Harmony Wants to Sit in the Front: Different Brain Responses to Violations in Chord Progressions.

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ABSTRACT

Deviations from auditory regularities elicit electric potentials distributed over the frontal regions of the scalp. The mismatch negativity (MMN) is elicited by change in repetitive auditory input, whereas the early right anterior negativity (ERAN) is elicited when sounds deviate from a hierarchically organized musical regularity. In this study we wished to disentangle the functional roles of these two brain processes associated with the detection of sequential vs. hierarchical musical violations by studying the localization of their neural generators. Subjects listened to musical cadences constituted by seven chords, each containing either harmonically congruous chords, harmonically incongruous chords (Neapolitan subdominant), or harmonically congruous but mistuned chords (5th raised 50 cents). Electroencephalography (EEG) was recorded and source analysis was performed. Incongruous chords violating the rules of harmony elicited a bilateral ERAN, whereas mistuned chords within chord sequences elicited a right-lateralized MMN. We found that the dominant neural sources for the ERAN were localized in Broca's area and its right homologue, whereas the MMN generators were localized in auditory cortex. These findings demonstrate the predominant role of the auditory cortices in detecting sequential scale regularities and of the prefrontal cortex in parsing hierarchical regularities in music.

I. SOUND & MUSIC PROCESSING

A. Regularity vs Harmony

Using Magnetoencephalography (MEG), Maess et al (2001) showed that Western musical harmony (or "syntax" as they call it) is processed in Broca's area and its right hemispheric homologue. Since then, the processing of musical harmony has been a very important but also quite controversial subject of study. To talk about music processing, first we must understand how the human brain processes sequences of sounds. Regularities in language sounds and other domains are extracted and organized by the brain. These regularities may be the repetition of one feature of the sounds such as e.g. the pitch, or rules of succession of particular sound features e.g., the higher the pitch, the louder the sound intensity is expected to be (Paavilainen et al. 2001). The extraction of sound regularities allows for adaptation to the environment and detection of sound deviations that may be important for survival (Pincze et al. 2002; Bendixen et al. 2007). This is true for humans as well as for animals but, unlike animals, humans can also form hierarchic structures adopted for aesthetic purposes (e.g., (Koelsch and Sammler 2008)), like in visual art and music. A way to study auditory regularities is by using the mismatch negativity (MMN), a component of the event-related potential (Näätänen 1995; Picton et al. 2000). The MMN is an early frontocentral negative potential peaking at around 150-250 ms, which is elicited by deviant stimuli randomly introduced in a train of repetitive stimuli. It occurs automatically, i.e. without any attentional effort or even awareness. The cortical main sources of the MMN are in the auditory cortex (the supratemporal plane), sometimes additional sources in the right inferior frontal gyrus (Opitz et al. 2002), and inferior parietal lobule (Park et al. 2002). The reason for this wide localization of the MMN may be that these cortical sources detect the auditory change, and assess whether it is salient or novel enough to trigger attention (Schonwiesner et al. 2007). The MMN may reflect the automatic formation of brief neural models of regularities in the auditory environment (Winkler et al. 1996). However, the extent to which auditory regularities can be encoded by the auditory-cortex MMN neurons have not yet been fully determined, and to investigate this question we need to further study musical regularities, characterized by different levels of structural complexity.

B. More than a word about Music

1) Music theory.

The way we perceive and create music is strongly governed by cultural constrains or rules, with pitch as a central, cultural-dependant, dimension. Pitch can be defined as the human perception and categorization of the fundamental frequency of a sound wave (tone) as being "higher" or "lower" based on the changes within the sound's frequency. Western tonal music is founded only on a small subset of 12 pitches included in the chromatic equal-tempered scale, where the smallest relation or interval between pitches is the semitone (100 cents difference). The rules of the equal-tempered scale concern sequential aspects of sound pitches are extracted by comparing the pitch of the incoming sound with that of the immediately preceding one. The human sensitivity to pitch deviations goes from 10 to 30 cents (Krumhansl 2000; Lehmann 2008). Violations of pitch rules elicit an MMN, with main generators in the non-primary auditory cortex (Brattico et al. 2006).

Western music is mostly based on subsets derived from the chromatic scale. This configuration defines hierarchical relations between sounds by means of the rules of tonality, whereas when several sounds are played simultaneously (musical chords), harmony rules determine their relations simultaneously combined with the rules of voice leading (Grove and Colles 1944). The rules of harmony also determine the order and structural importance of the harmonic events within a musical sequence, thus determining a hierarchical structure within the musical piece. Chord progressions, like the plagal cadence (Tonic-Subdominant-Tonic) or the authentic cadence (Tonic-Subdominant-Dominant-Tonic), are representative examples of this type of structure and are main carriers of harmony in Western music (Piston 1941).

