lancker and Sidtis, 1992; Starkstein et al., 1994). The right hemisphere has therefore been proposed to be special-

ized for emotional comprehension; however, recent neuroimaging studies have demonstrated widely distributed involvement in both hemispheres and subcortical structures (Schirmer and Kotz, 2006), indicating that the functional aspects of emotional comprehension are region dependent. Activity in the right frontal (Buchanan et al., 2000; Wildgruber et al., 2005, 2006) and temporal areas (Beaucousin et al., 2007) has been observed during emotion detection using prosodic features, whereas activity in the left frontal and temporal areas appears to reflect emotional semantic content (Beaucousin et al., 2007).

On the other hand, numerous lesion and neuroimaging studies have provided evidence that linguistic semantic processing recruits the left frontotemporal areas (Price, 2000; Bookheimer, 2002), suggesting that the anterior temporal cortex is involved in bottom-up or automatic processing (Marinkovic et al., 2003; Fujimaki et al., 2009) and that the inferior frontal cortex is involved in top-down or controlled processing (Thompson-Schill et al., 1999; Cardillo et al., 2004; Badre et al., 2005; Gold et al., 2006; Ihara et al., 2007; Wei et al., 2007). How then does emotional context affect the way we interpret language? In order to answer this question, it is necessary to examine the top-down processing dependent on emotional context and the integration between linguistic and paralinguistic

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emotional information in the brain. To date, however, few studies have focused on these aspects.

The objective of the present study was therefore to clarify the effect of emotional context on language processing. We performed experiments using a cross-modal priming paradigm with an auditorily presented prime and a visually presented target. The primes we used were the names of people, e.g., “Mr. Aoki,” which were spoken with happy, neutral, or sad intonation; the targets were interrogative one-word sentences, which consisted of a verb, e.g., “walk?,” having emotionally neutral content. The reason for presenting the targets visually and not auditorily was that the subjects were made to read the words influenced only by the emotional context derived from the preceding prime. It was expected that interpretation of the targets would vary depending on the emotional context. For example, “walk?” in a happy context might be felt as a pleasant offer, whereas “walk?” in a sad context might be construed as an unattractive proposition, even though the prelexical and lexical (i.e., orthographical, phonological, and semantic) properties of the target are the same in both happy and sad contexts. Using magnetoencephalography (MEG), we measured the neural activities during silent reading of the targets presented in an emotional context.

2. Methods

2.1. Subjects

Ten native speakers of Japanese (6 males and 4 females, 21–56 years old) participated in the present study. All were right-handed (mean laterality quotient = +94.1) as confirmed by the Edinburgh Handedness Inventory (Oldfield, 1971). They had normal or corrected-to-normal vision, and had no history of neurological or psychiatric disease. The study was approved in advance by the Ethics Committee for Human and Animal Research of the National Institute of Information and Communications Technology, Japan. Informed consent to participate in the study was obtained from all subjects.

2.2. Stimuli and conditions

A cross-modal priming paradigm with auditorily presented primes and visually presented targets was applied (Table 1). The primes were 120 Japanese popular names with five morae, e.g., “Aoki-san” (English translation: “Mr./Ms. Aoki”) that were spoken by a trained female speaker with happy, neutral, or sad intonation and which were selected using the following procedure. In a previous study, we recorded 145 names spoken by the trained speaker and performed a preliminary investigation as follows: 23 participants (10 males and 13 females, 20–34 years old) evaluated the emotional impression of the sound of a name on a 7-grade

scale ranging from –3 to 3 (–3 being the saddest grade, 3 being the happiest grade, and 0 being neutral) (Yagura et al., 2006). On the basis of the results, we selected the 30 most positive-sounding names that were graded closest to 3 on the scale [mean \pm standard deviation (SD), 1.8 ± 0.2] for the Happy condition, the 30 names graded closest to 0 (-0.1 ± 0.1) for the Neutral condition, and the 30 most negative-sounding names (-1.6 ± 0.3) for the Sad condition. In addition, 30 out of the remaining 55 names were randomly selected for the Pseudo condition as described below.

The targets consisted of a Japanese verb, e.g., “歩く /aruku/” (English translation: “walk?”) or a pseudo-verb, e.g., “風ぶ /kazebu/” (pronounceable but not comprehensible: the Pseudo condition). They were written in one morphogram (kanji) and one syllabogram (kana) and pronounced with three morae. We informed the subjects that the target was to be presented as the sequel of the prime; i.e., the prime and the following target consisted of one comprehensible or incomprehensible interrogative sentence. We performed a preliminary investigation as follows: 20 participants (15 males and 5 females, 26–58 years old) evaluated the emotional impression of the verbs on a 5-grade scale ranging from –2 to 2 (–2 being the strongly negative, 0 being neutral and 2 being the strongly positive). Ninety verbs with emotionally neutral content (emotional impression value: 0.2 ± 0.2) were selected: Verbs with emotional content, such as “laugh,” “enjoy,” “cry,” and “regret,” were excluded. The targets had high familiarity values of 6.1 ± 0.3 on a 7-grade scale calculated on the basis of the database of lexical properties of Japanese (Amano and Kondo, 1999). The 90 verbs were used commonly in the three conditions.

