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Effects of Harmonic Expectations and Musical Expertise on Auditory Cortical Responses

- A Magnetoencephalography Study -

화성적 기대감과 전문성이 청각피질의 반응에 미치는 영향: 뇌자도 연구

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Abstract

Effects of Harmonic Expectations and Musical Expertise on Auditory Cortical Responses

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The present study investigated the effects of harmonic expectations and musical expertise on auditory cortical processing using magnetoencephalography (MEG). Numerous studies have demonstrated that musical experiences enhance auditory cortical processing; however, few studies have examined the effect of harmonic expectations on auditory cortical processing. Most studies regarding auditory cortical response enhancement have investigated acoustical sound without harmonic contexts as stimuli. Studies have demonstrated that harmonic expectations are processed in the inferior frontal gyri and elicit an early right anterior negativity (ERAN); however, the effect on the auditory cortex has rarely been examined.

The processing of auditory stimuli depends on both afferent and efferent auditory pathways. Behavioral studies have indicated that the chords harmonically related to the preceding context are more rapidly processed than unrelated chords. P2 (the positive auditory-evoked potential at approximately 200 ms) is principally affected by musical experience, and the source of P2 is the associative auditory temporal regions, with additional contributions from the frontal area. Based on anatomical evidence of interconnections between the frontal cortex and the belt and parabelt regions in the auditory cortex, we hypothesized that musical expectations would affect neural activities in the auditory cortex via an efferent pathway. To test this hypothesis, we created five-chord progressions with the third chord manipulated (highly expected, less expected, and unexpected) and measured the auditory-evoked fields (AEFs) of seven musicians and seven non-musicians while they listened to musical stimuli.

The results indicated that the highly expected chords elicited shorter N1m (negative AEF at approximately 100 ms) and P2m (a magnetic counterpart of P2) latencies and larger P2m amplitudes in the auditory cortex than the less-expected and unexpected chords. The relations between P2m amplitudes/latencies and harmonic expectations were similar between the groups; however, the results were more remarkable for the musicians than the non-musicians. These findings suggest that auditory cortical processing is enhanced by musical knowledge and long-term training in an efferent pathway, which is reflected by shortened N1m and P2m latencies and enhanced P2m amplitudes in the auditory cortex.

Keywords: auditory cortex, harmonic expectation, latency, musician, P2m

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1. Introduction

Western tonal music has a harmonic hierarchy that evokes musical expectancy along sequential chords. Thus, the same chords may be perceived to have different relationships, depending on the harmonic context. For example, “G-B-D and C-E-G” may be regarded as both “a dominant (V) and tonic chord (I)” in a key of C major and “a tonic and subdominant chord (IV)” in a key of G major (Poulin-Charronnat, Bigand, & Koelsch, 2006; Regnault, Bigand, & Besson, 2001).

These regularities establish musical syntax, which has been reported to be processed in right-lateralized structures in the frontal cortex (S.-G. Kim, Kim, & Chung, 2011; Koelsch, Rohrmeier, Torrecuso, & Jentschke, 2013; Leino, Brattico, Tervaniemi, & Vuust, 2007; Maess, Koelsch, Gunter, & Friederici, 2001), whereas the effects of the spectral properties of sound, training or experience, regardless of musical context, have been predominantly associated with subcortical regions or auditory cortices (Bidelman, Weiss, Moreno, & Alain, 2014; Fritz et al., 2013; Marmel, Parbery-Clark, Skoe, Nicol, & Kraus, 2011). The present question is whether harmonic expectancies generated in the frontal cortex influence auditory cortical processing in an efferent pathway.

However, most previous studies on auditory cortical representations have not focused on the effects of context; they have focused on the effects of training or experience. Neuroscientific studies have indicated that auditory-evoked potentials, including N1 (the negative component with a latency of approximately 90-110 ms) and P2 (the positive component with a latency of approximately 200 ms), for sounds are enhanced by musical training (Atienza, Cantero, & Dominguez-Marin, 2002; Itoh, Okumiya-Kanke, Nakayama, Kwee, & Nakada, 2012; Kaganovich et al., 2013; Pantev & Herholz, 2011; Pantev et al., 1998; Seppänen, Hämäläinen, Pesonen, & Tervaniemi, 2012; Tremblay, Ross, Inoue, McClannahan, & Collet, 2014), musical expertise (Itoh et al., 2012; Shahin, Bosnyak, Trainor, & Roberts, 2003), musical experience (Kuriki, Kanda, & Hirata, 2006; Pantev, Roberts, Schulz, Engelien, & Ross, 2001), and the degree of consonance (Itoh, Suwazono, & Nakada, 2003).

Behavioral studies have suggested that harmonic expectations enhance auditory processing. Previous behavioral studies have indicated that tonal expectations influence response times (Bharucha & Stoeckig, 1986; Tillmann, Janata, Birk, & Bharucha, 2008; Tillmann & Lebrun-Guillaud, 2006). Tonally expected chords are processed more rapidly than other chords (Tillmann & Lebrun-Guillaud, 2006), and response-time patterns reflect chord ranking according to the tonal structure, with faster processing for tonic chords, followed by dominant and subdominant chords (Tillmann et al., 2008). These findings may reflect enhanced auditory processing as a result of harmonically expected chords. Furthermore, as the auditory cortex (specifically, the belt and parabelt regions of the auditory cortex) is interconnected with the frontal cortex (Hackett, Stepniewska, & Kaas, 1999; Kaas & Hackett, 2000), harmonic expectations generated in the frontal cortex (Maess et al., 2001) might influence auditory cortical processing. In a study on musical perception, Platel et al. (1997) reported that familiar musical tasks activate both the left inferior frontal gyrus and superior temporal gyrus, and the results indicate an interconnection between the frontal and temporal gyri in processing music. Marmel, Perrin, and Tillmann (2011) demonstrated that cognitive tonal expectations modulate early pitch processing by eliciting Nb / P1 complexes of different amplitudes. In addition, Marmel, Parbery-Clark, et al. (2011) reported that harmonic relationships influence the auditory brainstem when encoding chords. However, there has been minimal research regarding the effects of expectations according to harmonic context on auditory cortical representations. Thus, the present study investigated the effects of musical context on the auditory cortical processing of sequential chords using magnetoencephalography (MEG).

2. Background

2.1. Musical Expectation

2.1.1. Musical Expectation and Behavioral Research

Western tonal music has harmonic rules or syntax, which may be defined as a set of principles that govern the combination of discrete structural elements into sequences (Jackendoff, 2002). Experienced listeners obtain implicit knowledge of these rules, which provoke expectations in their minds (Meyer, 2008). Expectancies built by extensive experience with Western tonal music reflect the learned mental representation of tonal relationships, or tonality (Leino et al., 2007).

Tonality refers to the organization of pitches in a way that one central pitch or chord dominates and attracts the other pitches or chords and provides names to the keys, such as tonic (I), supertonic (II), and mediant (III) (Bharucha, 1984; Bharucha & Krumhansl, 1983). The tonic note, the first note in the diatonic scale (major and minor scale), which consists of 7 tones, is in the center of Western tonality, which consists of 12 tones. Fig. 1 presents a slightly idealized configuration that displays the psychological distance among 13 tones (C, C#, D, D#, E, F, F#, G, G#, A, A#, B, C’) from C. Four tones in the core form the tonic triad in the key of C major, and tones within the second level become the diatonic scale (major or minor). The tones in the third level are out-of-key notes in the key of C major.

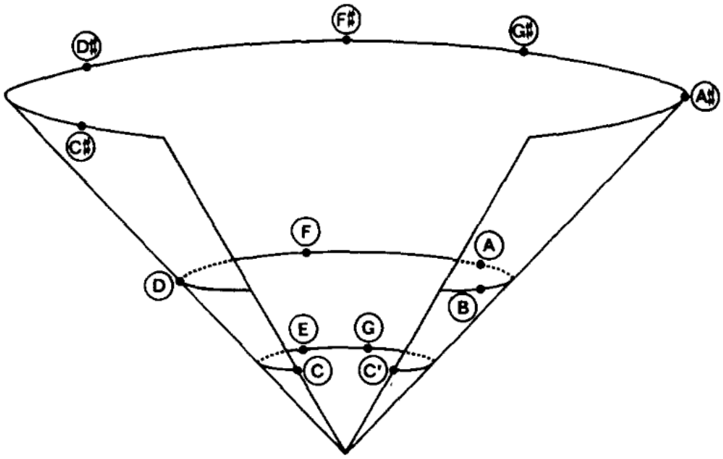

Figure 1. Idealized three-dimensional conical configuration for thirteen pitches to the ‘C’ note (from Krumhansl, 1979)

In Western music theory, chords are formed by the addition of the third and fifth notes on each diatonic scale note, which comprise seven chord-functions referred to as Roman numerals such as I, II, III, IV, V, VI, and VII. Among the seven chord-functions, a tonic chord (I) built on the tonic note is perceived as the most stable. A dominant chord (V) on the fifth note is regarded as tension-creating, demanding resolution to the stable state of a tonic chord (I) (Leino et al., 2007). Thus, the progression of “V – I” is referred to as an authentic cadence, particularly at the end of a musical phrase, which arouses strong expectancies. The tonic, dominant, and subdominant chords (IV; built on the fourth note) are the core of every key. Similarly, seven chords have their own functions in each key.

Fig. 2A shows seven chords in the two keys of C major and F# major respectively. There is no common chord between the two keys of C major and F# major. All chords in Fig. 2 are major triads, which are consonant. In Fig. 2B, the psychological distances between the chords are represented as spatial distances (Bharucha & Krumhansl, 1983). Even in the absence of a context, the fundamental three chords (I, IV, and V) are close to each other (Fig. 2B). However, if a context is presented prior to a target chord, the chords in the same key become closer to each other, whereas the chords in the different keys become farther apart (Fig. 2C) (Bharucha & Krumhansl, 1983).

