Language and Music: Differential Hemispheric Dominance in Detecting Unexpected Errors in the Lyrics and Melody of Memorized Songs

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Abstract: Using magnetoencephalography (MEG), we report here the hemispheric dominance of the auditory cortex that is selectively modulated by unexpected errors in the lyrics and melody of songs (lyrics and melody deviants), thereby elucidating under which conditions the lateralization of auditory processing changes. In experiment 1 using familiar songs, we found that the dipole strength of responses to the lyrics deviants was left-dominant at 140 ms (M140), whereas that of responses to the melody deviants was right-dominant at 130 ms (M130). In experiment 2 using familiar songs with a constant syllable or pitch, the dipole strength of frequency mismatch negativity elicited by oddballs was left-dominant. There were significant main effects of experiment (1 and 2) for the peak latencies and for the coordinates of the dipoles, indicating that the M140 and M130 were not the frequency mismatch negativity. In experiment 3 using newly memorized songs, the right-dominant M130 was observed only when the presented note was unexpected one, independent of perceiving unnatural pitch transitions (i.e., perceptual saliency) and of selective attention to the melody of songs. The consistent right-dominance of the M130 between experiments 1 and 3 suggests that the M130 in experiment 1 is due to unexpected notes deviating from well-memorized songs. On the other hand, the left-dominant M140 was elicited by lyrics deviants, suggesting the influence of top-down linguistic information and the memory of the familiar songs. We thus conclude that the left-lateralized M140 and right-lateralized M130 reflect the expectation based on top-down information of language and music, respectively. *Hum Brain Mapp 30:588–601, 2009.* ©2008 Wiley-Liss, Inc.

Key words: hemispheric dominance; auditory processing; temporal cortex; magnetoencephalography; mismatch negativity

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INTRODUCTION

The higher brain functions related to language and music are thought to involve uniquely human abilities [Lerdahl and Jackendoff, 1983; Patel, 2003], and they are known to have a strong tendency for hemispheric dominance in the brain. Syntax, semantics, and phonology are generally lateralized with left hemispheric dominance [Gazzaniga, 2000; Geschwind, 1979; Price, 2000; Sakai, 2005], whereas the right hemispheric dominance in processing prosodic information has been reported in frontal

and temporal regions [Hesling et al., 2005; Nicholson et al., 2003; Plante et al., 2002; Ross, 1981]. On the other hand, right temporal lesions are reported to cause amusia, or deficits in the discrimination of melodies [Ayotte et al., 2000; Dennis and Hopyan, 2001; Griffiths et al., 1997; Liégeois-Chauvel et al., 1998; Murayama et al., 2004; Nicholson et al., 2003]. A positron emission tomography study on healthy participants has also reported that activation of the right superior temporal cortex is enhanced during passive listening to melodies [Zatorre et al., 1994]. Active listening to instrumental music activates both hemispheres, with right-hemispheric weighting [Koelsch et al., 2002; Kraemer et al., 2005], and previous lesion studies have indicated that long-term memory of musical information, in contrast to verbal information, is not clearly lateralized in one hemisphere [Samson, 1999; Stewart et al., 2006]. To establish the right hemispheric dominance of auditory processing more conclusively, cortical activation should be further examined with sufficient temporal resolution.

Recent magnetoencephalography (MEG) studies with speech sounds have reported that phoneme or voice oddballs induce the left-dominant mismatch negativity (MMNm) [Knösche et al., 2002; Näätänen et al., 1997]. This type of "frequency MMNm" is generated by an automatic detection of frequency errors (deviants) occurring in a series of standard stimuli, and the frequency MMNm can be elicited even by auditory oddballs eliciting no N1 response [Näätänen et al., 2005]. An MEG study has reported that the frequency MMNm for chord oddballs was larger than that for phoneme oddballs in the right hemisphere, but the right dominance of the MMNm for chord oddballs was not significant [Tervaniemi et al., 1999]. In these previous studies, speech sounds were used for language stimuli, while the instrumental sounds or chords were used for music stimuli. Thus the bottom-up processes for the acoustic features of stimuli can explain the contrasting hemispheric dominance between language and music processing. Speech sounds are highly dependent on rapidly changing sounds whereas tonal music patterns tend to be slower; thus, hemispheric dominance of the superior temporal cortex may depend on the temporal and spectral properties of the acoustic stimuli and associated bottom-up processes [Boemio et al., 2005; Zatorre et al., 2002]. However, it remains unclear how the hemispheric dominance is influenced by top-down processes including attention and memory.

A previous event-related brain potential (ERP) study examined the effect of familiar melodies with a regular but unexpected ending, or with an irregular tone, and reported that a late positive component with the peak latency of 300 ms was elicited by these wrong notes [Besson and Faïta, 1995]. Another ERP study reported that the N400 component was elicited by memory violations, whereas an early right anterior negativity (ERAN) with the peak latency of 200 ms was elicited by out-of-key violations [Miranda and Ullman, 2007]. The ERAN was also associated with expectancy based on musical regularity [Koelsch

et al., 2000; Maess et al., 2001]. It remains to be elucidated how the expectancy of melody itself based on stored memory affects early components. If the exact timing of the first component reflecting the top-down processes based on stored memory could be clarified, this would further elucidate basic auditory processing.

To examine such top-down processes, experiments in which participants listen actively to song stimuli with both properties of lyrics and melody would be ideal, because the temporal and spectral properties of the song stimuli can be equated as much as possible. Figure 1A shows one example of song stimuli used in the present study, which was made with a speech synthesis program that can be configured to produce songs by assigning musical notes and lyrics. Using this program, the duration, pitch, and power of each note can be held constant. We used a forced-choice error-detection paradigm, which has been established in previous studies [Embick et al., 2000]; in each trial, there were always one or two unexpected errors in the lyrics and melody of songs (lyrics and melody deviants). In experiment 1 using familiar songs, we first compared the hemispheric dominance between language and music tasks, where identical song stimuli were used without any instrumental accompaniment or chords. We detected event-related MEG responses to either the lyrics or melody deviants in two tasks performed separately: a lyrics and a melody task (Fig. 1B). Here the stored memory of songs was required, since there was no cue in the acoustic features per se to discriminate deviants from the normal reference stimuli. In experiment 2 using familiar songs with a constant syllable or pitch, which did not require stored memory of songs, we examined the effect of oddballs in two tasks performed separately: a syllable and a pitch task (Fig. 1C). We tried to clarify whether the deviant-induced fields observed in experiment 1 were different from the frequency MMNm. In experiment 3 using unfamiliar and newly memorized songs, we further tried to separate the top-down expectation processes from the bottom-up perception of unnatural pitch transitions in the melody task (Fig. 1D), thereby confirming the consistency of the deviant-induced fields between experiments 1 and 3.