2.3. Procedure

The prime and target were presented with a stimulus onset asynchrony of 1500 ms (Fig. 1). The primes [761 ± 125 -ms (mean \pm SD) duration] were presented binaurally via nonmagnetic ear tubes at ~ 75 dB, and then the targets (300-ms duration) were projected on a gray screen centered in front of the subject. Subjects were instructed to read the target words silently as the sequel of the prime voices while gazing at the fixation point, and to judge whether the targets included a verb or pseudo-verb. The fixation point became larger 1500 ms after the onset of target word presentation, which was the cue for subjects to press a button with their index finger for “verb,” or to press another button with their middle finger for “pseudo-verb.” To avoid any effect of motor preparation on the response in either hemisphere, we divided the subjects into two groups: half of the subjects were instructed to use their right hand, and the other half were instructed to use their left hand. The prime in the next trial was randomly presented 2000–2500 ms after the cue for the button press. The height of each target subtended a visual angle of 1° , the length of each word subtended a visual angle

Table 1
Experimental conditions and stimuli.

Condition	Prime			Target	
	Auditory stimulus	Prosody	Example “English translation”	Visual stimulus	Example “English translation”
Happy	Name	Happy	Aoki-san “Mr./Ms. Aoki”	Verb + “?”	歩く /aruku/? “walk?”
Neutral	Name	Neutral	Asano-san “Mr./Ms. Asano”	Verb + “?”	歩く /aruku/? “walk?”
Sad	Name	Sad	Araki-san “Mr./Ms. Araki”	Verb + “?”	歩く /aruku/? “walk?”
Pseudo	Name	Happy/ Neutral/ Sad	Akita-san “Mr./Ms. Akita”	Pseudo-verb + “?”	風ぶ /kazebu/? -meaningless-

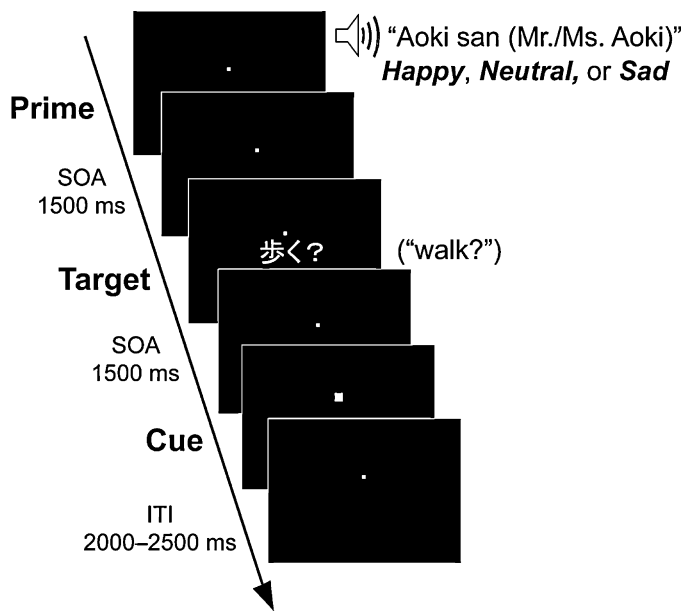


Fig. 1. Schematic representation of the stimulus sequence. The auditory prime and visual target were presented at a stimulus onset asynchrony (SOA) of 1500 ms, and the cue for subjects to press the buttons for lexical judgment was presented 1500 ms after the onset of the target. The intertrial interval (ITI) between the onset of the cue and the next prime was randomly set at 2000–2500 ms.

of 4° , and each target was displayed 0.1° below the fixation point. The luminance of the stimuli and their background were respectively 120 and 2 cd/m^2 . An experimental session was divided into six blocks, each consisting of 60 stimulus pairs, and each word pair in the four experimental conditions was delivered in a pseudorandom order. The subjects were allowed to rest for a few minutes after each block.

2.4. Data acquisition

Neuromagnetic signals were recorded with a 148-channel whole-head system (Magnet 2500WH; 4-D Neuroimaging, San Diego, CA) in a magnetically shielded room. MEG signals in a frequency bandwidth from 0.1 to 200 Hz were sampled at 678 Hz and recorded continuously throughout the experiments. Magnetic resonance imaging (MRI) was performed using a 1.5-T scanner (Magnetom Vision; Siemens A.G., Erlangen, Germany). Whole-brain T1-weighted coronal, axial, and sagittal MR images with a contiguous 1.0-mm slice thickness were used for overlay for the equivalent current dipole sources calculated from the MEG data. In the MRI acquisition, three high-contrast oil capsules were attached to the same anatomical landmarks (the nasion and the entrance of the auditory meatus of each ear) that were then digitized by a sensor position indicator on MEG acquisition. These common landmarks allowed the coordinate systems for MEG and MRI to be aligned so that the MEG source locations could be overlaid onto the corresponding MRI.