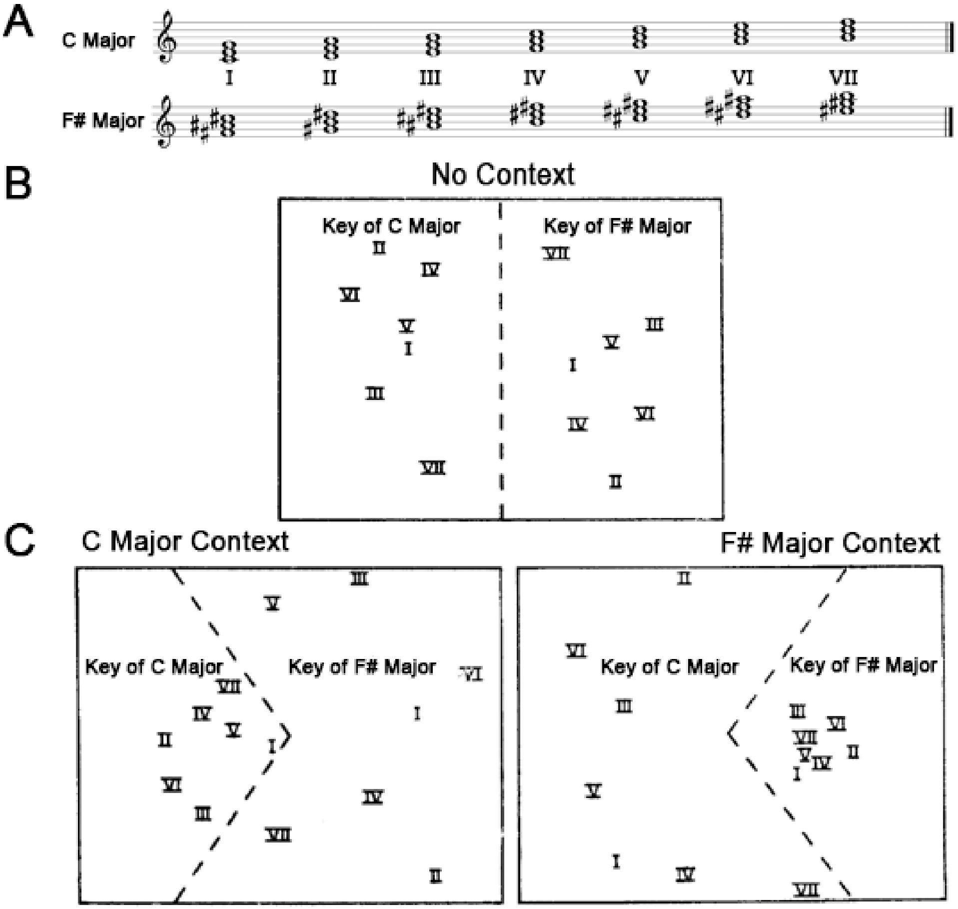

Figure 2. Fourteen chords in the keys of C major and F# major and psychological distances between the chords with/without context (from Bharucha & Krumhansl., 1983)

A chord can prime tonality, which affects the reaction time for processing the following chords. For a task of in-tune/out-of-tune decision, the reaction time was faster when related than when unrelated (Bharucha & Stoeckig, 1986). The harmonic context that consists of a chord sequence primes the processing of chords in accordance with the context and induces expectations in a listener’s mind (Bharucha & Stoeckig, 1986). The processing of the 2-chord endings with the relationship of the fifth (i.e., G-B-D & C-E-G) was affected by the previous musical context, including 6-chord sequences (Tillmann & Lebrun-Guillaud, 2006), because the 2-chord endings with the relationship of the fifth may be an authentic cadence depending on the previous musical context, which is highly expected. In this case (expected), the reaction time is faster than the other (unexpected) (Tillmann & Lebrun-Guillaud, 2006). The reaction time patterns reflect the harmonic hierarchy: Processing is the fastest for I, followed by V and then IV (Tillmann et al., 2008). Schmuckler and Boltz (1994) reported that harmonic and rhythmic variation also influenced the reaction times of musical processing.

2.1.2. Musical Expectation and Neuroscientific Research

We may perceive the same chords to be different in accordance with the musical context or musical syntax. For example, a C major chord – F major chord may be regarded as the dominant (V) – tonic chord (I), the so-called authentic cadence, in the key of F major and may also be regarded as the tonic (I) – subdominant (IV) in the key of C major. The former is more stable than the latter according to musical context; however, they are acoustically the same. Poulin-Charronnat et al. (2006) investigated the brain responses for these types of musical stimuli using event-related potentials (ERPs). They determined that an N5-like frontal negative component was larger for subdominant than tonic chords and attained significance only in musically expert listeners (Poulin-Charronnat et al., 2006). In some cases, the early right anterior negativity (ERAN) was followed by an N5 (Koelsch, Gunter, Friederici, & Schröger, 2000; Loui, Grent-'t-Jong, Torpey, & Woldorff, 2005), which has been interpreted as reflecting the integration of musical events into their tonal context (Koelsch et al., 2000). Most studies on harmonic expectations have demonstrated that the processing of harmonic expectations is associated with the frontal cortex (Koelsch et al., 2000; Koelsch et al., 2001; Maess et al., 2001).

Many neuroscientific studies have reported that an ERAN with a latency of approximately 180 ms over the right anterior electrode sites is elicited when a harmonically unexpected chord is heard (C. H. Kim et al., 2014; S.-G. Kim et al., 2011; Koelsch et al., 2000; Koelsch, Jentschke, Sammler, & Mietchen, 2007; Koelsch & Sammler, 2008; Koelsch, Schmidt, & Kansok, 2002; Maess et al., 2001). Koelsch et al. (2000) indicated the violation of harmonic expectancy to be reflected in the ERP as an ERAN and the processing of musical integration to be reflected as a late-bilateral negativity (N5). An ERAN was elicited by irregular chords under both task-relevant and task-irrelevant conditions (Koelsch et al., 2007).

The ERAN occurs at an early latency (150-250 ms after stimulus onset) and is maximal over anterior regions of the scalp with a tendency to be lateralized to the right (Leino et al., 2007). The source of the mERAN (the magnetic counterpart of the ERAN) was determined to be in the Broca’s area (BA44), which is related to producing language and processing syntax, using MEG, and its right hemispheric homologue, with a tendency towards right hemispheric dominance (Maess et al., 2001). Other studies have reported that the response elicited by a harmonically inappropriate chord occurred found bilaterally (Leino et al., 2007; Loui et al., 2005). Thus, a similar nomenclature of EAN (the early anterior negativity) has recently been adopted to designate the component associated with processing musical syntax or harmony and elicited in the frontal area (Loui et al., 2005).

Patel, Gibson, Ratner, Besson, and Holcomb (1998) reported that out-of-key target chords elicited a positive ERP component with a maximum at approximately 600 ms (P600) and right anterior temporal negativity (RATN) after onset. The P600 component has been shown to be elicited by harmonically unexpected events (Besson & Faïta, 1995; Besson, Faïta, & Requin, 1994; Besson & Macar, 1987; Levett & Martin, 1992).

The P3 component was larger in response to the less expected chord (IV) than the most expected chord (I) (Regnault et al., 2001). The P3b was largest in response to unrelated chords, followed by minor chords, whereas it was smallest in response to tonic chords (Janata, 1995). The diversity of the observed components suggests that tonal expectations modulated perception at several processing stages (Marmel, Perrin, et al., 2011).

2.2. Musical Expertise and the Brain

A musician’s brain has been regarded as an ideal model for plasticity studies (Sittiprapaporn, 2012). Most musicians started playing musical instruments at a very early age and continue to practice intensively for a very long period of time. Intensive music training for a long-term period has a substantial influence on the brain (Sittiprapaporn, 2012). Learning to play an instrument is a highly complex task that involves the interaction of several modalities and sophisticated cognitive functions, and it results in behavioral, structural, and functional changes in the brain (Herholz & Zatorre, 2012).

Previous studies have demonstrated that musicianship enhances functional plasticity across multiple sensory modalities that benefit a wide range of perceptual-cognitive capacities (Herholz & Zatorre, 2012). Musicianship may cause neuro-plastic changes in the brainstem and cortical structures, as well as improved acuity for behaviorally relevant sounds including speech, which may result in linguistic advantages (Bidelman et al., 2014). Musicians’ subcortical and cortical neural enhancements have been correlated with their years of formal music training (Bidelman et al., 2014). Although the effects of musical training on cortical representations may be larger if training is initiated in childhood, the adult brain may also change (Trainor, Shahin, & Roberts, 2003).

Learning or training creates physiological changes in synaptic transmissions, which occur in the nervous system (Lamprecht & LeDoux, 2004). The changes may be explained by Hebbian learning rules: “when an axon of cell *A* is sufficiently near to excite cell *B* and repeatedly or persistently participates in firing it, a growth process or metabolic change occurs in one or both cells such that *A*'s efficiency, as one of the cells firing *B*, is increased” (Hebb, 1949). The brain plasticity gained by learning or training may be explained by long-term potentiation (LTP), which is a persistent strengthening of synapses (Cooke & Bliss, 2006). In general, LTP is considered one of the major cellular mechanisms that underlie learning and memory (Bliss & Collingridge, 1993; Cooke & Bliss, 2006) and is important for rapid learning.

Previous ERP studies have reported that non-musicians can process harmonic regularities (Koelsch et al., 2000; Koelsch, Schroger, & Gunter, 2002). However, other studies have indicated that less salient harmonic irregularities are processed only by musically expert listeners (Koelsch, Schroger, et al., 2002; Poulin-Charronnat et al., 2006). The ERAN has been shown to be larger in musical experts than novices (Koelsch, Schmidt, et al., 2002), and amateur musicians are slightly more sensitive to musical irregularities than non-musicians (Koelsch et al., 2007). Moreover, an N5-like frontal negative component for musical expectations attained significance only in musically expert listeners (Poulin-Charronnat et al., 2006).

Highly skilled musicians also exhibit enhanced auditory cortical representations (N1) for musical timbres associated with their principal instrument compared with those associated with other instruments (Pantev et al., 2001). The effect may be interpreted as use-dependent plasticity, in which more neurons were involved in representing and processing the musical sounds produced by their principal instruments or that neurons serving these functions fired more synchronously (Pantev et al., 2001).

Previous studies have demonstrated that the P2 amplitude was enhanced by various types of auditory training experiences, including music and speech-sound training (Kuriki, Ohta, & Koyama, 2007; Shahin et al., 2003; Tremblay et al., 2014). The P2 amplitude increased across repeated EEG sessions, which form a type of auditory training, and this effect was retained for months (Tremblay et al., 2014). The P2m amplitude for successive stimuli was significantly larger in musicians than non-musicians (Kuriki et al., 2006).

Moreover, the P2 amplitudes are larger in musicians than non-musicians (Pantev et al., 2001; Shahin et al., 2003). Recent neuroscientific studies have highlighted the effect of musical expertise on pitch processing by showing that musicians have better pitch encoding than non-musicians at the subcortical level of the brainstem (Musacchia, Sams, Skoe, & Kraus, 2007; Wong, Skoe, Russo, Dees, & Kraus, 2007).

2.3. Music and Auditory Cortical Responses (N1 & P2)

While previous studies on the cognitive processing of music, including harmonic expectations or musical syntax, have reported it to be associated with the frontal area or ERAN, most studies on auditory cortical responses for music have mainly reported the processing of acoustical features for auditory stimuli or an enhancement of perceptual processing by musical training or expertise.

2.3.1. Auditory Cortical Responses

The auditory P1 component dominates the ERP response to auditory stimuli in early childhood, has a latency of approximately 100 ms and originates from the lateral portion of Heschl’s gyrus (Ponton, Eggermont, Kwong, & Don, 2000; Sharma, Kraus, McGee, & Nicol, 1997; Wunderlich, Cone-Wesson, & Shepherd, 2006). The auditory P1 is followed by the N1, which is generated within the primary and secondary auditory cortices (Habibi, Cahn, Damasio, & Damasio, 2016; Näätänen & Picton, 1987). The development of the central auditory pathway leads to a decrease in the P1 amplitude and latency and an increase in the N1 amplitude, which is completed by young adulthood (Habibi et al., 2016; Ponton et al., 2000; Shahin, Trainor, Roberts, Backer, & Miller, 2010; Sharma et al., 1997; Tierney, Krizman, & Kraus, 2015; Wunderlich & Cone-Wesson, 2006).