2) EEG correlates of musical harmony.

An ERP component called early the right anterior negativity (ERAN) is elicited by violations of the harmonic structure; occurring at an early latency (150-250 ms after stimulus onset) and being maximal over anterior regions of the scalp it has a tendency to be lateralized to the right hemisphere (Koelsch et al. 1999; Koelsch et al. 2000; Leino et al. 2007) and is most commonly recorded in semi-attended paradigms (Koelsch et al. 2000) where the subject's attention is directed towards the music by asking them to respond to infrequent chords played on a deviant instrument. The ERAN's amplitude is modulated by voluntary attention towards the sounds and it is higher in musical experts than in novices (Koelsch et al. 2002; Loui et al. 2005). It is elicited by the incongruity of harmonically unexpected events in musical sequences e.g. by a Neapolitan subdominant (Sn) or double dominant chords (DD), at the tonic (T) position (Maess et al. 2001; Tramo et al. 2001; Leino et al. 2007; Koelsch and Sammler 2008); and contrary to the MMN, the ERAN has longer peak latency and higher amplitude that specifically depends on the degree of harmonic violation (Koelsch et al. 2001). Therefore, we can see that the ERAN and the MMN have similar temporal and scalp distributions and electrical behavior towards violations (Koelsch et al. 2001). Both ERPs can be elicited pre-attentively, but the MMN is the only one that can be elicited under deep sedation by anesthesia, thus it seems to be more strictly automatic (Heinke et al. 2004; Koelsch et al. 2006), and it can also be elicited by grammatically incorrect words (Pulvermüller and Shtyrov 2003; Shtyrov et al. 2003), syntax and semantic errors (Menning et al. 2005). The ERAN and the MMN, two ERP components elicited by deviants in auditory streams, are very similar in amplitude, latency and scalp distribution and it can thus be difficult to think about these two ERP components as being different. Nevertheless several authors suggest that ERAN and MMN are indeed different ERP components, with different functional role and neural generators (Koelsch and Sammler 2008).

C. Is the ERAN a musical MMN?

Previous studies have attempted to differentiate the ERAN from the MMN. Koelsch et al. (2001) compared the MMN and the ERAN. They wished to determine whether the ERAN is an abstract feature MMN or a completely distinct ERP component. They compared ERPs from Neapolitans inserted harmonically incongruently in chord sequences (ERAN-condition) with ERPs to deviant pitches (frequency-MMN condition) as well as ERPS to tone pairs falling in pitch in trains of rising tone pairs (abstract feature MMN-condition) in participants playing a videogame. The results showed that the ERAN amplitude was specifically dependent on placement within the stimulus train i.e. dependent on the rules of harmony or chord succession, whereas the MMN was not. One problem with the design of this study however is that the context of the ERAN condition, chord sequences, is fundamentally different from the lines of single notes that constitute the context of the MMNs.

In an attempt to further separate the ERAN and the MMN, various studies have tried to determine the neural generators of the ERAN. Using MEG Maess et al. (2001) localized the sources of the magnetic ERAN response in pars opercularis of the Broca's area (BA44) and its right hemispheric homologue. This bilateral localization is supported by other studies, calling the component simply early anterior negativity (EAN) (Loui et al. 2005; Leino et al. 2007). Other studies provide evidence for a right-lateralized ERAN (Koelsch et al. 2000; Koelsch et al. 2001; Koelsch et al. 2002; Koelsch et al. 2005).

Leino et al. (2007) directly compared the ERAN and MMN, using deviant sounds embedded in the same harmonic context. Their results indicated that the harmonically incongruous chords elicited an ERAN, whereas the mistuned chords elicited an MMN. They showed that the ERAN amplitude was affected by the harmonic hierarchy of the sequence as it was larger when the chord succession was less expected (when the Neapolitan was placed instead of the tonic, following a Dominant chord) than when it was more expected (as when the Neapolitan was placed instead of the subdominant following a Tonic chord). The MMN amplitude elicited by mistuned chords, in contrast to the ERAN, was not affected by the position of the mistuned chord in the sequence.