2.5. Data analysis

MEG responses from 300 ms before the prime onset to 1000 ms after the target onset were selectively averaged for each condition. Epochs in which MEG signal variations exceeded a threshold ranging from 4 to 6 pT were regarded as artifactual noise and were therefore excluded from the averages. The threshold value for removing artifacts was determined by inspecting the raw data for each subject. A band-pass filter (0.1–40 Hz) was applied to the averaged responses, and removal of the DC component of the magnetic

signals was achieved by using the 300-ms period before the target onset as the baseline.

Spatiotemporal characterization of neural source activities has been described in greater detail in our previous papers (Ihara et al., 2007; Wei et al., 2007; Fujimaki et al., 2009). Dipole locations were estimated using the selective minimum-norm method (Matsuura and Okabe, 1995). The estimation was carried out for each condition every ~ 6 ms, using a spatial mesh size of 7 mm, by employing a spherical head-shaped model and a noise level of five times the root-mean-square value of the MEG signals during the 200-ms period before the target onset (Matsuura and Okabe, 1996). All dipole locations obtained for the three conditions, excluding the neighbors within 2 cm, were equally used in the next step for each condition. The moments of the dipoles were fitted to the MEG signals with ASA software Version 2.22 (ANT software B.V., Enschede, the Netherlands) by means of the least squares of the difference between measured and calculated fields employing a realistic head-shaped model. The inseparable dipoles were grouped according to the criterion for separation and temporal correlation (Fujimaki et al., 2002). For each location, the offset of the dipole moment strengths was computed using the 100-ms period before the target onset as the baseline. Finally, we computed a grand average dipole moment waveform across subjects for each location. Moreover, the dipole locations were transformed into Talairach coordinates (Talairach and Tournoux, 1988) using ASA software Version 4.6.0.3 (ANT software B.V., Enschede, the Netherlands) so that neural activations with similar locations could be averaged across subjects.

For statistical analysis, the moment strengths were averaged over sampling points in 100-ms latency windows from 100 to 600 ms relative to the target onset (i.e., 100–200 ms, 200–300 ms, 300–400 ms, 400–500 ms, and 500–600 ms). Differences in the moment strengths for each location were assessed by two-way repeated-measures analysis of variance (ANOVA) (condition \times latency window) using SPSS 16.0J software (SPSS Inc., Chicago, IL). Significance level was set at 5%. When Mauchly's test showed that homogeneity of variance was violated, the degree of freedom was adjusted by Huynh–Feldt procedure. For a significant main effect of condition, Fisher's least significant difference (LSD) post-hoc test was performed. For a significant interaction, one-way repeated-measures ANOVA was subsequently performed with the significance level of 1% (i.e., 5% with a Bonferroni correction of multiple comparison) for each latency window, followed by Fisher's LSD post-hoc tests. Furthermore, to investigate the effect of the side used for pushing the button, we conducted a two-way ANOVA (group \times condition), though the number of subjects in each group was small ($n = 5$ for each). Differences in the accuracy rate across the conditions were assessed by one-way repeated measures ANOVA.

3. Results

3.1. Behavioral results

The accuracy rates for the lexical judgment task (verb or pseudo-verb) were $96.8 \pm 1.0\%$ (mean \pm standard error) for the Happy condition, $96.2 \pm 1.0\%$ for the Neutral condition, and $96.7 \pm 0.7\%$ for the Sad condition. ANOVA for the accuracy rate showed no significant main effect of condition [$F(2, 18) = 0.212$, $p = 0.811$].

3.2. Locations of neural sources and grand average dipole moment waveforms

Dipole locations that were consistently estimated in at least 9 out of the 10 subjects were identified in the following 11 areas (Table 2): the left posterior inferior frontal cortex [LpIFC, Brodmann's area (BA) 44/45/9/6]; the left anterior medial temporal

Table 2

Mean locations (Talairach and Tournoux, 1988) for neural sources estimated in more than nine subjects.