Mismatch negativity (MMN) is a brain response to violations of a rule established by a sequence of sensory stimuli, particularly auditory stimuli (Saarinen, Paavilainen, Schöger, Tervaniemi, & Näätänen, 1992). MMN is elicited by sudden changes in stimulation and peaks at approximately 100-250 ms from the change onset in the temporal and frontal areas (Sams, Paavilainen, Alho, &

Näätänen, 1985). MMN reflects the brain’s ability to perform automatic comparisons between consecutive stimuli and provides an electrophysiological index of sensory learning and perceptual accuracy (Garrido, Kilner, Stephan, & Friston, 2009).

The robustness of the P2m response to repetitive stimuli may be related to object analysis in the “what” pathway of auditory information, whereas N1/N1m responses may be related to spatial analysis or the “where” pathway of auditory information (Jääskeläinen et al., 2004; May et al., 1999; Rauschecker & Tian, 2000; Romanski, Bates, & Goldman-Rakic, 1999).

2.3.2. Auditory Cortical Responses by Acoustical Features

Harmonically incongruous chords elicit an ERAN, whereas mistuned chords elicit a bilateral fronto-central negativity (the mismatch negativity, MMN) (Leino et al., 2007). In general, MMN is considered to be elicited by physical or abstract deviants (Koelsch, 2009; Saarinen et al., 1992). Thus, the generation of MMN is based on representations of the regularities of relationships between sounds that are extracted from the acoustic environment (Koelsch, 2009).

Acoustical features for simultaneous sounding tones or the complexity of a tone or harmonics are mainly associated with P2. The auditory P2 is a positive potential generated at approximately 200 ms in the region lateral to Heschl’s gyrus in the secondary auditory cortex (Pantev, Eulitz, Hampson, Ross, & Roberts, 1996;

Picton et al., 1999; Scherg, Vajsar, & Picton, 1989; Shahin, Roberts, Pantev, Trainor, & Ross, 2005). P2 amplitudes are significantly modulated by the pitch interval of dyads, and they are most negative for 1 semitone (minor second, dissonance) and most positive for 7 semitones (perfect fifth, consonance) (Itoh et al., 2003).

The dipole moment of P2m (the magnetic counterpart of P2) was significantly larger for chord tones than single tones (Kuriki et al., 2006). P2m activity may be specialized for the processing of multifrequency sounds, such as musical timbre that consists of abundant harmonics (Kuriki et al., 2006).

Lütkenhöner, Seither-Preisler, and Seither (2006) reported that N1 components were also increased to piano tones compared with sine tones. However, Shahin et al. (2005) demonstrated that there was no difference in the N1 amplitude to instrumental tones compared with sine tones; in contrast, there was difference in the P2 amplitude, although only in musicians.

The P2 enhancement is specific to the instrument of practice (Shahin, Roberts, & Trainor, 2004). Early musical experience may account for the timbre-specific P2 and N1 enhancements that were present for the instrument for practice. P1, N1, and P2 enhancements in young music students are predominately a result of their musical experience (Shahin et al., 2004).

2.3.3. Enhancement of N1 and P2 by Training

The auditory N1 and P2 components reflect the processing of stimulus features that may be modulated by factors such as task demands (Pantev & Herholz, 2011). In general, P2 has been considered to be an automatic response, which is modulated only by the stimulus; however, it has been reported that its latency and amplitude are affected by learning and attentional processes (Lappe, Trainor, Herholz, & Pantev, 2011). Crowley and Colrain (2004) suggested that P2 activity may reflect auditory processing beyond sensation. Most studies have indicated that P2 amplitudes are larger in musicians than non-musicians (Pantev et al., 2001; Shahin et al., 2003).

In the preceding chapter, the enhancement of P2 to sound with abundant harmonics was discussed. In particular, the effect is more remarkable in musicians than non-musicians (Pantev et al., 1998; Shahin et al., 2005). The P2/P2m amplitudes for musical timbre are also increased by musical expertise (Kuriki et al., 2006; Shahin et al., 2003). The auditory cortical strength (N1 and P2) of musicians was larger for piano or instrumental tones than for pure tones, whereas there was no significant difference between the two types of tones in non-musicians (Pantev et al., 1998; Shahin et al., 2005). The N1 response is also enhanced by timbre training. Pantev et al. (2001) reported that N1 amplitudes were increased for the timbres of the instrument of training in violinists and trumpeters. Kaganovich et al. (2013) discovered that musicians had larger N1 and P2 components not only in musical sounds but also in other complex sounds, such as voice and artificial sounds.

The differences between musicians and non-musicians in auditory cortical responses may originate from their innate factors; however, they may be primarily affected by musical training or experience. Previous studies have indicated that musical training enhances the sensory encoding of musical sounds, thereby eliciting increased amplitudes of the N1 and P2 ERP components in musicians compared with those in non-musicians (Fujioka, Ross, Kakigi, Pantev, & Trainor, 2006; Pantev et al., 1998; Shahin et al., 2003; Shahin et al., 2004). Music training enhances rapid neural plasticity of N1 and P2 source activation for unattended sounds, which indicates faster auditory perceptual learning in musicians (Seppänen et al., 2012). The P2/P2m amplitude is larger in musicians than non-musicians; however, auditory training enhances this component in non-musicians (Kuriki et al., 2006; Shahin et al., 2003). The P2 amplitude is enhanced by training in acoustic discrimination with complex sounds (Atienza et al., 2002; Reinke, He, Wang, & Alain, 2003; Tremblay et al., 2001).

Musicians also exhibited a larger MMN amplitude in response to changes in chords, melody and rhythm (Brattico, Tervaniemi, Näätänen, & Peretz, 2006; Koelsch, Schröger, & Tervaniemi, 1999; Vuust et al., 2005). Music training influence on the early auditory cortical representation of pitch transitions as indexed by so-called change-N1s, which were more posterior in scalp distribution (Itoh et al., 2012). In general, the enhancement effects were right-dominant at temporal electrode sites (Itoh et al., 2012). Musicians have been reported to have enhanced N1/N1m for musical stimuli (Pantev et al., 1998; Shahin et al., 2003). Atienza et al. (2002) demonstrated an enhanced P2 at 24 hours after training and an enhanced MMN at 36 hours after training. Musical training may influence brain processing over time.

The instrumental sound for long-term training may activate many more regions in the brain than other sounds. According to an fMRI study, when listening to a real musical piece (J.S. Bach Partita) played on the instrument of expertise (i.e., when violinists listened to violin music and when flutists listened to flute music), an extensive cerebral network of expertise, including the BA 44, auditory association cortex, and precentral gyrus, was identified compared with when the same piece was played on an instrument of non-expertise (i.e., when subjects listened to music played on an instrument other than the one they play) (Margulis, Mlsna, Uppunda, Parrish, & Wong, 2009). Therefore, the effect of musical training on the auditory cortical responses should be investigated in the context of the interactive neural network.

2.4. The Efferent Pathway

The processing of auditory stimuli depends on the integrity of the afferent and efferent auditory pathways (Burguetti & Carvallo, 2008). Among the largest pathways in the brain, descending projections from sensory areas of the cerebral cortex play an important role in subcortical processing (Bajo, Nodal, Moore, & King, 2010). Subcortical and cortical processing dynamically interact in an experience-dependent manner in auditory information perception (Bajo et al., 2010; Tzounopoulos & Kraus, 2009).

Previous behavioral studies have indicated that tonal expectations may influence music perception (Bigand & Poulin-Charronnat, 2006; Krumhansl, 2001; Tillmann, Bharucha, & Bigand, 2000). Marmel, Tillmann, and Dowling (2008) reported the behavioral result that tonal expectations influence pitch perception even at the perceptual processing stage.

Neuroscientific research has also identified the effect of musical knowledge or expectations on auditory processing in the efferent pathway. Marmel, Perrin, et al. (2011) reported that cognitive tonal expectations modulated pitch perception, with a difference in an Nb/P1 complex or N2/P3 amplitude between tonally related and less-related conditions. The N1 was largest for a dominant note among notes in a diatonic scale with the exception of a tonic note (Krohn, Brattico, Välimäki, & Tervaniemi, 2007). When five-note melodies were simultaneously presented in the visual and auditory modalities, the N1 was larger for an implausible than plausible note in terms of tonal expectations. (Schön & Besson, 2005). Context and familiarity enhanced the MMN amplitude and musical expertise shortened the MMN latency for pitch perception under pre-attentive conditions (Brattico, Näätänen, & Tervaniemi, 2001).

According to previous auditory brainstem research, higher spectral response magnitudes exist in the harmonically related than in the unrelated or repeated conditions for both musician and non-musician listeners (Marmel, Parbery-Clark, et al., 2011). The result suggested that listeners' implicit knowledge of musical regularities influences subcortical auditory processing via an efferent pathway (Marmel, Parbery-Clark, et al., 2011; Tzounopoulos & Kraus, 2009).

Previous anatomical studies have shown connections between prefrontal and auditory cortices (Hackett et al., 1999; Kaas & Hackett, 2000). An fMRI study reported that activation for a familiarity music task occurred in the left frontal gyrus and superior temporal areas (Platel et al., 1997). Thus, even if harmonic expectations may be primarily processed in the frontal areas that elicit an ERAN (Koelsch et al., 2000; Maess et al., 2001), expectations may affect processing at the lower levels, including the auditory cortex and subcortical regions.

Among auditory ERPs, P2 is the most affected by musical training or expertise. Previous studies have indicated that the P2 component is larger in musically trained participants than in non-trained participants and have suggested that the P2 component is principally neuroplastic of the cortical sound representation affected by auditory experience (Shahin et al., 2003; Shahin et al., 2004; Trainor et al., 2003). The source of P2 is the associative auditory temporal regions, with additional contributions from the frontal area (Bishop, Anderson, Reid, & Fox, 2011; Tremblay et al., 2001). Although P2 is principally affected by musical experience, few studies have examined the effect of musical expectations on P2. Therefore, we aimed to investigate the effect of harmonic expectations on auditory cortical responses, particularly P2m using MEG.

2.5. Magnetoencephalography

MEG is a noninvasive technique that detects the magnetic fields produced by the electrical current of neuronal activity with multichannel superconducting quantum interference device (SQUID) gradiometers (Hämäläinen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993). When the brain is processing information, extremely small currents flow in the neural system and generate a weak magnetic field, which may be measured by a SQUID magnetometer set outside the skull (Hämäläinen et al., 1993).

Various imaging methods for the human brain have become available (Martin & Pechura, 1991). Brain structures may be explored via computer-assisted X-ray tomography (CT) and magnetic resonance imaging (MRI). Brain functions may be investigated with single-photon-emission computed tomography (SPECT) and positron-emission tomography (PET). A novel echo-planar technique enables functional imaging with MRI (fMRI) with a one-second time resolution (Belliveau et al., 1991). These methodologies enable brain research to explore brain structures and functions without opening the skull; however, the participant is exposed to X-rays, radioactive tracers, or strong static magnetic fields (Hämäläinen et al., 1993).

Electroencephalography (EEG) is the measurement of electric potential differences from electrodes on the scalp. MEG and EEG are related in terms of their measurement of signals generated by the same synchronized neuronal activity in the brain (Hämäläinen et al., 1993). The time resolution of MEG and EEG is in the millisecond range, which is a strong advantage for inspecting the rapid changes in cortical activities (Hämäläinen et al., 1993). Another principal benefit of MEG and EEG is their noninvasiveness.