MATERIALS AND METHODS

Participants

Sixteen native Japanese speakers participated in the present study (aged 21–32 years, mean 27 years; eight females). Fourteen participants participated in experiment 1, nine of whom also participated in experiment 2 along with an additional participant (a total of 10 participants). Eleven participants participated in experiment 3, eight of whom also participated in both experiments 1 and 2 but one of them was discarded due to low performance at the training stage (a total of 10 participants), and another two of whom had participated in either experiment 1 or 2. All participants showed right-handedness by the Edinburgh inventory
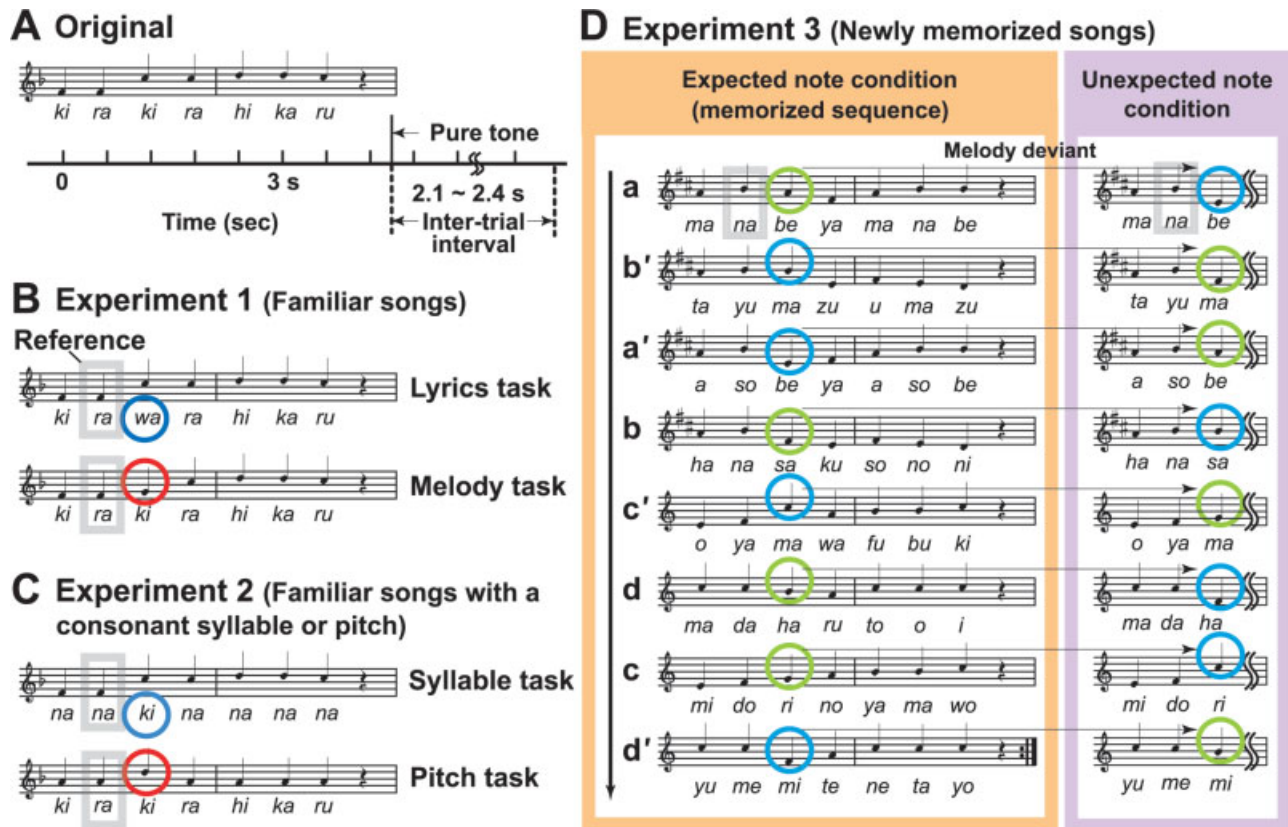
Figure 1.

The experimental paradigm with songs to examine the differences between lyrics and melody processing. **A**: An example of 12 original songs used in experiments 1 and 2 (e.g., a French folk song "Twinkle, twinkle, little star" with typical Japanese lyrics). Each song has seven notes, and is sung without any instrumental accompaniment and chords. The time line of one trial is shown below the musical score. In experiment 3, a different set of songs was used with the same time sequence. **B**: Experiment 1, employing lyrics and melody tasks on familiar songs. There were one or two deviants in lyrics (a blue circle) or melody (a red circle) among the third to the seventh notes. The normal note preceding the first appearing deviant was used as the reference for deviant-induced fields (gray rectangles). **C**: Experiment 2, employing syllable and pitch tasks on familiar songs with a constant syllable or pitch. In the syllable task, lyrics were replaced with the constant syllable of "*na*." A blue circle denotes a syllable oddball. In the pitch task, the melody was replaced with the constant note of A4 (440 Hz). A red circle denotes a pitch oddball. The note preceding the first appearing oddball was used as the reference (gray rectangles). **D**: Experiment 3, employing the melody task on newly memorized songs. See Materials and Methods for full explanation.

[Oldfield, 1971], and had normal hearing abilities without professional singing or instrument training besides school education. The study was approved by the institutional review board of The University of Tokyo, Komaba.

Stimuli and Tasks

The song stimuli without accompaniment were produced with SMARTTALK software (Oki Electric Industry, Tokyo, Japan). For each trial in all experiments, a song stimulus with seven notes (600 ms each) was presented at a sound pressure level of about 85 dB (Fig. 1A). There were always one or two deviants among the third to the seventh notes, and the second deviant appeared two or three sounds apart from the first one, but in a pseudo-randomized position, so that the melody after the first deviant clearly returned to the original one. After the song stimulus, a pure tone of 1,000 Hz was presented for 50 ms to initiate the button press within the following 2 s. The participants were informed that there would always be one or two deviants in each trial, and they indicated the number of deviants by pushing one of two buttons. In experiments 1 and 2, MEG responses to the first appearing deviant/oddball and those to a reference note just before it were used for the analysis; the responses to the second deviant/oddball were not used because they might reflect priming or habituation effects. In experiment 3, MEG responses to the third note and those to the second reference

note were used for the analysis. The trial interval was randomized within the range of ±2% at 6.8 s to reduce any periodical noises. The stimuli were delivered binaurally to participants via plastic tubes (length, 6.5 m), which were connected to insert earphones (Etymotic ER-30; Etymotic Research, Elk Grove Village, IL). Stimulus presentation and behavioral data collection were controlled using the LabVIEW software and interface (National Instruments, Austin, TX).

Experiment 1

We prepared for a sequence of 12 familiar songs (original songs), each consisting of seven quarter notes. The order of these 12 song stimuli was always fixed, so that the participants could expect lyrics and melody even from the beginning of each song. For the lyrics task, lyrics deviants were made by changing both consonants and vowels in two ways for each syllable (e.g., "*wa*" and "*bu*" from "*ki*"), while retaining the original melody (Fig. 1B). The songs with lyrics deviants were phonotactically legal, but they were syntactically and semantically anomalous. On the basis of such top-down linguistic information and the memory of familiar songs, the participants responded to one or two lyrics deviants. For the melody task, melody deviants were made by raising or lowering the original note by five semitones, while retaining the original lyrics (Fig. 1B). On the basis of the memory of familiar songs, the participants responded to one or two melody deviants. For each task, 228 trials were conducted for about 25 min; the last three trials were excluded from the analysis because of technical problems with the program. Behavioral data were not successfully collected from three participants due to technical problems with the buttons. The order of the two tasks was counterbalanced among the participants.

Experiment 2

In the syllable task, all lyrics were replaced with the constant syllable of "*na*" while keeping the original melody used in experiment 1. The participants responded to one or two oddballs consisting of the syllables "*ki*" or "*so*" in each song stimulus (Fig. 1C). In the pitch task, all melodies were replaced with the constant note of A4 (440 Hz) while keeping the original lyrics used in experiment 1. The participants responded to one or two oddballs, which were made by raising or lowering the constant note by five semitones. The location and number of oddballs in this experiment were the same as those of the deviants in experiment 1. For each task, 228 trials were conducted for about 25 min; the last three trials were excluded from the analysis due to technical problems with the program. The order of the two tasks was counterbalanced among the participants.

Experiment 3

As shown in Figure 1D (orange column), the participants memorized a sequence of the eight unfamiliar songs (a, b', a', ...) just before the MEG recordings. The order of these eight songs was always fixed, so that the participants could expect lyrics and melody even from the beginning of each song. On the basis of the memorized sequence, the participants responded to one or two melody deviants. Here, we define the expected note condition as presenting a note from the memorized sequence (the third note in the orange column), and the unexpected note condition as presenting a melody deviant (the third note in the purple column). If the expected note condition consisted of the originally composed notes alone whereas the unexpected note condition included the experimentally modified notes, it was not possible to separate the top-down expectation processes from the bottom-up perception of unnatural pitch transitions. To equate the melody stimuli between these conditions, each condition included both originally composed notes (green circles) and experimentally modified notes (blue circles), whereas the second notes were used as the reference (gray rectangles). From an original song (a, b, c, and d), each modified song (a', b', c', and d') was made by raising or lowering the third note alone by five semitones. This procedure was identical with that for making melody deviants, but the presence of modified songs did not hamper memorization, since the original songs were totally unfamiliar to the participants before the experiment. Moreover, a melody deviant at the third note of a modified song (e.g., a') was made always identical with the third note of the corresponding original song (a for a'), thereby strictly equating the stimulus properties. Melody deviants were also present in the fourth to the seventh notes as in experiment 1, but they were not used for the analysis.

After an initial self-paced memorization block for 10 min, a confirmation test consisting of eight trials of the melody task was performed twice. If participants failed to score seven out of eight, another memorization block was administered. All but one participant successfully scored seven out of eight in two consecutive tests, within two or three memorization blocks (20–30 min in total). The MEG recordings were then started for the successfully passed participants. During the MEG recordings, only the melody task was performed, using the same design as in experiment 1. In each of three separate blocks, 128 trials were performed for about 15 min each.