Location	BA	Talairach coordinates (SE)		
		x	y	z
Left posterior inferior frontal cortex (LpIFC)	44/45/9/6	–51 (3)	10 (2)	18 (4)
Left anterior medial temporal lobe (LaMedTL)	34/28	–11 (1)	–2 (3)	–25 (2)
Left anterior temporal area (LaT)	38	–49 (2)	16 (2)	–22 (3)
Left posterior superior temporal area and inferior parietal lobe (LpST/IP)	40/41/13/42/22	–53 (3)	–36 (3)	19 (3)
Left ventral occipitotemporal area (LvOT)	37	–44 (3)	–60 (3)	–24 (2)
Right posterior inferior frontal and middle frontal cortices (RpIFC/MFC)	9/46/45/44	50 (2)	18 (3)	22 (6)
Right anterior medial temporal lobe (RaMedTL)	28/34/36/38	18 (2)	3 (3)	–26 (2)
Right anterior temporal area (RaT)	38/21	50 (2)	12 (2)	–26 (2)
Right posterior superior temporal area and inferior parietal lobe (RpST/IP)	40	53 (2)	–35 (3)	27 (3)
Right ventral occipitotemporal area (RvOT)	37/19	46 (2)	–64 (3)	–18 (4)
Occipital cortex (Occ)	18/17/23/30	–2 (5)	–77 (1)	5 (4)

BA: Brodmann's area; SE: standard error; coordinates are in mm.

lobe (LaMedTL, BA 34/28); the left anterior temporal area (LaT, BA 38); the left posterior superior temporal area and inferior parietal lobe, including the supramarginal and angular gyri (LpST/IP, BA 40/41/13/42/22); the left ventral occipitotemporal area, including the posterior inferior temporal area and fusiform gyri (LvOT, BA 37); the right posterior inferior and middle frontal cortices (RpIFC/MFC, BA 9/46/45/44); the right anterior medial temporal lobe (RaMedTL, BA 28/34/36/38); the right anterior temporal area (RaT, BA 38/21); the left posterior superior temporal and inferior parietal lobe (RpST/IP, BA 40); the right ventral occipitotemporal area (RvOT, BA 37/19); and the occipital cortex (Occ, BA 18/17/23/30). For each region, the mean locations among the subjects were overlaid on a standard brain (Fig. 2). The grand average dipole moment

waveforms showed that earlier activations occurred in the Occ and bilateral vOT with a peak at a latency of ~150 ms and that other activations started at ~200 ms. In all 11 regions, the grand average dipole moment waveforms for the three conditions were similar.

3.3. Statistical results

Significant between-condition differences in moment strengths were found in the RpIFC/MFC and LpIFC, but not in the remaining nine regions (Fig. 2).

Two-way ANOVA for the RpIFC/MFC showed a significant main effect of condition [$F(2, 16) = 6.455, p = 0.009$], and a post-hoc test revealed that the activation was smaller for the Happy ($p = 0.003$)