The MEG equipment utilized in the present experiment was a 306-channel whole head MEG system (VectorView, Elekta Neromag Oy, Finland) with 102 identical triple-sensor elements. Each sensor comprises two orthogonal planar gradiometers and one magnetometer on the same wafer.

3. Objectives and Hypothesis

The present study aimed at identifying the effects of harmonic context and musical expertise on the auditory cortical processing of sequential chords using MEG. The hypothesis was that harmonically expected chords would enhance auditory cortical responses, and that the effect would be more remarkable in musicians than in non-musicians.

4. Methods

4.1. Participants

Fourteen subjects, including seven female musicians (mean age ± SD, 23.6 ± 10.91 years) and five female and two male non-musicians (mean age ± SD, 20.4 ± 1.72 years) participated in the experiment. The study was approved by the Ethics Committee of Seoul National University, Korea. All of the participants signed informed consent forms in accordance with the Institutional Review Board, and the experiment was performed in accordance with the Declaration of Helsinki. The participants were right-handed and had Edinburgh Handedness Inventory scores exceeding 79%. The participants in the musician group had majored in piano, violin, and composition and had spent an average of 25,370 hours (minimum of 19,580 hours) studying music throughout their lives, whereas the participants in the non-musician group had taken less than 600 hours of formal music lessons.

4.2. Stimuli

The harmonic progressions used in the experiment consisted of five chords and a rest. The durations of the first to fourth chords were 800 ms, the fifth chord lasted 1,200 ms, and the rest (silence) lasted 400 ms. Each chord was a major triad (e.g., C-E-G and G-B-D), representing a consonance. The standard progression was I – I – V – V – I. We manipulated harmonic expectations at the third trigger (T3) to create three conditions with different degrees of harmonic expectancies (Fig. 3). First, a dominant chord (V) at T3 was highly expected. Second, a Neapolitan 6th chord (N^6: F-$A^\flat$-$D^\flat$ in the key of C major) at T3 was less expected than a dominant chord but remained plausible because N^6 functions as a predominant chord (before V), which is similar to a subdominant (IV) chord according to Western traditional music theory, although N^6 has two out-of-key notes. Third, a flatted mediant chord (♭III) at T3 was unexpected and implausible in the musical context, although ♭III had two out-of-key notes similar to N^6. A dominant (V), Neapolitan 6th (N^6), and flatted mediant chord (♭III) at T3 are all consonances, as major triads, but have different expectancies depending on the musical context. The three types of stimuli were transposed into 12 keys, and each sequence was presented five times in a pseudorandom order to avoid repeating the same keys twice in a row.

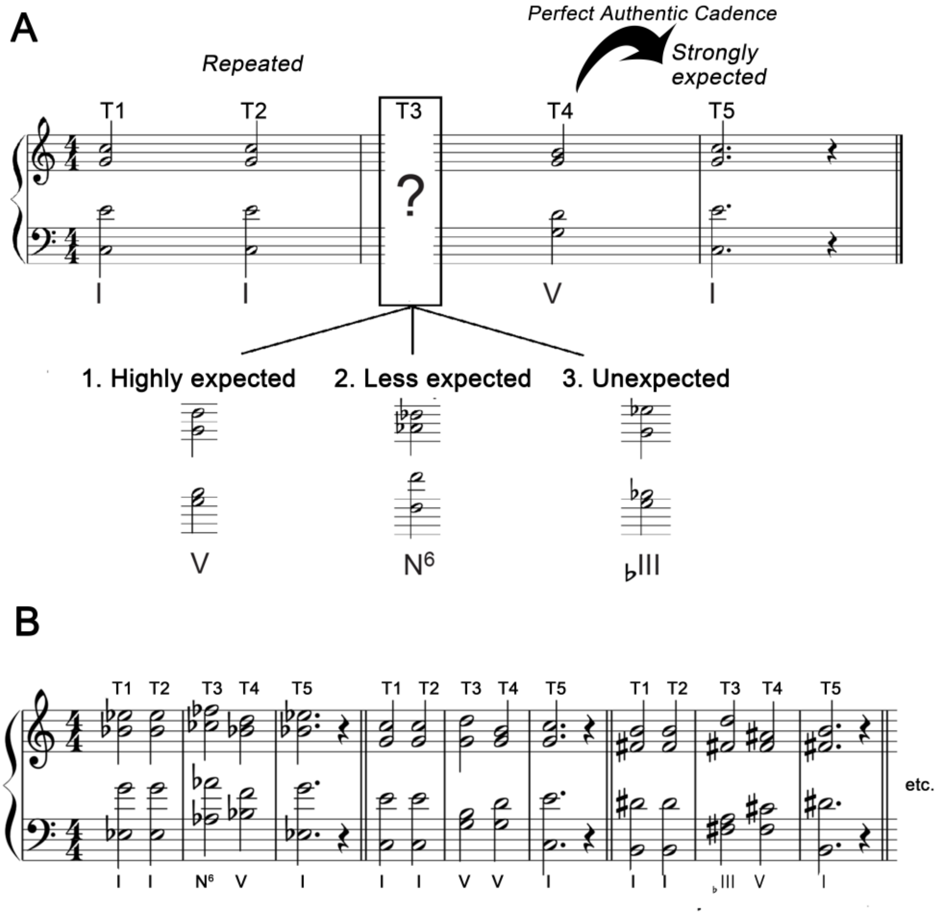

Figure 3. (A) Stimuli. At the 3rd trigger (T3) of a chord progression, a dominant chord (V) was highly expected, a Neapolitan chord (N^6) was less expected, and a flatted mediant chord ($\flat$III) was unexpected based on the musical context. T2 and T5 were identical tonic chords (I), although T2 was repeatedly presented after the previous chord (T1) and T5 was strongly expected because the final two chords (V – I) built a perfect authentic cadence. (B) Stimuli sequence. The three stimuli types were transposed into 12 keys, and each progression was presented five times in a

pseudorandom order to avoid repeating the previous key. Thus, T1 could not be expected and T5 was strongly expected.

Although T1, T2, and T5 were identical as tonic chords, T2 was simply a repetition of T1, and T5 was presented with strong expectations because T4 and T5 built a perfect authentic cadence (V – I) (Fig. 3). T2 was superior to T5 in terms of acoustic similarities between previous chords, whereas T5 was superior to T2 in terms of harmonic expectations. Thus, the former (acoustical similarities) is related to a bottom-up process, whereas the latter (harmonic expectations) is related to a top-down process. Hence, a comparison between the effects of T2 and T5 helps untangle the two types of processes.

4.3. Procedures

The participants sat in a magnetically shielded room listening to the musical stimuli at a sound pressure level of approximately 60 dB using a STIM 2 system (Neuroscan, Charlotte, NC, USA) via MEG-compatible tubal-insert earphones during the MEG recording. Before the experiment, the participants were instructed to stay awake and to view a fixation cross at a comfortable distance to reduce retinal movement while the evoked magnetic fields were being recorded. Two sessions were conducted, and in each session, the participants listened to 180 sequences consisting of five chords. Participants wanting to rest between the sessions were allowed to do so. Each of the two sessions lasted approximately 11 minutes.

4.4. Magnetoencephalography Recordings

AEF recordings were acquired using a 306-channel whole-head MEG system (VectorView, Elekta Neuromag Oy, Helsinki, Finland) at the Seoul National University Hospital. This system measured magnetic field strength in 102 locations, which were covered by a triplet of sensors (two planar gradiometers and one magnetometer). The MEG signals were analog-filtered between 0.1 and 200 Hz at a sampling frequency of 600.615 Hz. Head movements were tracked with four additional head position indicator coils attached to each participant's head. To remove MEG artifacts, the temporal signal space separation (tSSS) method was used with MaxFilter software (Elekta Neuromag Oy, Helsinki, Finland). Source localization was performed in three-dimensional space, with the x-axis from left to right, the y-axis toward the nasion, and the z-axis toward the vertex.

4.5. Data Analysis

The MEG signals were bandpass filtered between 1 and 20 Hz by IIR filters and averaged using MATLAB 7.5.0.342 software (MathWorks Inc., Natick, MA, USA), the MATLAB toolbox (Fiff Access 1.2, Brain Research Unit, Low-Temperature Laboratory, Helsinki University of Technology, Helsinki, Finland) and in-house software. Epochs in the data were defined from 100 ms prior to 800 ms after each chord onset, and a baseline correction with the pre-stimulus period average (-100 to 0 ms) was performed. Epochs with electrooculography (EOG) artifacts were excluded automatically using MATLAB to retain approximately 90% of the data. For this, we determined threshold values individually. To investigate auditory cortical responses, we selected 26 gradiometer channels around the bilateral temporal lobes as the regions of interest (ROIs) as shown in Fig. 4. The AEFs from the ROIs were averaged, and root mean square (RMS) values were calculated using MATLAB software. In Fig. 4, the blue lines indicate the AEFs from 26 gradiometer-channels, and the red lines indicate the RMS values of the ROIs. To obtain individual N1m and P2m amplitudes and latencies, we selected the peak points in the RMS waveforms in the temporal ROIs at approximately 100 (70 – 170 ms) and 200 ms (140 – 250 ms), respectively. Overall, the second peak on the RMS waveforms was regarded as N1m, and the third peak was regarded as P2m. The data were statistically evaluated with a repeated-measures analysis of variance (ANOVA) and paired *t*-tests using IBM SPSS Statistics 19 software (SPSS Inc., Chicago, IL, USA). As a post hoc analysis, we conducted Bonferroni-corrected multiple comparisons.

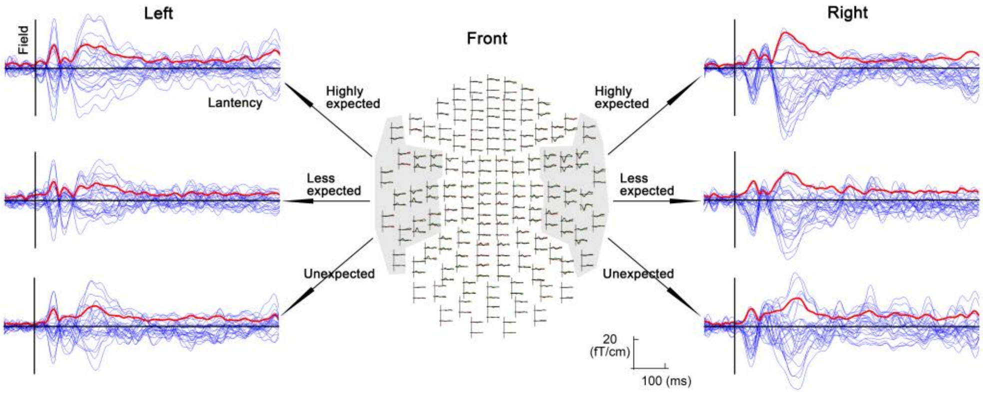

Figure 4. A participant's AEFs in the bilateral temporal ROIs. The middle section shows a participant's AEFs for three conditions of the musical expectations in 204 gradiometers; The shaded regions are the selected ROIs used to investigate auditory processing, and they include 26 gradiometer channels around the bilateral temporal lobes. In the left and right graphs, the blue lines indicate the 26 AEFs from each channel, and the red lines indicate the RMS waveforms from the 26 channels. The top graphs are the waveforms for the highly expected chords, the middle graphs are for the less-expected chords, and the bottom graphs are for the unexpected chords.