MEG Recordings and Analyses

The MEG data were acquired with a 160-channel whole-head recording system (MEGvision; Yokogawa Electric Corporation, Kanazawa-city, Japan). Signals were digitized on-line with a bandwidth of 0.3–1,000 Hz at a sampling rate of 2,000 Hz. From the MEG data, only artifact-free trials (peak-to-peak amplitude <3,000 fT and without eye movement) were selected and averaged separately for the different types of deviant/oddball and reference stimuli. In experiments 1 and 2, both correct and incorrect trials were analyzed, whereas in experiment 3, only correct trials

were used for analyses because the accuracies were lower. The averaged data were further filtered with an off-line band-pass filter of 1–20 Hz [Sinkkonen and Tervaniemi, 2000].

The MEG responses from −100 ms to 600 ms (0 ms at the onset of each note) were analyzed with a time window of 0.5 ms, and those from −100 ms to 0 ms were regarded as a baseline. For each MEG component (e.g., P1m), a temporal peak latency and a spatial peak channel (the posterior peak of a source/sink pair) were simultaneously searched and determined in each hemisphere of a participant. The selected peak channels did not necessarily coincide among the participants. With a software package (MEG Laboratory; Yokogawa Electric Corporation, Kanazawa-city, Japan) based on previously established procedures [Sarvas, 1987], an equivalent current dipole (ECD) at the latency of each component was calculated for artifact-free channels corresponding to a source/sink pair of MEG responses in each hemisphere, and a spherical model was used to determine ECDs without the use of seed-points or other constraints. In experiments 1 and 2, the criterion for an acceptable dipole solution was a goodness-of-fit of at least 90% for each participant, whereas in experiment 3, a goodness-of-fit of at least 85% was required. Each ECD location was plotted as a point on individual MR images using MRIcro software (http://www.mricro.com). Individual MR images were then normalized with SPM2 software (Welcome Department of Imaging Neuroscience, London, UK), and the ECD points were transformed with the same normalization parameters using the MRIcro subroutine (lesionmask.m). In the present study, we used the MNI (Montreal Neurological Institute) coordinate system. The MNI coordinates of each ECD were plotted onto the standard brain, and their positions relative to Heschl's sulcus were determined on the standard brain. For the statistical analysis within each experiment, repeated measures analysis of variance (ANOVA) was performed. If an interaction among several factors was significant, further analyses with one-way ANOVAs were performed. Regarding the ECD location in each hemisphere, the unsigned x coordinates (more medial or lateral within the hemisphere), as well as the signed y and z coordinates, were used for comparisons.

RESULTS

Experiment 1

The accuracies of the lyrics and melody tasks for the 11 participants were $(94 \pm 1.0)\%$ (mean $\pm$ SEM) and $(94 \pm 1.3)\%$, respectively, and these two values were not significantly different ($F(1, 10) = 0.066$, $P = 0.8$). Figure 2A shows event-related MEG responses to the reference stimuli, lyrics deviants, and melody deviants; these responses were taken from the same posterior peak channel in each hemisphere of one representative participant. The first detectable peak, a P1m, was observed with the latency of 50 ms for all types of stimuli, whereas the second peak, an N1m, was observed with the latency of 100 ms for reference stimuli (Fig. 2A, black lines). From all 28 hemispheres, we obtained the peak latencies of the P1m induced by reference stimuli (52 ± 2.4 ms), as well as those induced by both types of deviants (lyrics deviants, 55 ± 1.6 ms; melody deviants, 56 ± 1.1 ms). According to a two-way repeated measures ANOVA, neither the main effects of task and hemisphere nor their interaction were significant for the peak latencies (Table I). The grand-average of the ECD locations for the P1m is shown in Figure 2B. The ECDs in the lyrics task [MNI coordinates, left: (x, y, z) = (-47 ± 3.0, -25 ± 2.9, 11 ± 3.1); right: (50 ± 1.8, -20 ± 2.6, 8.4 ± 1.5)] and those in the melody task [left: (-52 ± 2.7, -23 ± 3.1, 16 ± 2.7); right: (52 ± 1.9, -19 ± 2.6, 13 ± 2.3)] were located in the posterior region of Heschl's gyrus. The significant main effects of task for the ECD locations were observed, such that the ECDs of the P1m in the lyrics task were significantly superior to those in the melody task (Table I). Neither the main effects of task and hemisphere nor their interaction were significant for the ECD strength (Fig. 2C, Table I). The N1m for reference stimuli (peak latency, 111 ± 4.3 ms) was not always induced (nine hemispheres), presumably due to the rapid succession of notes [Hari et al., 1982]. The P1m and N1m are also known as P50m and N100m [McEvoy et al., 1994].

In contrast, prominent deviant-induced fields with the latency of 130–150 ms were elicited by both the lyrics and melody deviants (Fig. 2A, blue and red lines). The distribution of these magnetic fields with an inverse polarity in each hemisphere suggests the existence of symmetrical dipoles that point to the infero-posterior direction (Fig. 2A, upper panel). To extract pure deviant-induced fields, the event-related responses to reference stimuli were subtracted from the responses to deviants (Fig. 2D, blue and red lines), which resulted in a similar distribution pattern of magnetic fields for this representative participant (Fig. 2D, upper panel for melody deviants). Because the reference notes include both features of syllable and pitch used in the deviants, the subtracted MEG responses are selective to the temporal properties of either lyrics or melody, which are independent from particular languages, songs, and constant acoustic features. In all 14 participants tested, these deviant-induced fields were consistently observed. In the lyrics task, their temporal peak latencies in the left and right hemispheres, simultaneously determined with spatial peak channels from the subtracted data, were 149 ± 4.4 ms and 146 ± 3.0 ms, respectively. In the melody task, the peak latencies in the left and right hemispheres were 132 ± 4.6 ms and 130 ± 3.6 ms, respectively. The significant main effects of task for the peak latencies were observed, such that the peak latency in the lyrics task was significantly longer than that in the melody task (Table I). We thus named the deviants-induced fields in the lyrics and melody tasks the M140 and M130, respectively.

To evaluate the hemispheric dominance of deviant-induced fields in the lyrics and melody tasks, we calculated
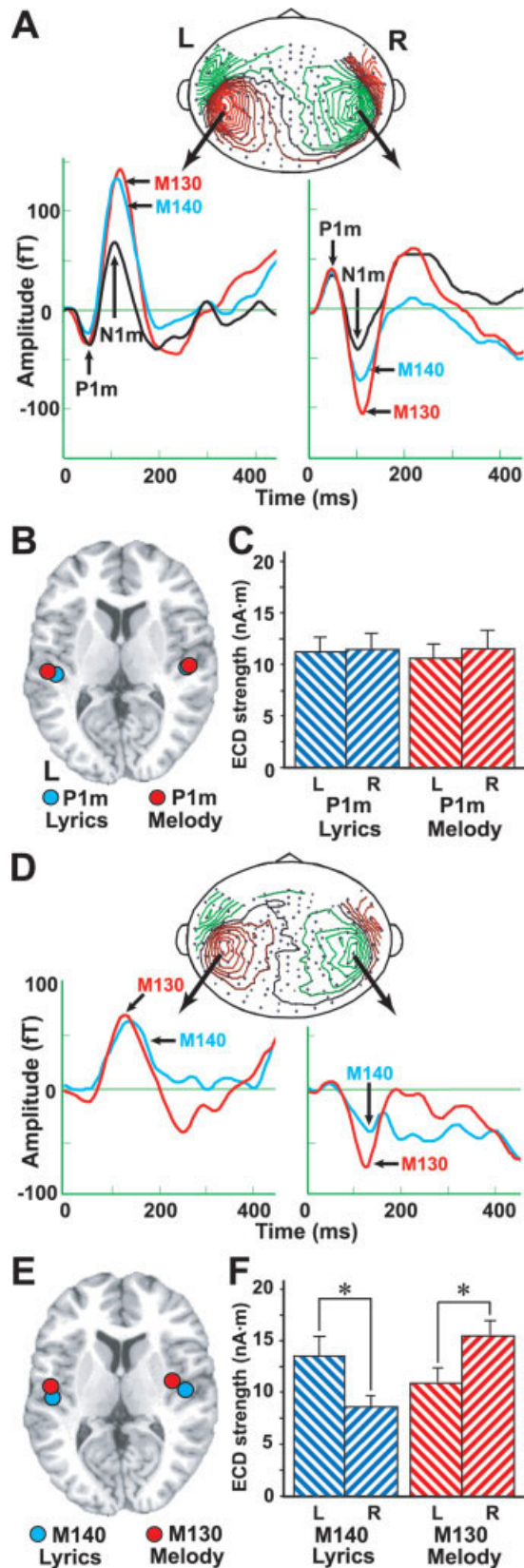
A: MEG responses

B:
○ P1m Lyrics
● P1m Melody

C: ECD strength (nA·m)
L R P1m Lyrics
L R P1m Melody

D:

E:
● M140 Lyrics
● M130 Melody

F: ECD strength (nA·m)
L R M140 Lyrics
L R M130 Melody

ECDs of the M140 and M130 from the subtracted data. The ECDs of the M140 [left: (-49 ± 3.3, -18 ± 3.0, 19 ± 4); right: (49 ± 2.3, -13 ± 3.4, 16 ± 2.6)] and those of the M130 [left: (-50 ± 2.9, -10 ± 4.2, 7.8 ± 2.0); right: (39 ± 1.7, -6.8 ± 5.4, 14 ± 3.3)] were located anterior to Heschl's gyrus (Fig. 2E). According to a two-way repeated measures ANOVA, the significant main effects of task for the z coordinate were significant, such that the ECDs of the M140 were significantly superior to those of the M130 (Table I). On the other hand, the main effects of task and an interaction between task and hemisphere were marginally significant for the x coordinate. The ECDs of the M140 were significantly more lateral to those of the M130 in the right hemisphere ($F(1, 13) = 16$, $P = 0.014$), while there was no such difference in the left hemisphere ($F(1, 13) = 0.009$, $P = 0.9$).