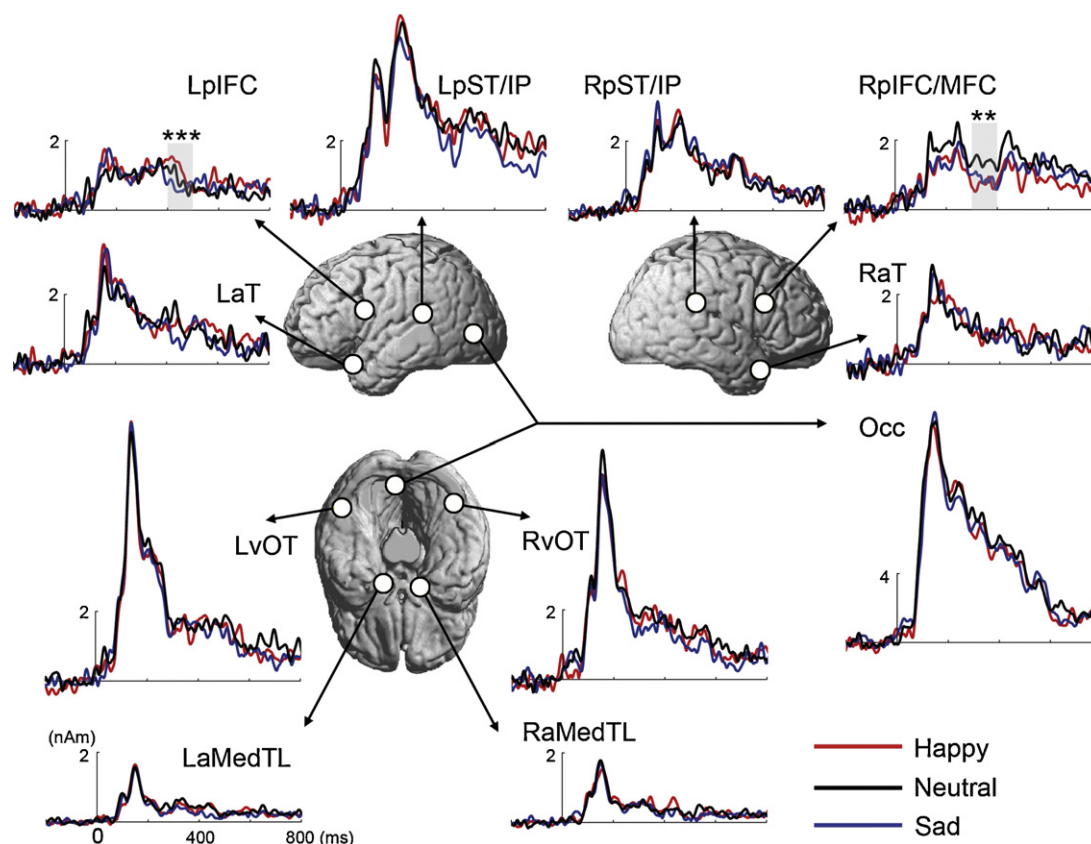


Fig. 2. Dipole locations and grand average moment waveforms. Eleven regions in both hemispheres were identified as common neural sources in at least 9 out of the 10 subjects. Dipole locations averaged across the subjects (see Table 2) were overlaid on a standard brain image (white circle). The moment strengths of each region were averaged across the subjects for the Happy (red), Neutral (black), and Sad (blue) conditions. Abbreviations for the locations are defined in Table 2. ** $p < 0.01$; *** $p < 0.005$.

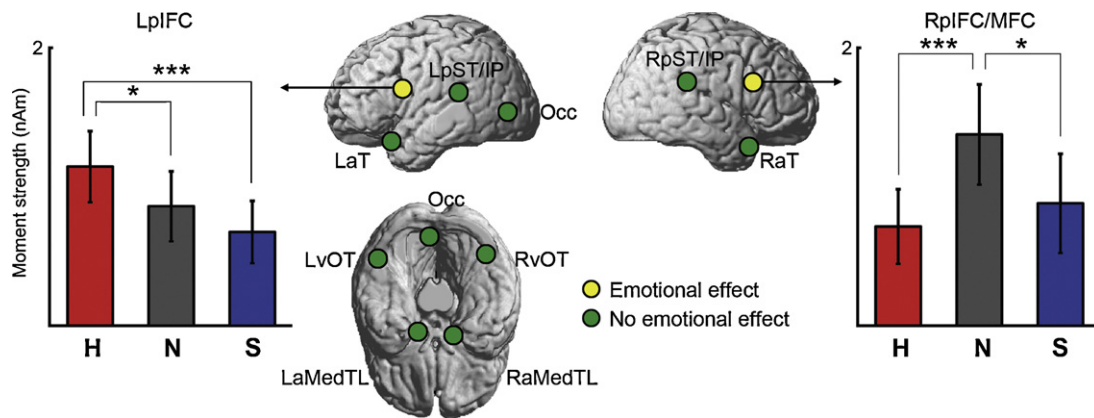


Fig. 3. Between-condition differences. In the RpIFC/MFC, the moment strength for the Happy (red) and Sad (blue) conditions was smaller than that for the Neutral condition (dark gray). On the other hand, in the LpIFC, the moment strength for the Happy (red) and Neutral (dark gray) conditions was greater than that for the Sad condition (blue). Means and standard errors of moment strength are shown for the RpIFC/MFC in the latency window from 300 to 400 ms as well as for the LpIFC in the latency window from 400 to 500 ms. Yellow and green circles on the standard brain image indicate the regions showing emotional effect and no emotional effect, respectively. Abbreviations for the locations are defined in Table 2. H, Happy; N, Neutral; S, Sad. * $p < 0.05$; *** $p < 0.005$.

and Sad ($p=0.021$) conditions than for the Neutral condition. Furthermore, as a planned comparison, we performed one-way ANOVA for each latency window. The results showed a significant main effect of condition only in the latency window from 300 to 400 ms [$F(2, 16)=6.539$, $p=0.008$] (Fig. 2); the activation was smaller for the Happy ($p=0.003$) and Sad ($p=0.019$) conditions than for the Neutral condition (Figs. 3 and 4). No significant difference was found in other latency windows.

Two-way ANOVA for the LpIFC showed a significant interaction between the condition and latency window [$F(8, 72)=2.586$, $p=0.015$]. Subsequent one-way ANOVA revealed a main effect of condition only in a latency window from 400 to 500 ms [$F(2, 18)=8.778$, $p=0.002$] (Fig. 2). In the latency window of 400–500 ms, the activation was larger for the Happy condition compared with the Sad ($p<0.001$) and Neutral ($p=0.021$) conditions (Figs. 3 and 4).

Differences in the moment strengths between the right and left hand groups were assessed by two-way ANOVA for the RpIFC/MFC in a latency window of 300–400 ms and the LpIFC in a latency window of 400–500 ms. The results showed no significant difference in these areas.