4.6. Source Localization

The parameters for equivalent current dipoles were estimated for the target chords using *xfit* (source modeling) by Neuromag^{TM}. A spherical model was applied to estimate volume conduction. To determine the sources of the differences between conditions, we first obtained the differences in waves by subtracting the AEFs of the highly expected chords from those of either the less-expected or unexpected chords (N^6 – V and ♭III – V). Then, to compare locations among the sources, we conducted dipole solutions of N1m and P2m for the highly expected chord. To conduct dipole solutions of N1m, P2m, N^6 – V, and ♭III – V, as shown in Fig. 5, we first chose the peak points of the overall wave, and at these points, we selected channels showing large amplitudes and then fitted dipoles to them with goodness-of-fit index values of over 0.91. The data from these processes were registered to an MRI image using MRIlab (Elekta-Neuromag Oy, Helsinki, Finland) (Fig. 5).

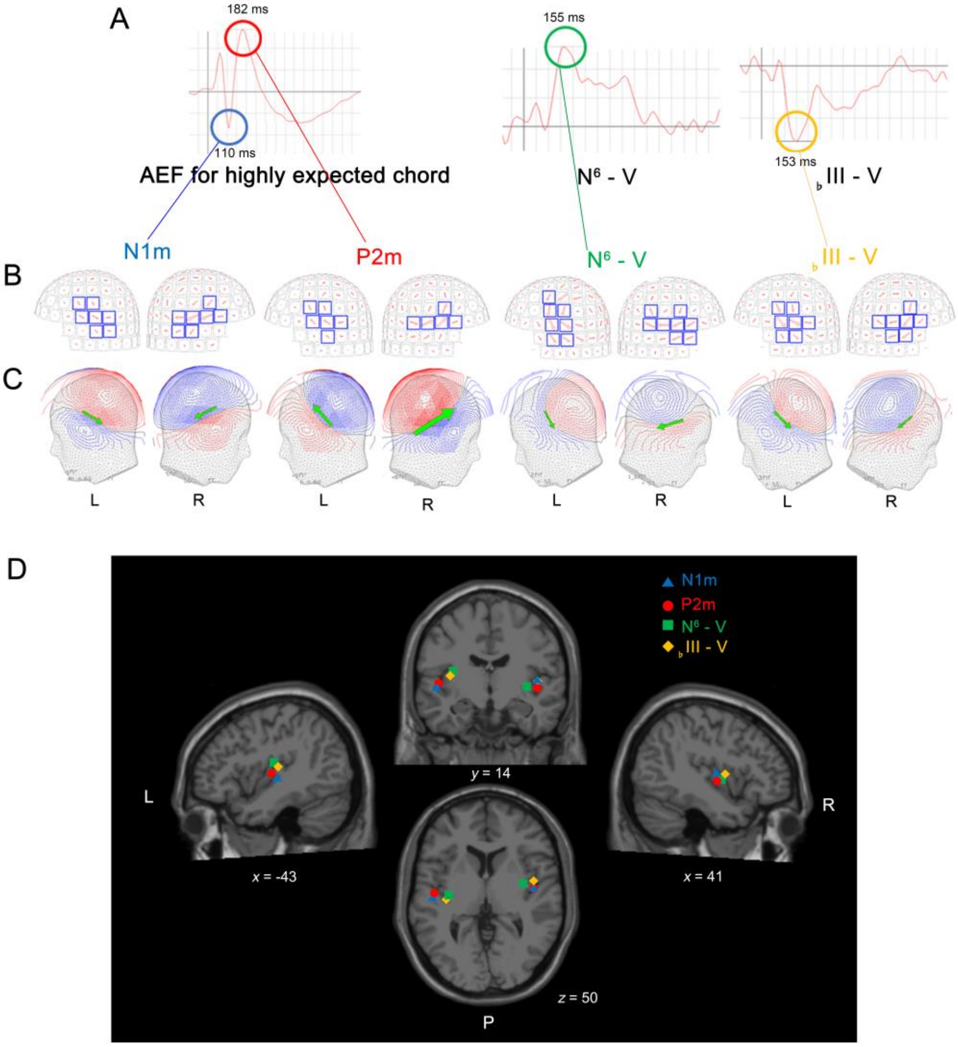

Figure 5. Dipole solutions for difference waveforms (N^6 – V and ♭III – V), N1m and P2m for the expected chord (V). (A) The peak points for dipole fitting on the grand averaged waves from all 204 gradiometers; N1m (110 ms), P2m (182 ms), N^6 – V (155 ms), and ♭III – V (153 ms). (B) Selected coils. Each coil has two gradiometers and one magnetometer. The coils showing large amplitudes were selected for dipole

fitting, which are outlined with blue lines. (C) Topographies of dipoles by the selected channels. The green arrows present the direction and moment of dipoles, the “L” indicates the left hemisphere and “R”indicates the right hemisphere. (D) Source localization. Four panels present two sagittal (left and right), a coronal, and an axial view (L: left, R: right, P: posterior). The blue triangles indicate N1m, the red circles indicate P2m, the green squares indicate N^6 – V, and the yellow diamonds indicate ♭III – V. The generators of N^6 – V and ♭III – V, N1m, and P2m were located in the auditory cortices.

5. Results

5.1. Auditory-Evoked Fields (AEFs) for Three Conditions at T3 (3rd Trigger)

For the peak latencies of AEFs, we identified significant results in both N1m and P2m (Fig. 6). Fig. 6 shows the RMS waveforms for the three conditions (highly expected, less expected, and unexpected) in the left and right temporal ROIs (A), as well as the N1m latencies and P2m amplitudes and latencies at approximately 100 and 200 ms, respectively (B).

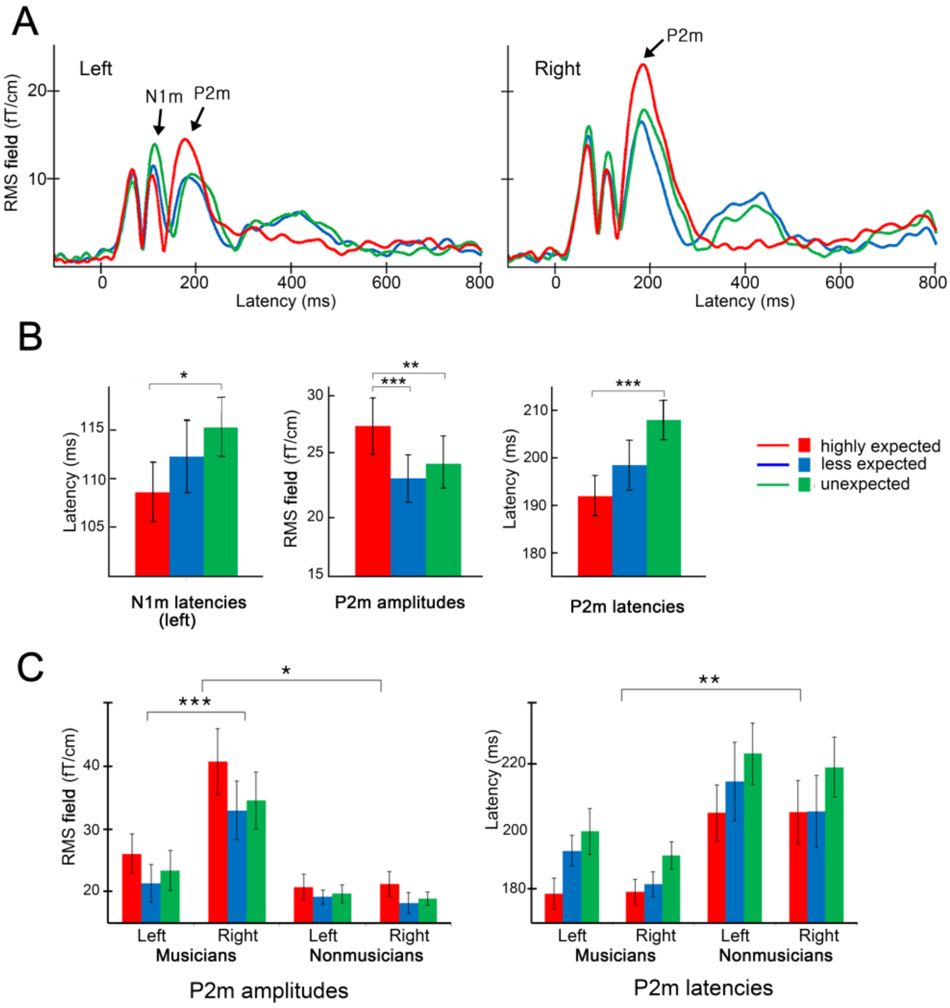

Figure 6. Grand-averaged RMS waveforms for all participants in the left and right temporal ROIs (A) and the amplitudes and latencies in N1m and P2m for the three conditions (B and C). Red indicates the highly expected chords (V), blue indicates the less-expected chords (N^6), and green indicates the unexpected chords (♭III) at T3. The vertical lines indicate the standard errors of the mean. The highly expected condition had the largest amplitude for P2m and the shortest latency for N1m and

P2m (B). The right hemisphere exhibited larger P2m amplitudes than the left hemisphere in musicians; moreover, the P2m amplitudes were significantly larger in musicians than non-musicians, and the P2m latencies were significantly shorter in musicians than non-musicians. However, the P2m tendencies for expectations were similar regardless of the hemisphere or group. *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

For the P2m latencies, we determined that the highly expected condition (mean = 192 ms, standard error of the mean (*SEM*) = 4) was the shortest among the three conditions (less expected: mean = 198 ms, *SEM* = 5; unexpected: mean = 208 ms, *SEM* = 4). A repeated-measures ANOVA of three factors (condition, hemisphere, and expertise) indicated significant main effects of conditions (highly expected, less expected, and unexpected) ($F(2, 52) = 12.818$, $p < 0.001$) and expertise (musicians and non-musicians) ($F(1, 26) = 8.418$, $p = 0.007$); however, there was no effect of hemisphere (left and right) ($F(1, 26) = 0.758$, $p = 0.392$) and no interaction effects (Table 1). After applying Bonferroni post hoc tests for the three conditions, we identified a significant difference between the highly expected and unexpected conditions ($p < 0.001$) and marginally significant differences between the highly expected and less-expected conditions ($p = 0.078$) and the less-expected conditions and the unexpected chords ($p = 0.053$). In the left hemisphere, the N1m latency in the highly expected condition (mean = 109 ms, *SEM* = 3) was the shortest among the three conditions (less expected: mean = 112 ms, *SEM* = 4; unexpected: mean = 115 ms, *SEM* = 3) ($F(2, 52) = 3.913$, $p = 0.026$), and the musicians' N1m latencies were significantly shorter than those of the non-musicians' ($F(1, 26) = 8.418$, $p = 0.037$) (Table 2).