Next, we compared the ECD locations between the P1m and M140/M130. According to a three-way repeated measures ANOVA for the y coordinate (Table I), the significant main effects of both component and hemisphere were observed. The ECDs of the M140/M130 were significantly more anterior to those of the P1m, while those of the M140/M130 and P1m were significantly more anterior in the right hemisphere to those in the left hemisphere. A significant interaction between component and task for the x and z coordinates, as well as that between task and hemisphere for the x coordinate, was also observed. The ECDs of the M140 were significantly more dorsal to those of the

Figure 2.

The results of experiment 1, showing the left-dominant M140 and right-dominant M130. **A:** MEG responses to the lyrics deviants (blue lines), melody deviants (red lines), and reference stimuli (black lines), taken from one representative participant. The upper panel shows the magnetic field distribution at 130 ms from the onset of the first melody deviants (source: red lines; sink: green lines). The lower left and lower right panels show the responses at the same posterior channels in the left and right hemispheres, respectively. **B:** The grand-averaged ECD locations of the P1m in the lyrics (blue circles) and melody tasks (red circles). The ECDs were superimposed on a structural image of the standard brain (Montreal Neurological Institute) showing a horizontal slice at $z = 9$. **C:** The ECD strength (mean ± SE) of the P1m in the lyrics and melody tasks. **D:** Time courses of the M140 (blue lines) and M130 (red lines), taken from one representative participant. The data were calculated by subtracting event-related responses to reference stimuli from those to the first appearing deviants. The upper panel is the magnetic field distribution of the M130 (after subtraction) at 130 ms from the onset of the first melody deviants. **E:** The grand-averaged ECD locations of the M140 (blue circles) and M130 (red circles). **F:** The ECD strength of the M140 and M130. The M140 was significantly larger in the left than in the right hemisphere (*$P < 0.05$). In contrast, the M130 was significantly larger in the right than in the left hemisphere.

TABLE I. Repeated measures ANOVAs for the P1m and M140/M130 in experiment 1

	df	x		y		z	
		F	P	F	P	F	P
P1m							
Task (lyrics, melody)	1, 13	2.2	0.2	0.16	0.7	6.5	0.024*
Hemisphere (L, R)	1, 13	0.23	0.6	3.1	0.1	1.4	0.3
Task × Hemisphere	1, 13	0.39	0.5	0.10	0.8	0.001	1
		Latency		ECD strength			
Task (lyrics, melody)	1, 13	0.57	0.5	0.060	0.8		
Hemisphere (L, R)	1, 13	0.43	0.5	0.22	0.6		
Task × Hemisphere	1, 13	0.44	0.5	0.41	0.5		
M140/M130							
Task (lyrics, melody)	1, 13	3.9	0.068	1.5	0.2	5.4	0.037*
Hemisphere (L, R)	1, 13	3.9	0.070	1.8	0.2	0.37	0.6
Task × Hemisphere	1, 13	4.2	0.062	0.097	0.8	0.15	0.2
		Latency		ECD strength			
Task (lyrics, melody)	1, 13	12	0.0043**	2.8	0.1		
Hemisphere (L, R)	1, 13	1.3	0.3	0.027	0.9		
Task × Hemisphere	1, 13	0.17	0.7	1.4	0.0022**		
Component (P1m, M140/M130)	1, 13	2.8	0.1	14	0.0027**	0.71	0.4
Task (lyrics, melody)	1, 13	0.2	0.7	2.0	0.2	0.28	0.6
Hemisphere (L, R)	1, 13	1.4	0.3	6.2	0.027*	0.17	0.7
Component × Task	1, 13	5.6	0.034*	0.67	0.4	18	0.0009**
Component × Hemisphere	1, 13	3.1	0.1	0.001	1	1.6	0.2
Task × Hemisphere	1, 13	4.9	0.046*	0.19	0.7	1.2	0.3
Hemisphere × Task × Component	1, 13	2.8	0.1	0.006	0.9	0.63	0.4

df, degree of freedom; L, left; R, right; *, $P < 0.05$; **, $P < 0.01$.

P1m in the right hemisphere ($F(1, 13) = 5.6$, $P = 0.034$). The ECDs of the M130 were marginally more ventral to those of the P1m in the left hemisphere ($F(1, 13) = 4.3$, $P = 0.058$), and those of the M130 were significantly medial in the right hemisphere ($F(1, 13) = 28$, $P = 0.0001$), while there was no significant difference for the other cases ($P > 0.1$). Therefore, the ECD locations of the M140 and M130 were significantly different from those of the P1m.

To evaluate the hemispheric dominance of M140 and M130, we compared the ECD strength of these two components between hemispheres. We found a significant interaction between task (i.e., component) and hemisphere for the ECD strength of the M140/M130 (Fig. 2F, Table I). In the lyrics task, the ECD strength of the M140 was significantly larger in the left than in the right hemisphere ($F(1, 13) = 6.4$, $P = 0.025$), whereas that of the M130 was significantly larger in the right than in the left hemisphere in the melody task ($F(1, 13) = 8.8$, $P = 0.011$). These results demonstrate the evidence of the left-dominant M140 in the lyrics task and the right-dominant M130 in the melody task.

Experiment 2

The latencies of M140 and M130 were within the range of those of the previously reported frequency MMNm (100–200 ms), and the deviants might be regarded as oddballs from the natural flow of songs. Moreover, it has been reported that the frequency MMNm was elicited even by oddballs at the second position (i.e., different from the first stimulus) [Jääskeläinen et al., 2004]. It is thus necessary to examine whether or not the M140 and M130 were identical with the frequency MMNm. For this purpose, we tested syllable and pitch tasks with an oddball paradigm, which did not require judgment based on the stored memory of songs. In the syllable task, all lyrics were replaced with a constant syllable, whereas in the pitch task, all notes were replaced with a constant pitch (Fig. 1C). Participants detected the oddballs by monitoring the constant syllable or pitch, where other features of the songs were identical with those tested in experiment 1. If the right dominance observed in the melody task in experiment 1 were due to the characteristics of the frequency MMNm, then the right dominance would be observed in the pitch task in experiment 2 as well, because the frequency MMNm is more likely to be produced by the pitch oddballs.

The accuracies in the syllable and pitch tasks for the 10 participants were $(97 \pm 1.7)\%$ and $(91 \pm 1.6)\%$, respectively, and these two values were significantly different ($F(1, 9) = 5.1$, $P = 0.050$). Figure 3A shows event-related MEG responses to pitch oddballs and reference stimuli in

the pitch task (Fig. 3A, red and black lines, respectively); these responses were taken from the same posterior channel in each hemisphere of one representative participant. At 120 ms, the oddballs at the positions of the third/fourth and fifth-seventh notes elicited larger responses than the reference stimuli. The distribution of these magnetic fields with an inverse polarity in each hemisphere suggests the existence of symmetrical dipoles that point to the infero-posterior direction (Fig. 3A, upper panel). To extract the MMNm, event-related responses to the reference stimuli, which were the notes just before the first appearing oddballs at all stimulus positions, were subtracted from the event-related responses to the oddballs (Fig. 3B, blue and red lines), which resulted in a similar distribution pattern of magnetic fields for this representative participant (Fig. 3B, upper panel for pitch oddballs).