II. DESIGN & METHODS

A. Aims and paradigm of the study

Using the stimuli of Leino et al. (2007) we wished to localize the cortical sources of the ERAN and MMN components, in a direct comparison between Neapolitans and mistuned chords embedded in a comparable context. To this aim, we used Brain Electric Source analysis (BESA) (Scherg 1984; Scherg and Von Cramon 1986; Grandori et al. 1990; Scherg and Berg 1991; Scherg and Picton 1991; Scherg 1994). We also wanted to correlate the ERP results with behavioral measures. We used the Leino et al paradigm in which different kinds of musical violations are embedded in the same context, presenting 7-chord cadences with harmonically incongruous Neapolitan subdominants (Sn) as well as mistuned chords (Mn). There were three types of seven chord long sequences: a harmonically congruous sequence adapted from the authentic cadence, a harmonically incongruous sequence (Sn chords in either the 3rd, 5th, or 7th position), and a harmonically congruous sequence that had a mistuned fifth note in positions 3rd, 5th, and 7th, in all 12 keys (Table 1). We hypothesized that the Mn, representing a violation of the chromatic musical scale, would elicit an MMN with predominant neural sources in the temporal cortex, whereas the Sn, violating the hierarchical rules of chord successions, would elicit an ERAN originating in the posterior prefrontal cortex (Näätänen 1995; Winkler et al. 1996; Näätänen et al. 2004; Brattico et al. 2006; Leino et al. 2007) . We also gathered subject's ratings valence and fittingness for each type of cadence (Standard, Harmonically incongruous and Mistuned) to study the subjective perception of the chord violations. We expected higher pleasantness and fittingness for cadences with Sn in the 5th position than the 3rd or 7th positions, and similar pleasantness and fittingness for the Mn in all three positions.

Table 1 - Cadences.

Position	1st	2nd	3rd	4th	5th	6th	7th
Standard	T	D	T	T3	S	D	T
H. Incongruous			Sn		Sn		Sn
Mistuned			Mn		Mn		Mn

T = tonic, T3 = inverted tonic, S = subdominant, D = dominant, Sn = Neapolitan subdominant, Mn = mistuned.

B. Methods

1) Subjects and stimuli.

15 right-handed healthy paid volunteers without musical education (5 male, 10 female; age range 18 – 30 years, mean age= 24.3 years) participated in the experiment. Ten of these subjects were also participants in the study by Leino et al. (2007). The subjects were sitting in a comfortable chair inside a soundproof room while they listened to the stimuli from headphones. The stimuli consisted on seven-chord long cadences digitally generated by piano and organ (deviant), presented randomly in twelve different keys (144 times in total) while preserving the musical meter in order to give an impression of real flowing music. The stimulus chords were prepared in accord with rules of voice leading of Western functional harmony and further edited to have equal duration and intensity. The cadences consisted of chords played with a piano timbre created for 7 different experimental conditions and in 12 different keys. These conditions were: Standard, Harmonically incongruous and Mistuned. Each condition was three-fold; with a deviant chord either in the 3rd, 5th or 7th position, replacing a Tonic (T) or Subdominant (S) chord. In the Standard conditions, each of the 7 chords in the cadence belonged to the same key and together they composed a simple chord sequence following the rules of the Western functional harmony. In the Harmonically incongruous conditions, the deviant chord was a Neapolitan subdominant (Sn). In the Mistuned conditions, the deviant chord was a mistuned major triad, in which the fifth of the chord (at pitch distance of a fifth, or seven semitones, from the lowest note of the chord) was increased by 50 cents.

2) Procedure and data acquisition.

Subjects were instructed to attend to the musical sequences and press the response button after hearing a random chord played on a deviant instrument (an organ; p = .08). The deviant organ chords were uniformly distributed among conditions and matched with the piano chords in all aspects except for timbre. The stimuli were presented in eight separate stimulus blocks of approximately 10 min. each in duration, while EEG was measured. The entire experimented lasted 3 hours including preparation. The EEG was measured using the BioSemi measuring system (BioSemi, Inc., Netherlands; http://www.biosemi.com), recorded with 128 active scalp electrodes fitted into a stretching cap and following the BioSemi ABC position system. Additionally, three active electrodes were placed on the subject's nose and mastoid areas, respectively, and four more around the eyes to monitor eye muscle activity. After the EEG measurements, subjects were instructed to relax and asked to rate 4 cadences taken randomly from each of the 7 experimental conditions according to valence and fittingness on a 5-point scale (with 1 being the lowest score and 5 the highest).

C. Source analysis

1) Source analysis.