As shown in Fig. 6C, the P2m latencies of the musician group were significantly shorter than those of the non-musician group ($F(1, 26) = 8.418$, $p = 0.007$); however, interaction effects (expertise × hemispheres, conditions × expertise, and conditions × hemispheres) were not identified, which indicates that the tendencies in P2m latencies depending on expectations were similar regardless of expertise and hemisphere (Fig. 6C).

Table 1. *F*-values and *P*-values of P2m amplitudes and latencies at T3

Factors	Amplitude		Latency	
	F-value	*P*-value	*F*-value	*P*-value
Condition	13.536	<0.001 ***	12.818	<0.001 ***
Hemisphere	24.605	<0.001 ***	0.758	0.392
Expertise	6.423	0.018 *	8.418	0.007 **
Condition × Hemisphere	1.800	0.175	1.732	0.187
Condition × Expertise	2.888	0.065	0.198	0.821
Hemisphere × Expertise	27.916	<0.001 ***	0.013	0.910

Note: $*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

Table 2. *F*-values and *P*-values of N1m amplitudes and latencies at T3 in the left hemisphere

Factors	Amplitude		Latency	
	F-value	*P*-value	*F*-value	*P*-value
Condition	0.745	0.480	3.913	0.026*
Expertise	0.013	0.909	8.418	0.037*
Condition × Expertise	0.200	0.819	1.468	0.240

Note: $*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

For the P2m amplitudes, a repeated-measures ANOVA with three factors (condition, hemisphere, and expertise) indicated a primary effect of condition (highly expected, less expected, and unexpected) ($F(2, 52) = 13.536$, $p < 0.001$), a main effect of hemisphere (left and right) ($F(1, 26) = 24.605$, $p < 0.001$), a main effect of expertise (musicians and non-musicians) ($F(1, 26) = 6.423$, $p = 0.018$), and an interaction effect between hemisphere and expertise ($F(1, 26) = 27.916$, $p < 0.001$). After applying Bonferroni post hoc tests to the three conditions, the value for the highly expected chords was significantly larger (mean = 27.22 fT/cm, *SEM* = 2.23) than those of the less-expected ($p < 0.001$) and unexpected ($p = 0.006$) chords, whereas there was no significant difference between the less-expected and unexpected chords ($p = 0.318$) in the P2m amplitudes. Nevertheless, the tendencies of the P2m amplitudes for the three conditions were similar regardless of hemisphere and expertise (Fig. 6C). For a post hoc test of the interaction effect between hemisphere and expertise, we conducted a paired *t*-test with each group, which showed that the musicians' P2m amplitudes in the right hemisphere were significantly larger than in the left hemisphere ($p < 0.001$), whereas the non-musicians' P2m amplitudes did not differ between hemispheres ($p = 0.678$).

To determine the location to generate the greatest difference in expectations between the three conditions, we conducted dipole solutions. Fig. 5 shows the sources of the peak amplitudes at approximately 200 ms of N^6 – V and ♭III – V, as well as the N1m and P2m values for the expected chord (V). The peak latencies for dipole fitting on the grand-averaged waves from all 204 gradiometers were 110 ms (N1m), 182 ms (P2m), 155 ms (N^6 – V), and 153 ms (♭III – V) (Fig. 5A). The coils that exhibited large amplitudes were selected for dipole fitting, which are outlined with blue lines in Fig. 5B. Fig. 5C shows the topographies for the dipoles by the selected channels, and the green arrows represent the direction and moment of the dipoles. The values of the *xyz*-coordinates and dipole moments (Q) for four dipoles are shown in Table 3. The generators of the N1m and P2m for V, and the peak amplitudes for N^6 – V and ♭III – V were located in the auditory cortices (Fig. 5D).

Table 3. Dipole coordinates (x, y, z) and dipole moments (Q) of N1m, P2m, and peak components of difference waveforms (N^6 – V and ♭III – V)

	N1m		P2m		N^6 – V		♭III – V	
	Left	Right	Left	Right	Left	Right	Left	Right
x (mm)	-51	44	-49	45	-35	34	-38	44
y (mm)	7	16	11	17	9	20	6	23
z (mm)	44	50	49	43	60	45	56	50
Q (nAm)	14	14	17	27	12	17	14	11

5.2. Acoustical Similarity and Harmonic Expectation

To untangle the effects of acoustical similarities and harmonic expectations on P2m, we also analyzed the P2m amplitudes and latencies evoked by repetition (T2: 2nd trigger) and the realization for harmonic expectation (T5: 5th trigger).

5.2.1. P2m for Acoustical Similarity

Fig. 7 shows the RMS waveforms of the five-chord progression and P2m amplitudes and latencies at T1 – T5 in the two groups. For the P2m amplitudes, a repeated-measures ANOVA that included trigger (T1 – T5), hemisphere (left and right), and expertise (musicians and non-musicians) as factors indicated main effects of the trigger ($F(4, 104) = 11.101$, $p < 0.001$), hemisphere ($F(1, 26) =$

29.672, $p < 0.001$), and expertise ($F(1, 26) = 7.471$, $p = 0.011$), as well as an interaction effect between trigger and expertise ($F(4, 104) = 2.847$, $p = 0.028$) (Table 4). After applying Bonferroni post hoc tests, we determined that the P2m amplitudes for T2 were significantly smaller than those for the other chords (T1, $p = 0.015$; T3, $p = 0.035$; T4, $p = 0.025$; T5, $p = 0.009$). Furthermore, we conducted paired *t*-tests between T1 and T2 and determined that T2 was significantly smaller than T1 ($t(55) = 5.883$, $p < 0.001$).

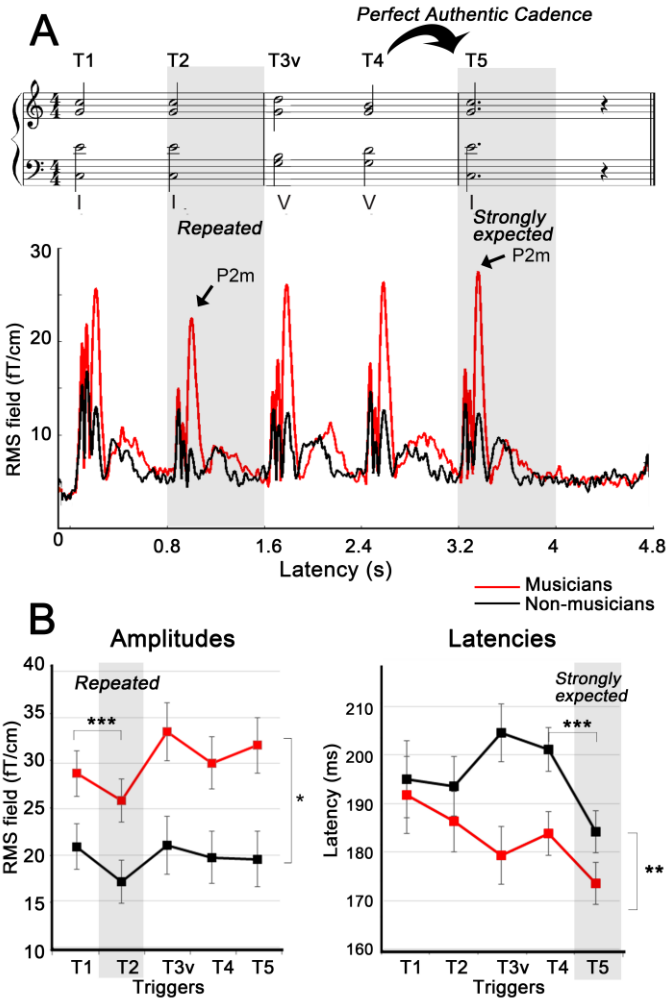

Figure 7. (A) RMS waveforms for T1 to T5. The red line indicates the musician group, and the black line indicates the non-musician group. The shaded regions show the repeated chord (T2) and the strongly expected chord (T5) and their responses. T2 repeated T1, and T5 was strongly expected based on a perfect authentic cadence, although T2 and T5 were identical. The arrows indicate P2m peaks at approximately 200 ms. (B) P2m amplitudes and latencies for T1 to T5. The

shaded regions show the effect of repetition (T1 – T2) and strong expectation (T4 – T5). For P2m amplitudes, T2 was significantly smaller than T1 while there was no significant difference between T4 and T5; for latencies, T5 was significantly shorter than T4, while there was no significant difference between T1 and T2. Additionally, musicians had significantly larger P2m amplitudes and shorter P2m latencies than non-musicians. $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

Table 4. *F*-values and *P*-values of P2m amplitudes and latencies at T1 to T5

Factors	Amplitude		Latency	
	F-value	*P*-value	*F*-value	*P*-value
Trigger	11.101	<0.001 ***	5.804	<0.001 ***
Hemisphere	29.672	<0.001 ***	24.332	<0.001 ***
Expertise	7.471	0.018 *	1.468	0.237
Trigger × Hemisphere	1.139	0.343	2.713	0.034 *
Trigger × Expertise	2.847	0.028 *	0.396	0.811
Hemisphere × Expertise	31.167	<0.001 ***	2.262	0.145

Note: $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

If T3 was a highly expected condition (V), T4 was similar to $\mathrm{T3_V}$ (in the case of V) because $\mathrm{T3_V}$ and T4 are V. However, $\mathrm{T3_V}$ was not acoustically the same as T4 because their voice arrangements differed (e.g., in a key of C major, T3 was G3-B3-G4-D5 and T4 was G3-D4-G4-B4; Fig. 8). After conducting a paired *t*-test between $\mathrm{T3_V}$ and $\mathrm{T4_V}$ (T4 after $\mathrm{T3_V}$), we found that the P2m amplitudes of $\mathrm{T4_V}$ (mean = 24.879 fT/cm, *SEM* = 1.692) decreased after $\mathrm{T3_V}$ (mean = 27.219 fT/cm, *SEM* = 1.967) (*t*(55) = 3.094, *p* = 0.003), whereas no significant differences were identified in the P2m latencies (*t*(55) = -0.135, *p* = 0.893).

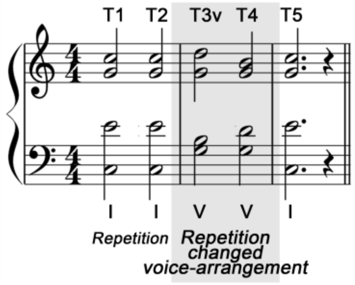

Figure 8. Repetition-changed voice-arrangement. T1 and T2 were identical, whereas T3$_V$ and T4 were not identical. Although the voice-arrangements of T3$_V$ and T4 differed, both functioned as dominant chords.

5.2.2. P2m for Harmonic Expectation

For the P2m latencies, a repeated-measures ANOVA that included trigger (T1 – T5), hemisphere (left and right), and expertise (musicians and non-musicians) as factors indicated main effects of the trigger (*F*(4, 104) = 5.017, *p* = 0.001) and hemisphere (*F*(1, 26) = 18.168, *p* < 0.001); however, the effect of expertise was only marginally significant (*F*(1, 26) = 3.407, *p* = 0.076). After applying Bonferroni post hoc tests, we determined that the P2m latencies for T5 were significantly shorter than those for the other chords (T1, *p* = 0.004; T2, *p* = 0.125; T3, *p* = 0.031; T4, *p* = 0.001) (Table 4). Furthermore, we conducted paired *t*-tests between T4 and T5, which indicated T5 was significantly shorter than T4 ($t(55) = 4.579$, $p < 0.001$). For the hemispheric effect, the P2m latencies on the right were significantly shorter than those on the left, and a significant interaction effect (trigger × expertise) was identified ($F(4,104) = 2.643$, $p = 0.038$). Moreover, there was no significant difference in the P2m latency of T1 and T2 ($t(55) = 0.865$, $p = 0.391$).