In all 10 participants, both syllable and pitch oddballs elicited larger magnetic responses than the reference stimuli in the left and right temporal cortices. In the syllable task, the temporal peak latencies of the MMNm in the left and right hemispheres, simultaneously determined with spatial peak channels from the subtracted data, were 136 ± 11 ms and 124 ± 12 ms, respectively. In the pitch task, the peak latencies in the left and right hemispheres were 123 ± 5.8 ms and 122 ± 6.0 ms, respectively. Regarding the peak latencies of the MMNm, neither the main effects of the task and hemisphere nor their interaction were significant (Table II). With these individually determined temporal peak latencies and spatial peak channels, the wave amplitudes of MEG responses were calculated for oddball and reference stimuli, as well as for stimulus positions (first and second halves of the five notes used for analyses), by using the data before the subtraction. In both tasks and hemispheres, the significant main effects of stimulus type for the wave amplitudes were observed, such that the wave amplitudes for oddballs were larger than those for reference stimuli. On the other hand, the main effects of stimulus position were not significant (Table II). An interaction between stimulus type and stimulus position
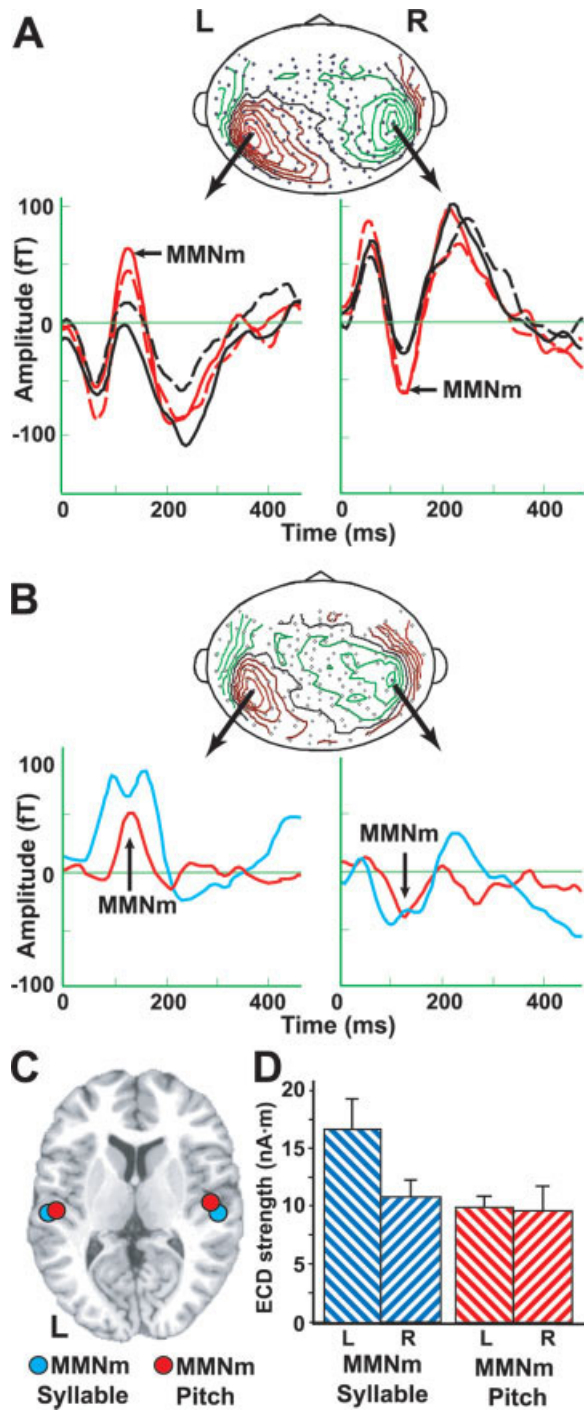

Figure 3.
The results of experiment 2, showing the MMNm in the syllable and pitch tasks. **A:** MEG responses to pitch oddballs at the third and fourth notes (solid red lines), pitch oddballs from the fifth to seventh notes (dashed red lines), reference stimuli at the second and third notes (solid black lines), and reference stimuli from the fourth to sixth notes (dashed black lines), all taken from one representative participant in the pitch task. The upper panel shows the magnetic field distribution at 130 ms from the onset of the pitch oddballs at the third and fourth notes. The lower left and lower right panels show the responses at the same posterior channels in the left and right hemispheres, respectively. **B:** Time courses of the MMNm in the syllable (blue lines) and pitch tasks (red lines), taken from one representative participant. The data were calculated by subtracting event-related responses to reference stimuli from those to pitch oddballs. The upper panel shows the magnetic field distribution of the MMNm (after subtraction) at 130 ms from the onset of the first pitch oddballs. **C:** The grand-averaged ECD locations of the MMNm in the syllable (blue circles) and pitch tasks (red circles). The ECDs were superimposed on a structural image showing a horizontal slice at z = 9. **D:** The ECD strength of the MMNm in the syllable (blue bars) and pitch tasks (red bars).

TABLE II. Repeated-measures ANOVAs for the MMNm in experiment 2

	df	Left		Right			
		F	P	F	P	F	P
Syllable task							
Stimulus type (oddball, reference)	1, 9	41	0.0001**	28	0.0005**		
Stimulus position (first, second half)	1, 9	3.2	0.1	0.97	0.4		
Stimulus type × Stimulus position	1, 9	0.16	0.7	3.9	0.08		
Pitch task							
Stimulus type (oddball, reference)	1, 9	40	0.0001**	51	<0.0001**		
Stimulus position (first, second half)	1, 9	2.3	0.2	1.5	0.3		
Stimulus type × Stimulus position	1, 9	2.2	0.2	4.8	0.056		
		x		y		z	
Task (syllable, pitch)	1, 9	1.5	0.2	1.4	0.3	0.001	1
Hemisphere (L, R)	1, 9	0.010	0.9	0.51	0.5	0.036	0.9
Task × Hemisphere	1, 9	0.003	1	0.47	0.5	0.015	0.9
		Latency		ECD strength			
Task (syllable, pitch)	1, 9	0.36	0.6	2.8	0.1		
Hemisphere (L, R)	1, 9	1.7	0.2	8.7	0.016*		
Task × Hemisphere	1, 9	1.5	0.2	2.8	0.1		

Regarding the stimulus position, oddballs at the third and fourth notes correspond to the first half of the five notes used for analyses (there were no oddballs at the first and two notes), and those from the fifth to the seventh notes correspond to the second half. Reference stimuli at the second and third notes correspond to the first half, and those from the fourth to the sixth notes correspond to the second half (reference notes just before the first appearing oddballs were used for analyses). *, $P < 0.05$; **, $P < 0.01$.

was marginally significant in the right hemisphere for the pitch task; the wave amplitudes for the oddballs on the second half were significantly smaller than that on the first half ($F(1, 9) = 11$, $P = 0.0089$), whereas no significant effect of stimulus position was observed for the reference stimuli ($F(1, 9) = 0.12$, $P = 0.7$). Therefore, the effect of stimulus position cannot account for the larger wave amplitudes of the oddballs that appeared later than the reference stimuli; moreover, this result was observed in the two tasks and both hemispheres (Table II). These results confirm that the observed MMNm was indeed due to the presence of oddballs.

Next, we calculated ECDs of the MMNm from the subtracted data, and the grand-average of the ECD locations for the MMNm is shown in Figure 3C. The ECDs of the MMNm in the syllable task [left: (-56 ± 3.7, -21 ± 3.9, 10 $\pm$ 2.3); right: (56 ± 3.6, -21 ± 6.1, 9.1 ± 2.9)] and those in the pitch task [left: (-51 ± 2.6, -19 ± 3.5, 9.4 ± 4.6), right: (51 ± 4.1, -14 ± 3.4, 9.4 ± 4.7)] were located in the posterior region of Heschl's gyrus. Neither the main effects of task and hemisphere nor their interaction were significant for all coordinates (Table II). Regarding the ECD strength of the MMNm, the significant main effects of hemisphere were observed, showing that the ECD strength was significantly larger in the left hemisphere than in the right hemisphere (Fig. 3D, Table II).

To compare the results of experiments 1 and 2, three-way ANOVAs of experiment (1 and 2) × task × hemisphere for the peak latency, dipole coordinates, and ECD strength were performed (Table III). By comparing the

M140/M130 and MMNm, the significant main effects of experiment were observed, such that the M140/M130 showed significantly longer peak latencies, and the ECD locations of the M140/M130 were significantly more medial, anterior, and marginally dorsal to those of the MMNm. An interaction between task and experiment, as well as that between task and hemisphere, were significant for the ECD strength. The ECD strength of the MMNm in the pitch task was significantly smaller than that of the M130 in the right hemisphere ($F(1, 9) = 5.7$, $P = 0.026$), while there was no significant difference between experiments 1 and 2 for the other cases ($P > 0.2$). These results strongly suggest that the M140 and M130 were unique and independent of the property of the frequency MMNm.