4. Discussion

The neural activities for the visually presented language differed depending on the emotional context derived from the prosody of the prime. As the targets were commonly used in each of the three conditions, the prelexical and lexical properties of the targets under these conditions were exactly the same. We believe that the conditional differences of activity reflect top-down processing for language comprehension using emotional context. We identified two conditional differences: (1) the Happy and Sad conditions produced less activity than the Neutral condition in the RpIFC/MFC from 300 to 400 ms, and (2) the Happy and Neutral conditions produced greater activity than the Sad condition in the LpIFC from 400 to 500 ms.

The results show that the bilateral frontal cortices play important roles in top-down processing for language comprehension using emotional context. Although only a few MEG studies are available on the emotional aspect of language processing, the frontal activity has been reported. Beta-low gamma band event-related-desynchronization in the LpIFC/MFC was of a greater magnitude during reading of a word with semantically emotional

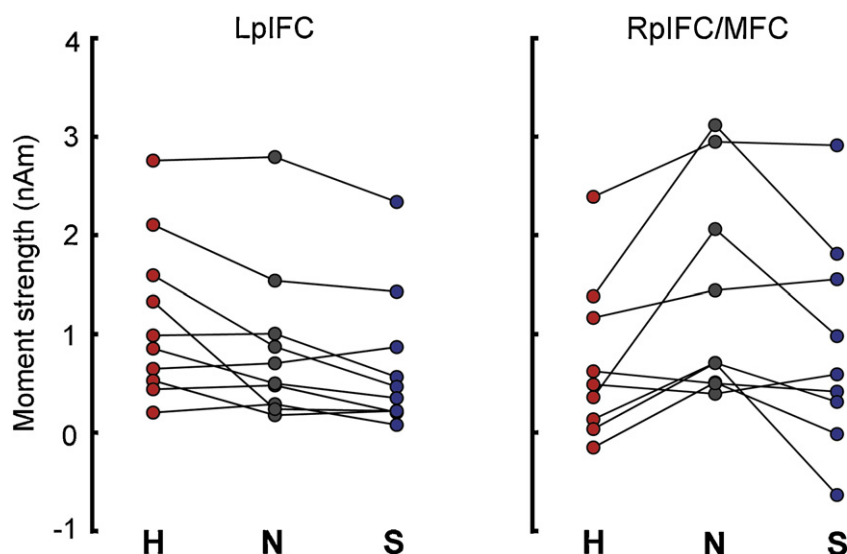


Fig. 4. Individuals' moment strength for the RpIFC/MFC in the latency window of 300–400 ms and the LpIFC in the latency window of 400–500 ms. H, Happy; N, Neutral; S, Sad.

content than during reading of an emotionless word (Hirata et al., 2007). The bilateral prefrontal cortices were activated when a joke was understood (Marinkovic et al., 2011).

A considerable number of neuroimaging studies have demonstrated linguistic top-down processing in the left hemispheric areas (Nobre and McCarthy, 1995; Helenius et al., 1998; Halgren et al., 2002; Marinkovic et al., 2003; Rossell et al., 2003; Cardillo et al., 2004; Dhond et al., 2005; Gold et al., 2006; Matsumoto et al., 2005; Wheatley et al., 2005; Wible et al., 2006; Ihara et al., 2007; Wei et al., 2007), whereas the present study found emotional top-down processing in both hemispheres. Regarding the processing of emotional prosody, hemispheric dominance is still controversial. Lesion studies have proposed specialization in the right hemisphere because right hemisphere damage leads to aprosodia, which presents as an impaired ability to comprehend or generate the emotional components of spoken language (Heilman et al., 1975; Tucker et al., 1977; Ross and Rush, 1981; Tompkins and Flowers, 1985; Bowers et al., 1987; Borod et al., 1990; Cancelliere and Kertesz, 1990; Blonder et al., 1991; Van Lancker and Sittis, 1992; Starkstein et al., 1994). In contrast, neuroimaging studies have demonstrated a widespread involvement of both hemispheres and the subcortical areas in emotional comprehension, indicating that the different functions are region dependent (Kotz et al., 2003; Schirmer and Kotz, 2006; Beaucois et al., 2007; Bach et al., 2008). On the basis of the results of the present study—that there were differences in the activities of right (i.e., RplIFC/MFC) and left (i.e., LplIFC) hemispheric regions associated with different emotional conditions—we consider that these right and left regions serve different functions in top-down processing for language comprehension using emotional context.