5.3. Correlation between Auditory and Frontal Responses

To investigate the connectivity between temporal and frontal regions, Pearson correlation analysis was conducted among the peak amplitudes of the bilateral temporal and frontal regions at approximately 200 ms. The result revealed brain responses in the left and right temporal and right frontal regions were significantly correlated with each other except for the left frontal region (Table 5). There was no significant difference between the latencies of four regions.

Table 5. Correlational Analysis between the Temporal and Frontal Responses

	1	2	3	4
1. Temporal-Left	-			
2. Temporal-Right	.85 ***	-		
3. Frontal-Left	.51	.24	-	
4. Frontal-Right	.60 *	.70 **	.32	-

Note: $*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

5.4. Correlation between Training Hours and Auditory Responses

To investigate the effect of training hours on P2m amplitudes and latencies, Pearson correlation analysis was conducted. The result showed that training hours were positively correlated with the P2m amplitudes in the right hemisphere (*r* = 0.603, *p* = 0.022) and negatively correlated with the latencies of difference waveforms (N^6 – V and ♭III – V) in the right hemisphere (*r* = -0.676, *p* = 0.008 and *r* = -0.538, *p* = 0.047, respectively).

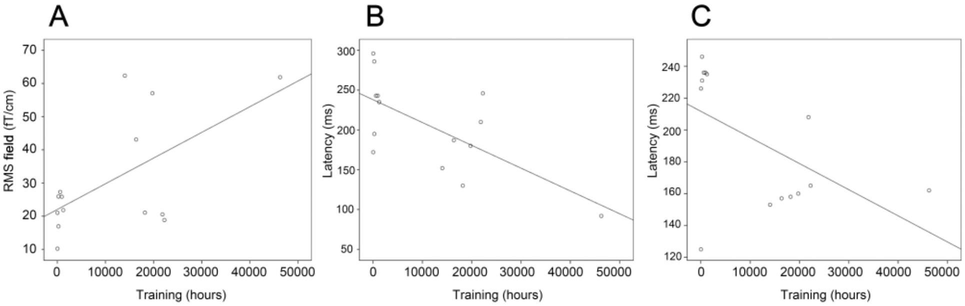

Figure 9. Scatter plots showing the correlation between training hours and P2m amplitudes in the right hemisphere (A), latency of the difference waveform (N^6 – V) in the right hemisphere (B), and latency of difference waveform (♭III – V) in the right hemisphere (C).

6. Discussion

6.1. Highlights of the Research

- Harmonic expectations reduced the latencies of N1m (only on the left side) and P2m and enhanced the amplitudes of P2m.
- The effect of harmonic expectations on the auditory cortical responses is more remarkable in musicians.
- Acoustical similarity (repetition) suppressed P2m amplitudes; however, it did not influence P2m latencies.
- Regardless of harmonic expectations, P2m amplitudes were larger in the musician group than in the non-musician group and were larger in the right hemisphere than in the left hemisphere in the musician group.
- Regardless of harmonic expectations, P2m latencies were shorter in the musician group than the non-musician group.

6.2. Implications

6.2.1. Shortened P2m Latencies and Increased P2m Amplitudes as a Result of Harmonic Expectations

In the present study, the primary finding was that the latencies were shortened, and the amplitudes were increased in P2m for harmonically expected chords relative to the values for less-expected and unexpected chords. This finding is consistent not only with previous behavioral studies that have reported shorter response times for harmonically related chords than less-related chords (Bharucha & Stoeckig, 1986; Bigand, Poulin, Tillmann, Madurell, & D'Adamo, 2003; Bigand, Tillmann, Poulin-Charronnat, & Manderlier, 2005; Schmuckler & Boltz, 1994; Tillmann et al., 2008; Tillmann & Lebrun-Guillaud, 2006) but also with neurophysiological results suggesting that there is an effect of harmonic relatedness on subcortical auditory encoding of chords in a top-down manner (Marmel, Parbery-Clark, et al., 2011). When listeners knew the chord progression in advance, the peak latency of the ERAN was earlier in both non-musicians and musicians and the result suggested that harmonic expectations modulate the speed (Guo & Koelsch, 2016). However, few studies have examined the effects of musical expectations according to harmonic context on auditory cortical representations.

The auditory P2 is a dipolar vertex-positive auditory-evoked potential generated by cortical sources lateral to Heschl's gyrus in the region of the secondary auditory cortex (Bosnyak, Eaton, & Roberts, 2004; Pantev, Roberts, Elbert, Roβ, & Wienbruch, 1996; Scherg et al., 1989). Most previous studies on P2 or auditory cortical responses have demonstrated effects of training, experience, or stimulation properties, regardless of context effects (Atienza et al., 2002; Itoh et al., 2012; Kaganovich et al., 2013; Kuriki et al., 2006; Pantev & Herholz, 2011; Pantev et al., 2001; Seppänen et al., 2012; Tremblay et al., 2014). Thus, although the P2 component is strongly associated with music and enhanced by musical training and experience, the effect of harmonic context on P2 remains unknown. Several studies have shown that harmonic sense is processed in Broca's area, eliciting an ERAN (S.-G. Kim et al., 2011; Koelsch et al., 2013; Leino et al., 2007; Maess et al., 2001). We may question whether the responses are affected by musical expectations in the present study because the latencies of P2 and ERAN are similar. However, the crucial difference between them is their sources. While the source of P2 is an auditory cortex, the source of ERAN is an interior frontal cortex (Maess et al., 2001). In the present study the source of P2m and difference waveforms at approximately 200 ms were found in the auditory cortex, so that we considered that the responses were different from an ERAN.

In this respect, our finding is novel because it indicates that P2m amplitudes and latencies reflect not only the processing of experienced sound at the perceptual level (Atienza et al., 2002; Itoh et al., 2012; Kaganovich et al., 2013; Kuriki et al., 2006; Pantev & Herholz, 2011; Pantev et al., 1998; Pantev et al., 2001; Seppänen et al., 2012; Tremblay et al., 2014) but also musical expectancy or context at the cognitive level. The result suggests that harmonic expectations generated in the frontal cortex (Koelsch et al., 2013; Maess et al., 2001; Rohrmeier, 2007) facilitate auditory cortical processing of expected chords via an efferent pathway. The present result that brain responses of temporal and frontal regions at approximately 200 ms were positively correlated supports the possibility of the connectivity between the temporal and frontal regions for processing musical expectation. Because the frontal and auditory cortices (specifically, the belt and parabelt regions in the auditory cortex) are interconnected in the auditory system (Hackett et al., 1999; Kaas & Hackett, 2000), efferent (corticofugal) mechanisms result in enhancements at the perceptual level in the auditory system (Angenstein, Scheich, & Brechmann, 2012; Kraus & Chandrasekaran, 2010a; Marmel, Parbery-Clark, et al., 2011; Marmel, Perrin, et al., 2011; Patel, 2012; Suga, 2008; Suga & Ma, 2003).

Furthermore, these findings strongly support the possibility that the principally neuroplastic P2 component of cortical sound representation is affected by auditory experience (Shahin et al., 2003; Shahin et al., 2004; Trainor et al., 2003), and the source of P2 is associative auditory temporal regions, with additional contributions from the frontal area (Bishop et al., 2011; Tremblay et al., 2001). Our findings extend the efferent mechanisms of the auditory system to auditory cortical representations indexed as P2m components.

6.2.2. Shortened P2m Latencies and Increased P2m Amplitudes as a Result of Musical Expertise

The P2m latencies were significantly shorter and the P2m amplitudes were significantly larger in musicians than in non-musicians; however, the patterns of P2m amplitudes and latencies according to musical expectancies were similar between the groups (Fig. 6). Moreover, the musicians exhibited more significant differences in the P2m latencies between the less-expected and unexpected chords than the non-musicians. These results suggest that long-term musical training strengthens top-down feedback pathways in musicians (Kraus & Chandrasekaran, 2010b) and facilitates auditory cortical processing for expected chords, which is indexed as shortened latencies and enhanced amplitudes in P2m. Thus, musicians may pre-attentively detect less salient harmonic irregularities (Poulin-Charronnat et al., 2006); however, the non-musicians could also detect musical syntactic violations, which elicited an ERAN (Koelsch et al., 2000).

For enhanced P2m amplitudes regardless of expectancy, we also obtained the following additional results: (1) the musicians produced larger amplitudes than the non-musicians, and (2) the right hemisphere of the musicians produced larger amplitudes than the left hemisphere.

Result (1), the enhancement of P2m amplitudes in musicians compared with those in non-musicians regardless of expectancy, is consistent with the results of previous studies. P2 amplitudes have been reported to be increased by perceptual training for sounds such as speech and musical tones (Atienza et al., 2002; Bosnyak et al., 2004; Kuriki et al., 2006; Moreno et al., 2011; Reinke et al., 2003; Seppänen et al., 2012; Tremblay et al., 2001; Tremblay et al., 2014), musical expertise (Pantev & Herholz, 2011; Shahin et al., 2003; Shahin et al., 2005) or a familiar timbre (Kuriki et al., 2006; Pantev & Herholz, 2011; Shahin et al., 2005). This effect may be explained by Hebbian learning rules ("cells that fire together, wire together") and brain plasticity caused by long-term musical training (Hebb, 1949).

Result (2), the right hemispheric dominance of P2m for musical stimuli in musicians, is consistent with previous research (Shahin et al., 2003); however, previous authors have identified a right hemispheric dominance of the N1c component in musicians. This finding is also in line with research that indicated preferential encoding of spectral information in the right hemisphere (Schönwiesner, Rübsamen, & Von Cramon, 2005; Zatorre & Halpern, 1993; Zatorre & Samson, 1991). However, the finding that the right hemispheric dominance of P2m was only identified in musicians indicates that the result is caused by training. According to studies on training effects, linguistic training enhances P2m amplitudes in the left hemisphere (Reinke et al., 2003), whereas musical training enhances MMNm amplitudes in the right auditory cortex more than in the left auditory cortex (Lappe, Herholz, Trainor, & Pantev, 2008) and improves pitch processing (Pantev & Herholz, 2011). Our finding extends evidence of the right hemispheric dominance in musicians to the P2m component.

To determine whether the effects were caused by innate nature or training, a correlation analysis was necessary. The result revealed that the more the participants had trained, the greater the P2m amplitudes were in the right hemisphere (r = 0.603, p = 0.022). For processing harmonic expectations, the more the participants had trained, the shorter the latencies of the difference waveforms (N^6 – V and ♭III – V) in the right hemisphere were (r = -0.676, p = 0.008 and r = -0.538, p = 0.047, respectively). The results suggest that musical training enhances auditory processing particularly in the right hemisphere.