Experiment 3

To examine which factors modulated the M130 observed in experiment 1, we introduced newly memorized songs in the melody task (Fig. 1D). It is possible that the M130 was elicited by unexpected notes deviating from well-memorized songs. An alternative possibility is that the M130 was induced by perceiving unnatural pitch transitions, independent from the stored memory of songs. In experiment 3, the participants were trained with a fixed sequence of original and modified songs before the MEG recordings, and performed the melody task based on these newly memorized songs. If the M130 was elicited by unexpected notes deviating from well-memorized songs, a right-dominant M130 would be observed under the unex-

TABLE III. ANOVAs for the comparison between the M140/M130 in experiment 1 and the MMNm in experiment 2

	df	x		y		z	
		F	P	F	P	F	P
Experiment (1, 2)	1, 88	9.2	0.0032**	5.0	0.028*	3.6	0.064
Task (lyrics/syllable, melody/pitch)	1, 88	5.2	0.025*	3.2	0.08	2.0	0.2
Hemisphere (L, R)	1, 88	1.5	0.2	1.3	0.3	0.043	0.8
Experiment × Task	1, 88	<0.001	1	0.14	0.7	0.88	0.4
Experiment × Hemisphere	1, 88	2.0	0.2	0.083	0.8	0.16	0.7
Task × Hemisphere	1, 88	1.4	0.2	0.048	0.8	1.0	0.3
Experiment × Task × Hemisphere	1, 88	1.7	0.2	0.25	0.6	0.70	0.4
		Latency		ECD strength			
Experiment (1, 2)	1, 88	9.1	0.033*	0.065	0.8		
Task (lyrics/syllable, melody/pitch)	1, 88	7.5	0.0074**	0.68	0.4		
Hemisphere (L, R)	1, 88	1.1	0.3	2.1	0.1		
Experiment × Task	1, 88	1.0	0.3	7.0	0.0095**		
Experiment × Hemisphere	1, 88	0.19	0.7	1.7	0.2		
Task × Hemisphere	1, 88	0.53	0.5	11	0.0013**		
Experiment × Task × Hemisphere	1, 88	0.25	0.6	0.60	0.4		

*, $P < 0.05$; **, $P < 0.01$.

pected note condition (the purple column in Fig. 1D), but not under the expected note condition (the orange column). On the other hand, if the M130 was induced by perceiving unnatural pitch transitions, independent from the stored memory of songs, a right-dominant M130 would be observed for the modified songs (blue circles), but not for the original songs (green circles).

The accuracies under the expected note and unexpected note conditions for the 10 participants were $(87 \pm 2.2)\%$ and $(83 \pm 2.9)\%$, respectively, and these two values were not significantly different $(F(1, 9) = 2.3, P = 0.2)$. To extract pure deviant-induced fields, the event-related responses to the second notes were subtracted from the responses to the third notes. Regarding the peak latencies of the M130, neither the main effects of the expectation and hemisphere nor their interaction were significant (Table IV). Next, the ECDs were calculated from the subtracted data. The grand-average of the ECD locations for the M130 is shown in Figure 4A. The ECDs of the M130 under the unexpected note condition [left: $(-46 \pm 6.2, -17 \pm 4.4, 19 \pm 5.2)$; right: $(45 \pm 3.6, -9.7 \pm 4.4, 9.9 \pm 6.0)$] were located anterior to Heschl's gyrus. The ECDs of the M130 under the expected note condition [left: $(-45 \pm 5.7, -18 \pm 8.5, 6.3 \pm 6.3)$; right: $(52 \pm 4.3, -27 \pm 5.4, 8.3 \pm 8.9)$] were located anterior to Heschl's gyrus in the left hemisphere, and located in the posterior region of Heschl's

TABLE IV. Repeated measures ANOVAs for the effect of expectation or melody on the M130 in experiment 3

		x		y		z	
		F	P	F	P	F	P
Effect of expectation							
Expectation (expected note, unexpected note)	1, 9	0.56	0.5	2.9	0.1	1.0	0.3
Hemisphere (L, R)	1, 9	0.15	0.7	0.007	0.9	0.30	0.6
Expectation × Hemisphere	1, 9	2.4	0.2	1.1	0.3	1.6	0.2
		Latency		ECD strength			
Expectation (expected note, unexpected note)	1, 9	0.025	0.9	5.4	0.045*		
Hemisphere (L, R)	1, 9	0.017	0.9	3.4	0.1		
Expectation × Hemisphere	1, 9	0.10	0.8	4.6	0.060		
Effect of melody							
Melody (original, modified)	1, 9	0.71	0.4	0.002	1	3.0	0.1
Hemisphere (L, R)	1, 9	0.45	0.5	1.2	0.3	0.25	0.6
Melody × Hemisphere	1, 9	0.054	0.8	<0.001	1	0.47	0.5
		Latency		ECD strength			
Melody (original, modified)	1, 9	0.035	0.9	0.069	0.8		
Hemisphere (L, R)	1, 9	0.043	0.8	0.33	0.6		
Melody × Hemisphere	1, 9	0.50	0.5	0.021	0.9		

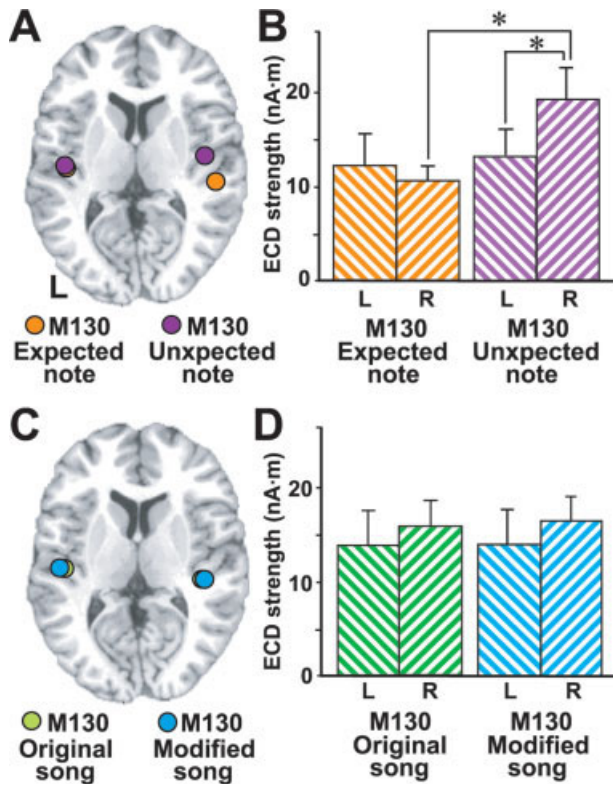*, $P < 0.05$; **, $P < 0.01$.

Figure 4.
The results of experiment 3, showing the right-dominant M130 under the unexpected note condition alone. **A:** The grand-averaged ECD locations of the M130 under the expected note (orange circles) and unexpected note conditions (purple circles). The ECDs were superimposed on a structural image showing a horizontal slice at $z = 9$. **B:** The ECD strength of the M130 under the expected note (orange bars) and unexpected note conditions (purple bars). Under the unexpected note condition, the M130 was significantly larger in the right than in the left hemisphere. **C:** The grand-averaged ECD locations of the M130 for the original (green circles) and modified songs (blue circles). **D:** The ECD strength of the M130 for the original (green bars) and modified songs (blue bars).

gyrus in the right hemisphere. Neither the main effects of expectation and hemisphere nor their interaction were significant for any of the coordinates (Table IV). Regarding the ECD strength, the main effects of expectation (expected note and unexpected note) were significant, while an interaction between expectation and hemisphere was marginally significant (Fig. 4B, Table IV). Under the unexpected note condition, the ECD strength of the M130 was significantly larger in the right than in the left hemisphere ($F(1, 9) = 5.8$, $P = 0.039$), whereas there was no hemispheric dominance under the expected note condition ($F(1, 9) = 0.042$, $P = 0.8$). In the right hemisphere, the ECD strength was significantly larger under the unexpected note than under the expected note condition ($F(1, 9) = 9.1$, $P = $

0.014), whereas there was no such difference in the left hemisphere ($F(1, 9) = 0.82$, $P = 0.4$).

Next, we examined whether or not the right-dominant M130 was elicited automatically by the modified songs. The accuracies for the original and modified songs for the 10 participants were (87 ± 2.2)% and (84 ± 2.6)%, respectively, and these two values were not significantly different ($F(1, 9) = 0.94$, $P = 0.4$). Neither the main effects of melody and hemisphere nor their interaction were significant for the peak latency, any of the ECD coordinates, or the ECD strength (Fig. 4C,D, Table IV).