4.1. Different activity in the RplIFC/MFC between emotional and neutral conditions

RplIFC/MFC activity differed depending on whether the primes were spoken with emotional (i.e., Happy and Sad) or neutral prosody (Fig. 3). In previous positron emission tomography (PET) and functional MRI (fMRI) studies, greater activity in the right frontal cortex, particularly the inferior region (BA 44, 45, and 47), was observed during emotional judgment of prosodic expressions compared with during resting or a verbal task (George et al., 1996; Buchanan et al., 2000; Wildgruber et al., 2002, 2004, 2005; Gandour et al., 2003). Schirmer and Kotz (2006) have proposed different functional roles within the right inferior frontal cortex: the more cognitive aspects of emotional judgments, such as the labeling of emotional expressions, occur in the posterior part (BA 45), whereas retrieval of their reward value occurs in the anterior part (BA 47). Accordingly, the present study suggests that the RplIFC/MFC might be engaged in the emotional labeling of the prime; i.e., “happy,” “sad,” or “neutral.” On the basis of the results reported by Kotz et al. (2003)—that positive (happy) and negative (angry) prosodies elicited greater activity in the RplIFC/MFC as well as in the left hemispheric regions compared with neutral prosody during an emotional judgment task—we expected activity in response to the primes to be greater for the Happy and Sad conditions than for the Neutral condition.

The question then arises as to why the targets under the Happy and Sad conditions elicited less activity than those for the Neutral condition. One possible explanation is that due to the emotional information from the primes, the subjects read the targets for the Happy and Sad conditions with happy and sad tones, respectively, in their minds. As a consequence, the emotional priming effect (Schirmer et al., 2002, 2005) reduced the RplIFC/MFC activity for the Happy and Sad conditions. This suggests that the emotional labels elicited by the primes were used as the contexts for paralinguistic comprehension of the targets. Given this interpretation, the emotional priming effect in the RplIFC/MFC indicates that

the emotional context is constructed and stored in this region. Furthermore, the present results suggest that the use of the emotional context stored in the RplIFC/MFC for the paralinguistic comprehension of a sentence starts at ~300 ms.

4.2. Different activity in the LplIFC between Happy and Sad conditions

Different responses to the two emotional conditions, i.e., Happy and Sad, were detected in the LplIFC, in which neural activities for the Happy (and Neutral) condition were greater than those for the Sad condition (Fig. 3). This result is consistent with previous electroencephalography (EEG) data showing greater activation in the left frontal area when a positive emotion (happiness or pleasure) is elicited (Davidson and Fox, 1982; Wheeler et al., 1993; Sutton and Davidson, 2000; Light et al., 2009). However, during emotion-judgment tasks, no difference in left frontal activity has been observed between happy and sad prosody (Buchanan et al., 2000; Wildgruber et al., 2005). These previous results suggest that left frontal activity is increased by eliciting a happy emotion, but not by the mere emotional judgment of happy prosody. In the present experiment, we instructed the subjects to read the targets (i.e., interrogative one-word sentences) silently as a sequel of the prime (i.e., names of people). Accordingly, the subjects were assumed to comprehend the targets with their own feelings by using the emotional context. Therefore, the greater activity for the Happy condition is attributed to the fact that the subjects could elicit a happy emotion for the targets in the Happy condition even when the targets were commonly used in the three conditions examined.

MEG and intracranial recording studies have reported that the LplIFC, as well as the left temporal area, are generators of N400, an event-related potential (ERP) component peaking at ~400 ms after stimulus onset (Halgren et al., 2002; Ihara et al., 2007; Wei et al., 2007). N400 is known to vary with semantic processing. Originally, Kutas and Hillyard (1980) observed N400 as a component reflecting semantically incongruent words in a sentence context. N400 is now considered to be a part of the brain's normal response to word or word-like stimuli, the amplitude of which changes with the ease of accessing information from long-term memory and integration of the semantic representation with a preceding context (Kutas and Federmeier, 2000). It appears that the left lateral temporal area is involved in lexical access, whereas the LplIFC is involved in contextual integration (Marinkovic et al., 2003; Ihara et al., 2007; Fujimaki et al., 2009). In addition, evidence is accruing that the LplIFC subserves controlled semantic inhibition and selection of semantic knowledge among competing alternatives (Thompson-Schill et al., 1999; Cardillo et al., 2004; Badre et al., 2005; Gold et al., 2006; Ihara et al., 2007; Wei et al., 2007). In the present study, activity in the LplIFC was influenced by emotional context, which occurred following an emotional priming effect in the RplIFC/MFC. This suggests that activities in the LplIFC are modulated by those in the RplIFC/MFC and that, consequently, the left frontal area is involved in the integration of linguistic information with linguistic context, as well as with paralinguistic emotional context, for sentence comprehension dependent on emotional context.