6.2.3. Reduced P2m Amplitudes by Acoustical Similarity

The result that acoustically similar chords with the previous chords (T2 (I - I) and T4 (V - V; altered voice-arrangement)) reduced P2m amplitudes may be interpreted as repetition suppression. Repeated auditory stimulation typically results in a reduced response in event-related potential components (Rosburg, Zimmerer, & Huonker, 2010; Todorovic & de Lange, 2012; Todorovic, van Ede, Maris, & de Lange, 2011), which may be a result of refractoriness in the cell assemblies involved in P2 component generation (Rosburg et al., 2010). Notably, these repetition-suppression effects were reflected in P2m amplitudes rather than P2m latencies. These results indicate that harmonic expectations are better reflected in P2m latencies, whereas acoustic similarities are better reflected in P2m amplitudes.

Interestingly, the result of a reduced P2m amplitude was also identified in acoustically similar chords as well as the same chords. When T3 was a highly expected condition ($T3_V$), T4 was similar to $T3_V$ but not the same as $T3_V$. $T3_V$ and T4 do not have the same pitch, but they do have the same pitch classes (e.g., in the key of C major, $T3_V$ was G3-B3-G4-D5 and T4 was G3-D4-G4-B4 in terms of pitches; $T3_V$ was G-B-D and T4 was G-B-D in terms of pitch classes; Fig. 8). That is, $T3_V$ is different from T4 in terms of voice arrangements. The result indicated that acoustically similar chords reduced P2m amplitudes in the same manner as the same chords did. Therefore, the effect of repetition suppression may occur by acoustically similar stimuli, and acoustical similarity and harmonic expectation are processed via different pathways. A high degree of similarity produced reduced P2m amplitudes, whereas a high degree of expectation enhanced P2m amplitudes and shortened P2m latencies. This result is consistent with brainstem research that demonstrated differences in the brainstem response between acoustically similar chords and harmonically related chords (Marmel, Parbery-Clark, et al., 2011). The research also exhibited that harmonically related chords produced enhanced brainstem responses, the effects were more remarkable in musicians, and musicians' responses were more enhanced regardless of harmonic relatedness (Marmel, Parbery-Clark, et al., 2011).

6.2.4. P2m Amplitude vs. Latency

The results showed that harmonic expectancy may be better reflected in the P2m latency than the P2m amplitude (i.e., highly < less < unexpected for latency and highly > unexpected > less expected for amplitudes). Although a significant difference between the less-expected and unexpected chords was identified only in the musicians' P2m latencies, similar patterns in the P2m amplitudes and latencies were identified among expectancies regardless of hemisphere or expertise (Fig. 6). Presumably, P2m amplitudes may reflect the distance between contiguous chords in terms of harmonic relatedness because V is the nearest to I and N^6 is more distant from I than $_{\flat}$III in terms of harmonic relatedness or the circle of fifths (Fig. 10). Fig. 10 shows the harmonic distances of V, $_{\flat}$III, and N^6 from I in the circle of fifths, in which the distances have an inverse relationship to the P2m amplitudes depending on the stimuli.

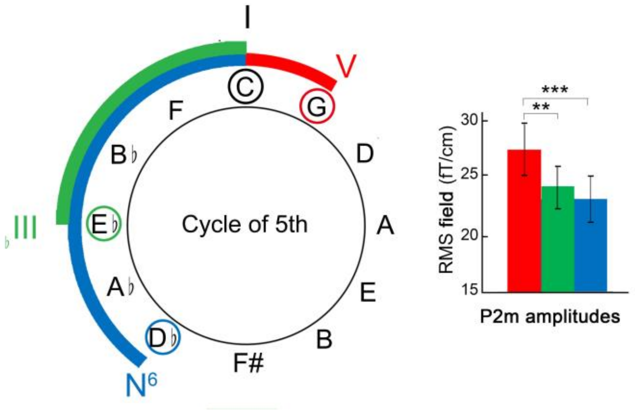

Figure 10. Circle of fifths and P2m amplitudes. According to the circle of fifths, the G chord (V) is the nearest to the C chord (I) in the key of C major, followed by the E$^{\flat}$ ($_{\flat}$III) and then the D$^{\flat}$ chord (N^6). Thus, in terms of harmonic relatedness

(distance) between two chords, ♭III is nearer to I than N^6. This tendency is similar to the results in P2m amplitudes. *Note: The circle of fifths shows the relationships of keys in music theory. Each letter indicates the tonic note or tonic chord for each key. Contiguous keys share six notes and vary in one note (e.g., C key = {C, D, E, F, G, A, B}; G key = {G, A, B, C, D, E, F#}). Therefore, the number of steps represents the harmonic distance.

The ♭III is unexpected in terms of harmonic context; however, it is nearer to the previous chord (I) in terms of harmonic relatedness (the circle of fifths) than N^6. N^6 is the most distant from I among stimuli in terms of harmonic relatedness, whereas it is more congruous than ♭III in terms of harmonic context (I – N^6 – V – I). In short, N^6 is superior in a harmonic context to ♭III, and ♭III is superior in harmonic relatedness to the preceding chord to N^6.

Taken together, the results suggest that P2m latencies reflect expectations for harmonic context (V > N^6 > ♭III), whereas P2m amplitudes reflect harmonic relatedness (V > ♭III > N^6). Note that if P2m amplitudes simply reflected acoustic similarity, a repeated tonic chord should have resulted in the greatest P2m amplitudes; however, repetition of the chords elicited significantly smaller P2m amplitudes (Fig. 7 and 8). Thus, we suggest that increments in P2m amplitudes reflect proximity in harmonic relatedness between contiguous chords via efferent processes, whereas decrements reflect repetition suppression via afferent processes.

6.3. Limitations and Future Directions

The musical stimuli used in this experiment were far from real music in that the harmonic progressions were too simple, and the timbre and musical expressions were artificial. These differences can cause differential effects from real situations. Thus, further studies utilizing musical stimuli closer to real music are needed to investigate brain responses in real situations. To control for the confounding effects of real music, it is necessary to collect additional data as well as to control for factors that may cause unexpected effects.

Although the result showed a significant correlation between temporal and frontal regions at approximately 200 ms, there were no significant differences in the latencies. To determine the causality of these results, further data are necessary in which the connectivity and causality among brain responses when listening to harmonic progression can be explored in several brain regions using a larger number of participants.

Few studies have investigated the effect of contextual expectations on auditory processing at the perceptual level. The present study indicated that the harmonic context influenced the auditory cortical response, particularly P2m. However, the number of participants in the experiment was insufficient to generalize the effect. To validate this effect, future studies must be conducted with a sufficient number of participants.

7. Conclusion

When we listen to music, dynamic cognitive processing occurs between actual and anticipated tones (Meyer, 2008). Although we cannot anticipate the first chord, once listening to the first chord, we anticipate the next chords dynamically according to the Western tonal scheme or probabilities generated by experience. It is necessary to design representation schemes that have musically and psychologically meaningful interpretations (Pearce & Wiggins, 2006). According to Narmour's *implication-realization*, there are two independent perceptual systems – the bottom-up (automatic, unconscious and universal) and top-down (learned and culture dependent) systems while we are processing music (Narmour, 1992). In the present musical stimuli, T1, T2, and T5 are the same chord in acoustical aspect and probabilities of appearance in the experiment but their meanings are different according to the Western tonal scheme. Our results showed that repeating T2 after T1 reduced P2m amplitudes in a bottom-up manner and that T5, realizing the expectation of a perfect authentic cadence, enhanced P2m amplitudes and shortened P2m latencies. These results may be neuroscientific evidence for schematic and veridical expectations.

The present study indicated that expected chords shortened N1m and P2m latencies (musical context) and enhanced P2m amplitudes (harmonic relatedness with the preceding chord), whereas acoustically similar chords reduced P2m amplitudes. The effects were more remarkable in musicians than non-musicians. We suggest that the effects of shortened P2m latencies and enhanced P2m amplitudes result from an efferent connection between the frontal and auditory cortices, whereas the effect of reduced P2m amplitudes results from repetition suppression via an afferent process. The greater significance of the effect and the promotion of P2m in musicians *versus* non-musicians may result from long-term training and neuronal plasticity. The findings suggest that auditory cortical processing is facilitated by musical knowledge and long-term musical training via an efferent pathway.

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Abstract in Korean

본 연구는 화성적 기대감과 음악적 전문성이 청각 피질에서의 화성진행 처리에 미치는 영향을 조사하였다. 많은 이전 연구들이 음악적 경험이나 전문성이 청각 피질의 청각정보 처리를 향상시킨다는 것을 밝힌 반면, 화성적 기대감이 청각 피질의 처리에 미치는 영향을 보여준 연구는 극히 드물다. 청각 피질 반응의 향상에 관한 대부분의 연구들은 화성적 맥락이 없는 자극을 사용하였고, 화성적 기대감에 관한 연구들의 경우에는 청각 피질 반응에 미치는 영향보다는 그 처리가 하전두이랑(inferior frontal gyrus)에서 처리되며 음악적 규칙에 위반되었을 때 ERAN(early right anterior negativity)이 유발된다는 것을 증명하였다.

신경계에서 청각자극의 처리는 상향적(afferent) 경로뿐만 아니라 하향적(efferent) 경로를 통해서도 함께 영향을 받는다. 행동실험 결과에 의하면, 화성진행에 있어서 앞선 화음과 화성적으로 관련된 화음이 제시될 경우에는 반응시간이 빨랐다. 청각 유발 전위 중 하나인 P2(200 ms 부근에서 유발되는 positive auditory evoked potential)는 주로 음악적 경험에 의해 영향을 받으며, 그 근원은 측두엽의 청각 연합 영역으로, 전두 영역에서 영향을 받는 부분이다. 전두피질과 청각피질의 주변부분(belt와 parabelt)이 상호 연결되어 있음을 보여준 해부학적

증거를 고려해 볼 때, 본 연구는 음악적 기대감이 하향식 경로로 청각피질의 화성진행 처리에 영향이 미칠 것이라 가설을 설정하였다. 이러한 가설을 확인하기 위해 5개의 화음으로 이루어진 화음진행에서 세번째 화음에 세 가지 단계의 기대감을 갖는 화음들(expected, less expected, and unexpected)을 무선배치 하였고, 7명의 음악가와 7명의 비음악가에게 들려주는 동안 뇌자도(magnetoencephalography)를 사용하여 청각유발 자기장(auditory evoked fields, AEFs)을 측정하였다.

연구 결과, 기대감이 높은 화음이 기대감이 낮은 화음들에 비해 청각 피질에서의 N1m(100 ms 부근의 negative AEF)과 P2m(P2에 대응하는 자기장)의 latency 가 짧았고, P2m 의 amplitude는 더 높게 나타나는 것을 확인하였다. 화성적 기대감 정도에 따른 P2m amplitude와 latency는 그룹에 상관없이 유사한 패턴을 보였으나, 음악가들의 결과가 더욱 주목할 만하였다. 이러한 발견은 음악지식과 오랜 기간의 음악훈련이 하향 경로에 의해 지각 수준의 청각 피질의 처리를 향상시킬 수 있음을 시사하며, 이러한 효과가 청각 피질에서의 짧아진 N1m 과 P2m latency와 상승된 P2m amplitude에 반영됨을 시사한다.

주요어: 청각피질, 화성적 기대감, latency, 음악가, P2m

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