To clarify whether the M130 observed under the unexpected note condition was consistent with the M130 in experiment 1, in which the same melody task was employed, we performed two-way ANOVAs of experiment (1 and 3) × hemisphere for the peak latency, dipole coordinates, and ECD strength (Table V). We confirmed that the peak latency of the M130 were consistent between experiments 1 and 3. Regarding the ECD locations, an interaction between experiment and hemisphere was marginally significant for the z coordinate alone. In the left hemisphere, the ECDs in experiment 3 were significantly more superior to those in experiment 1 ($F(1, 22) = 5.3$, $P = 0.031$); no significant difference was observed for the z coordinate in the right hemisphere ($F(1, 22) = 0.34$, $P = 0.6$). We also examined whether the ECD strength of the M130 was consistent between experiments 1 and 3. Regarding the main effects of task ($P = 0.1$), the difference between experiments 1 and 3 for the ECD strength in the right hemisphere was 4.2 ± 6.8 nA·m covering zero (with the confidence level of 95%). The main effects of hemisphere were significant for the ECD strength ($P = 0.016$), as expected from the right-dominant M130. The results of the right-dominant M130, as well as its matched peak latency, ECD locations, and ECD strength in the right hemisphere, suggest that the M130 in experiment 1 is consistent with that in experiment 3. Since the right-dominant M130 was clearly observed only under the unexpected note condi-

TABLE V. ANOVAs for the M130 under the unexpected note condition in experiment 3 and the M130 in the melody task in experiment 1

	df	x		y		z	
		F	P	F	P	F	P
Experiment (1, 3)	1, 44	0.12	0.7	1.0	0.3	0.91	0.3
Hemisphere (L, R)	1, 44	3.1	0.09	1.3	0.3	0.18	0.7
Experiment × Hemisphere	1, 44	1.8	0.2	0.16	0.7	3.5	0.067

	df	Latency		ECD strength	
		F	P	F	P
Experiment (1, 3)	1, 44	0.69	0.4	2.3	0.1
Hemisphere (L, R)	1, 44	0.024	0.9	6.3	0.016*
Experiment × Hemisphere	1, 44	0.17	0.7	0.17	0.7

*, $P < 0.05$; **, $P < 0.01$.

tion in experiment 3, we conclude that the M130 in experiment 1 was indeed modulated by memory-related factors.

DISCUSSION

In the present MEG study, we demonstrated the hemispheric dominance of the auditory cortex that is selectively modulated by deviant types of songs consisting of both lyrics and melody, thereby elucidating under which conditions the lateralization of auditory processing changes. In experiment 1 using familiar songs, we found that the ECD strength of the M140 to the lyrics deviants was left-dominant, whereas that of the M130 to the melody deviants was right-dominant (see Fig. 2). Moreover, the ECDs of the M130 were located significantly anterior to the P1m foci. In experiment 2 using familiar songs with a constant syllable or pitch, the ECD strength of the frequency MMNm elicited by oddballs was left-dominant (see Fig. 3). There were significant main effects of experiment (1 and 2) for the peak latencies and for the ECD coordinates, indicating that the M140 and M130 were not the frequency MMNm. In experiment 3 using newly memorized songs, the right-dominant M130 was observed only under the unexpected note condition (see Fig. 4), independent of perceiving unnatural pitch transitions (i.e., perceptual saliency). Moreover, the effect of selective attention to the melody of songs can also be excluded, as discussed in detail below. The consistent right-dominance of the M130, as well as its matched peak latency, ECD strength, and ECD coordinates between experiments 1 and 3, suggests that the M130 observed in experiment 1 is due to unexpected notes deviating from well-memorized songs, but not due to unnatural pitch transitions. On the other hand, the left-dominant M140 was elicited by lyrics deviants, suggesting the influence of top-down linguistic information and the memory of the familiar songs. We thus conclude that the left-lateralized M140 and right-lateralized M130 reflect the expectation based on top-down information of language and music, respectively.

The effect of selective attention has been examined by previous neuroimaging studies, and it is known that selective attention to auditory stimuli enhances neural responses in the auditory cortex [Alho et al., 1999; Hashimoto et al., 2000; Johnson and Zatorre, 2005; Neelon et al., 2006]. The differential modulation of hemispheric dominance in detecting the lyrics and melody deviants revealed in experiment 1 might also be due to selective attention to particular components of songs, although there have been no previous report comparing language and music components of the same stimuli. However, the frequency MMNm observed in the pitch task was comparable between the hemispheres (Fig. 3D), even when the selective attention to the music component was required. Moreover, the selective attention to the melody was required under all of the conditions in experiment 3, but nevertheless the right-dominant M130 was observed only under the unexpected note condition (Fig. 4B, D). Therefore, our results clearly established that memory-related components, independent of selective attention, specifically modulate the right-dominant M130.

A recent MEG study has reported an activity in the bilateral superior temporal area within 100–200 ms of auditory stimulus onset, which was observed only when participants could predict an incoming sound and the presented sound was an unexpected one [Aoyama et al., 2006]. The authors in this previous study suggested that this component was similar to the MMNm, whereas the ECD strength was not significantly different between hemispheres. Frequency MMNm responses are known to originate in the temporal cortex, and they are automatically elicited by oddballs even when participants are asked to ignore the stimuli [Alho et al., 1998; Imaizumi et al., 1998; Knösche et al., 2002; Näätänen et al., 2005]. However, the unexpected notes in the present experiments 1 and 3 were not frequency deviants, and the peak latency of the M140/M130 in experiment 1 were significantly longer than that of the MMNm in experiment 2. This difference might be due to the fact that the deviants in experiment 1 were harder to detect than the oddballs in experiment 2, but the right dominance of the M130 confirmed by experiment 3 suggests the expectation based on top-down information rather than bottom-up features like detectability of stimuli. Indeed, there was no cue in the acoustic features per se to discriminate deviants from the reference stimuli in the melody task of experiments 1 and 3. The melody deviants could be discriminated by using expectation based on stored memory of the melody sequence, and this process would probably elicit the M130. These results indicate the presence of memory-related sources in the superior temporal cortex, which are functionally distinct from the frequency MMNm.

The ECDs of the M140/M130 were located significantly anterior to that of the P1m located in the posterior region of Heschl's gyrus (Fig. 2B, E). One putative auditory region located anterior to the human primary auditory area (A1) has been proposed as the medial area (MA), based on the pattern of cytochrome oxidase and acetylcholinesterase activity [Rivier and Clarke, 1997]. This previous anatomical study regarded the MA as an upstream association area, defined as a unimodal association cortex receiving direct input from A1, and as an intermediate level between A1 and the superior temporal area. One might speculate that the ECDs of the M140/M130 are located in the MA, which subserves intermediate auditory processing and combines both bottom-up information from A1 and top-down information from the higher auditory areas. Furthermore, the M140/M130 reflecting top-down processes occurs at the latency of 140/130 ms, which is clearly later than the P1m. These results suggest that top-down information starts to influence auditory processing as early as 130 ms, which may be useful in a fast identification and detection of stimulus changes.

The right hemispheric dominance of frontal and temporal regions in processing prosodic information has been

indicated by both lesion studies [Nicholson et al., 2003; Ross, 1981] and functional magnetic resonance imaging studies [Hesling et al., 2005; Plante et al., 2002]. Prosody is often regarded as the melodic line of speech, including the variation in pitch, rhythm, and accent in common, whereas such semantic or emotional modulation is independent from other speech processing, e.g., syntax that is clearly lateralized in the brain [Sakai, 2005]. Songs also consist of two independent components, lyrics and melody, albeit coordinated in an artistic way. It is thus intriguing to note that these different aspects of speech processing (syntax vs. prosody), or of music processing (lyrics vs. melody), correspond to the dominance of left and right brains. Our results reported here may shed new light on the similarity and difference of language and music processing.

Previous MEG studies have reported possible top-down influences on auditory processing of music, such that a musical training or aptitude enhanced the ECD strength of the MMNm and N1m, as well as N19m–P30m, when auditory stimuli were presented under an ignored condition [Fujioka et al., 2004; Pantev et al., 1998; Schneider et al., 2002]. The ECD strength of the N19m–P30m, the gray matter volume of the anteromedial portion of Heschl's gyrus, and the musical aptitude were also correlated each other [Schneider et al., 2002]. However, it is still unknown which processes musical experiences actually affect in the auditory cortex. In the present study, we suggest that the expectation based on stored memory provides a top-down influence on the right-dominant M130. Our results are consistent with the previous studies, in that the skills of expectation and thinking ahead are experience-dependent and critically involved in on-line monitoring of speech and music, thereby quickly detecting and correcting production errors.