4.3. Prelexical and lexical processing independent of emotional context

In contrast to the RplIFC/MFC and LplIFC, activity in the remaining nine areas was elicited independent of emotional context (Figs. 2 and 3). These areas include those that have been reported to be involved in prelexical and lexical processing, i.e., bottom-up processing, in numerous lesion studies on aphasia and in neuroimaging studies. As summarized in these studies, the Occ and VOT are involved in visual form processing (Fiez and Petersen, 1998;

Koyama et al., 1998; Fujimaki et al., 1999; Tarkiainen et al., 1999; Price, 2000; Sakurai et al., 2000; Cohen et al., 2002; Ihara and Kakigi, 2006), whereas the LpST/IP, classically referred to as Wernicke's area, subserves phonological access of visually presented words (Fujimaki et al., 1999; Price, 2000; Jobard et al., 2003; Sekiguchi et al., 2004; Booth et al., 2006; Wei et al., 2007), acoustically perceptual analysis of speech (Demonet et al., 1992; Zatorre et al., 1996; Fiez and Petersen, 1998), and phonological storage (Paulesu et al., 1993; Baldo and Dronkers, 2006;). In addition, neuroimaging studies have demonstrated that the LaT is involved in lexico-semantic processing independent of sensory modalities, i.e., both visual and auditory inputs (Vandenberghe et al., 1996; Price, 2000; Scott et al., 2000, 2003; Marinkovic et al., 2003; Spitsyna et al., 2006; Pobric et al., 2007; Fujimaki et al., 2009, 2010). This proposal is also supported by lesion studies demonstrating that LaT damage causes semantic dementia—a selective impairment of semantic abilities that affects all modalities of reception and the expression of all types of concepts (Mummery et al., 1999; Gorno-Tempini et al., 2004; Noppeney et al., 2007; Patterson et al., 2007). Taken together, the results of the present study indicate that orthographic, phonological, and lexico-semantic processing is not affected by emotional context and that the involved regions deal with linguistic but not paralinguistic information.

4.4. Time-course of sentence comprehension dependent on emotional context

The time-course of neural activities for prelexical and lexical processing has been revealed using MEG and ERP. A survey of these studies reveals that Occ activity peaks at ~100 ms after stimulus onset for earlier or lower visual form processing, that vOT activity peaks at ~150 ms after stimulus onset for later or higher visual form processing, and that LpST/IP activity starts at 200–300 ms after stimulus onset for lexico-phonological processing (Talairach and Tournoux, 1988; Kuriki et al., 1996, 1998; Helenius et al., 1998; Koyama et al., 1998; Tarkiainen et al., 1999; Cornelissen et al., 2003; Sekiguchi et al., 2004; Vihla et al., 2006; Wei et al., 2007).

An MEG study by Halgren et al. (2002) has demonstrated that N400 comprises a sequence of differential activation, beginning in Wernicke's area at ~250 ms and then spreading to anterior temporal sites at ~270 ms, to Broca's area by ~300 ms, to the dorsolateral prefrontal cortices by ~320 ms, to the anterior orbital and frontopolar cortices by ~370 ms, and eventually to the right anterior temporal and orbital cortices by ~500 ms. This greater activity for semantically incongruent words than for semantically congruent words appears to reflect both lexical access and contextual integration (Kutas and Federmeier, 2000). Other MEG studies have shown that lexico-semantic access, separated from contextual integration, starts at ~200 ms in the LaT (Marinkovic et al., 2003; Fujimaki et al., 2009, 2010). Furthermore, it has been reported that an MEG component peaking at 300–400 ms, i.e., M350, reflects lexical, but not postlexical, processing (Embick et al., 2001; Pyllkanen et al., 2002; Pyllkanen and Marantz, 2003).

On the other hand, the present results indicate that paralinguistic processing for emotional comprehension occurs from 300 to 500 ms after stimulus onset in parallel with the abovementioned lexical processing. During this latency period, the RplFC/MFC is activated at 300–400 ms for the processing of emotional context, and then the LplFC is activated at 400–500 ms for emotional contextual integration. A series of ERP studies by Schirmer and colleagues has demonstrated an emotional priming effect at the right anterior site from 300 to 550 ms, showing that the N400 amplitude in response to congruent words with emotional prosody was smaller than that in response to incongruent words (Schirmer et al., 2002, 2005). Consistent with these studies, the emotional priming effect in the RplFC/MFC observed in the present study starts at ~300 ms.

Furthermore, the temporal characteristics of the emotional contextual effect in the LplFC are compatible with those of the linguistic contextual effect in the area reported in previous studies (Halgren et al., 2002; Ihara et al., 2007; Wei et al., 2007). This finding suggests that emotional context is integrated in the LplFC at latencies similar to those at which linguistic context is integrated.

5. Conclusion

Our study provides evidence that the bilateral frontal cortices play important roles in top-down processing for language comprehension using emotional context. These results suggest that the use of emotional context stored in the right posterior inferior and middle frontal cortices starts at ~300 ms, that integration of the linguistic information with the emotional context starts at ~400 ms in the left posterior inferior frontal cortex, and that language comprehension dependent on emotional context is achieved by ~500 ms.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neures.2011.09.011.

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