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REFERENCES

Alho K, Connolly JF, Cheour M, Lehtokoski A, Huotilainen M, Virtanen J, Aulanko R, Ilmoniemi RJ (1998): Hemispheric lateralization in preattentive processing of speech sounds. Neurosci Lett 258:9–12.

Alho K, Medvedev SV, Pakhomov SV, Roudas MS, Tervaniemi M, Reinikainen K, Zeffiro T, Näätänen R (1999): Selective tuning of the left and right auditory cortices during spatially directed attention. Cogn Brain Res 7:335–341.

Aoyama A, Endo H, Honda S, Takeda T (2006): Modulation of early auditory processing by visually based sound prediction. Brain Res 1068:194–204.

Ayotte J, Peretz I, Rousseau I, Bard C, Bojanowski M (2000): Patterns of music agnosia associated with middle cerebral artery infarcts. Brain 123:1926–1938.

Besson M, Faïta F (1995): An event-related potential (ERP) study of musical expectancy: Comparison of musicians with nonmusicians. J Exp Psychol (Hum Percept Perform) 21:1278–1296.

Boemio A, Fromm S, Braun A, Poeppel D (2005): Hierarchical and asymmetric temporal sensitivity in human auditory cortices. Nat Neurosci 8:389–395.

Dennis M, Hopyan T (2001): Rhythm and melody in children and adolescents after left or right temporal lobectomy. Brain Cogn 47:461–469.

Embick D, Marantz A, Miyashita Y, O'Neil W, Sakai KL (2000): A syntactic specialization for Broca's area. Proc Natl Acad Sci USA 97:6150–6154.

Fujioka T, Trainor LJ, Ross B, Kakigi R, Pantev C (2004): Musical training enhances automatic encoding of melodic contour and interval structure. J Cogn Neurosci 16:1010–1021.

Gazzaniga MS (2000): Cerebral specialization and interhemispheric communication—Does the corpus callosum enable the human condition? Brain 123:1293–1326.

Geschwind N (1979): Specializations of the human brain. Sci Am 241:158–168.

Griffiths TD, Rees A, Witton C, Cross PM, Shakir RA, Green GGR (1997): Spatial and temporal auditory processing deficits following right hemisphere infarction—A psychophysical study. Brain 120:785–794.

Hari R, Kaila K, Katila T, Tuomisto T, Varpula T (1982): Interstimulus interval dependence of the auditory vertex response and its magnetic counterpart: Implications for their neural generation. Electroencephalogr Clin Neurophysiol 54:561–569.

Hashimoto R, Homae F, Nakajima K, Miyashita Y, Sakai KL (2000): Functional differentiation in the human auditory and language areas revealed by a dichotic listening task. Neuroimage 12:147–158.

Hesling I, Clément S, Bordessoules M, Allard M (2005): Cerebral mechanisms of prosodic integration: Evidence from connected speech. Neuroimage 24:937–947.

Imaizumi S, Mori K, Kiritani S, Hosoi H, Tonoike M (1998): Task-dependent laterality for cue decoding during spoken language processing. Neuroreport 9:899–903.

Jääskeläinen IP, Ahveninen J, Bonmassar G, Dale AM, Ilmoniemi RJ, Levänen S, Lin FH, May P, Melcher J, Stufflebeam S, Tiitinen H, Belliveau JW (2004): Human posterior auditory cortex gates novel sounds to consciousness. Proc Natl Acad Sci USA 101:6809–6814.

Johnson JA, Zatorre RJ (2005): Attention to simultaneous unrelated auditory and visual events: Behavioral and neural correlates. Cereb Cortex 15:1609–1620.

Knösche TR, Lattner S, Maess B, Schauer M, Friederici AD (2002): Early parallel processing of auditory word and voice information. Neuroimage 17:1493–1503.

Koelsch S, Gunter T, Friederici AD, Schröger E (2000): Brain indices of music processing: "Nonmusicians" are musical. J Cogn Neurosci 12:520–541.

Koelsch S, Gunter TC, von Cramon DY, Zysset S, Lohmann G, Friederici AD (2002): Bach speaks: A cortical "language-network" serves the processing of music. Neuroimage 17:956–966.

Kraemer DJM, Macrae CN, Green AE, Kelley WM (2005): Musical imagery—Sound of silence activates auditory cortex. Nature 434:158.

Lerdahl F, Jackendoff R (1983): A Generative Theory of Total Music. Cambridge, MA: The MIT Press.

Liégeois-Chauvel C, Peretz I, Babaï M, Laguitton V, Chauvel P (1998): Contribution of different cortical areas in the temporal lobes to music processing. Brain 121:1853–1867.

Maess B, Koelsch S, Gunter TC, Friederici AD (2001): Musical syntax is processed in Broca's area: an MEG study. Nat Neurosci 4:540–545.

McEvoy L, Mäkelä JP, Hämäläinen M, Hari R (1994): Effect of interaural time differences on middle-latency and late auditory evoked magnetic fields. Hear Res 78:249–257.

Miranda RA, Ullman MT: Double dissociation between rules and memory in music: An event-related potential study. Neuroimage 38:331–345.

Murayama J, Kashiwagi T, Kashiwagi A, Mimura M (2004): Impaired pitch production and preserved in a right brain-damaged patient rhythm production with amusia. Brain Cogn 56:36–42.

Näätänen R, Lehtokoski A, Lennes M, Cheour M, Huotilainen M, Iivonen A, Vainio M, Alku P, Ilmoniemi RJ, Luuk A, Allik J, Sinkkonen J, Alho K (1997): Language-specific phoneme representations revealed by electric and magnetic brain responses. Nature 385:432–434.

Näätänen R, Jacobsen T, Winkler I (2005): Memory-based or afferent processes in mismatch negativity (MMN): A review of the evidence. Psychophysiology 42:25–32.

Neelon MF, Williams J, Garell PC (2006): The effects of auditory attention measured from human electrocorticograms. Clin Neurophysiol 117:504–521.

Nicholson KG, Baum S, Kilgour A, Koh CK, Munhall KG, Cuddy LL (2003): Impaired processing of prosodic and musical patterns after right hemisphere damage. Brain Cogn 52:382–389.

Oldfield RC (1971): The assessment and analysis of handedness: The Edinburgh inventory. Neuropsychologia 9:97–113.

Pantev C, Oostenveld R, Engelien A, Ross B, Roberts LE, Hoke M (1998): Increased auditory cortical representation in musicians. Nature 392:811–814.

Patel AD (2003): Language, music, syntax and the brain. Nat Neurosci 6:674–681.

Plante E, Creusere M, Sabin C (2002): Dissociating sentential prosody from sentence processing: Activation interacts with task demands. Neuroimage 17:401–410.

Price CJ (2000): The anatomy of language: Contributions from functional neuroimaging. J Anat 197:335–359.

Rivier F, Clarke S (1997): Cytochrome oxidase, acetylcholinesterase, and NADPH-diaphorase staining in human supratemporal and insular cortex: Evidence for multiple auditory areas. Neuroimage 6:288–304.

Ross ED (1981): The aprosodias—Functional-anatomic organization of the affective components of language in the right hemisphere. Arch Neurol 38:561–569.

Sakai KL (2005): Language acquisition and brain development. Science 310:815–819.

Samson S (1999): Musical function and temporal lobe structures: A review of brain lesion studies. J New Music Res 28:217–228.

Sarvas J (1987): Basic mathematical and electromagnetic concepts of the biomagnetic inverse problem. Phys Med Biol 32:11–22.

Schneider P, Scherg M, Dosch HG, Specht HJ, Gutschalk A, Rupp A (2002): Morphology of Heschl's gyrus reflects enhanced activation in the auditory cortex of musicians. Nat Neurosci 5:688–694.

Sinkkonen J, Tervaniemi M (2000): Towards optimal recording and analysis of the mismatch negativity. Audiol Neurootol 5:235–246.

Stewart L, von Kriegstein K, Warren JD, Griffiths TD (2006): Music and the brain: Disorders of musical listening. Brain 129:2533–2553.

Tervaniemi M, Kujala A, Alho K, Virtanen J, Ilmoniemi RJ, Näätänen R (1999): Functional specialization of the human auditory cortex in processing phonetic and musical sounds: A magneto-encephalographic (MEG) study. Neuroimage 9:330–336.

Zatorre RJ, Evans AC, Meyer E (1994): Neural mechanisms underlying melodic perception and memory for pitch. J Neurosci 14:1908–1919.

Zatorre RJ, Belin P, Penhune VB (2002): Structure and function of auditory cortex: Music and speech. Trends Cogn Sci 6:37–46.