We averaged the ERPs for each condition and cadence, then we offline filtered them to 0.5 – 40 Hz and re-referenced them to the average of both mastoids. Difference waveforms were calculated by subtracting the responses to the standard chords from those to the Sn or Mn chords. Regional source analysis was performed for each experimental condition (ERAN3, ERAN5, ERAN7, MMN3, MMN5, MMN7), and the results were registered according to the Talairach coordinate system (Talairach and Tournoux 1988). The differences in the coordinate locations between the ERAN and MMN regional sources were separately studied for each axis (hemispheres were not taken into account because the regional sources were symmetric). The mean coordinates were measured for the x, y and z axes in all conditions and graphed in the Talairach system. A distributed source analysis was performed with low resolution electromagnetic tomography (LORETA) (Pascual-Marqui et al. 1994) on the grand-average waveforms for each experimental condition. In this type of analysis the spherical head model is segmented into small voxels, each of them representing a regional source. We localized the maximum activity of the grand-average waveforms and thereafter we localized the maxima coordinates for each condition.

3) Behavioral Analysis.

The data were transformed to compensate for the individual response-style variation, in both rating criteria. Each subject's average of all ratings was subtracted from his/her average of grades for a given condition. The resulting "balanced" score (BS) was then used to perform repeated-measure ANOVA with Rating, Position and Violation Conditions as factors.

III. RESULTS & DISCUSSION

A. General results

The Neapolitan chords elicited an ERAN at around 230 ms whereas the mistuned chords elicited an MMN at around 270 ms. The ERAN regional sources were located significantly anterior to those of the MMN, with gray matter relationships to BA45 and BA46 (Broca's area) for the ERAN and BA22 and BA41 (non-primary auditory cortex) for the MMN. The LORETA distributed source analysis coordinates of the maximum activity for each condition were localized and compared to the regional source coordinates. The ERAN maximum was located at (x=-32, y=11, z=3) with gray matter relations to BA45, BA44 and BA13. The MMN maximum of activity was located at (x=38, y=-17, z=12) with gray matter relation to BA14, and BA42 (Figure 1). The behavioral part of the study showed that in the harmonically incongruous cadence, subjects rated the ERAN5 as the most pleasant, whereas ERAN7 was the least pleasant and fitting. The best fitting was ERAN3. In the mistuned cadence the MMN3 was the most pleasant and fitting, followed by the MMN5 and MMN7 in sequential order.

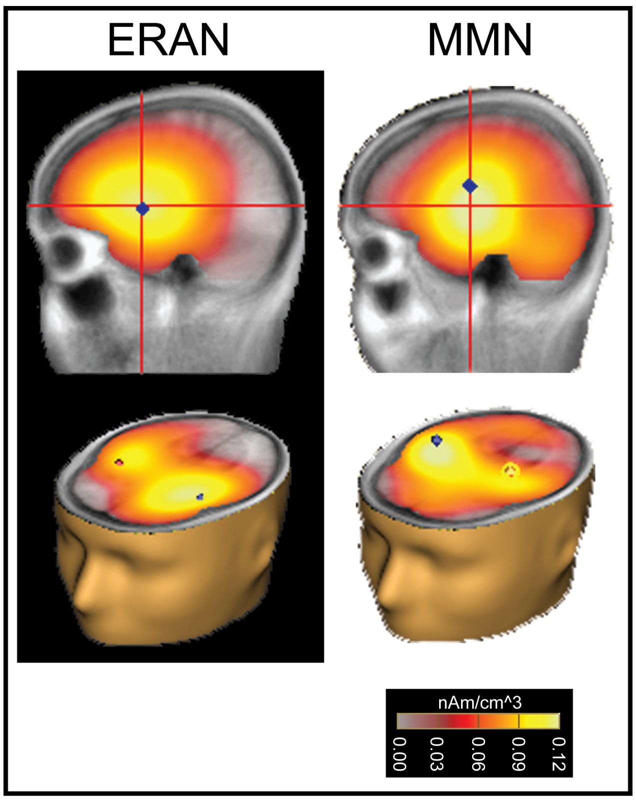

Figure 1. Source localization of the grand-average using discrete and distributed analysis.

B. Interpretation of the results

The present study was conducted to differentiate the ERAN and MMN, and to localize their underlying cortical generators when elicited in the same musical context. Some earlier studies have tried to differentiate the MMN from the ERAN (REF), but there are no previous studies that directly compare the MMN and ERAN localizations against each other within the same musical context. Context plays an important role when studying the influence of stimuli on brain processing. (Friston 2005) suggested a model of brain function, in which predictive coding, as a central principle of brain function, provides an account of how the brain identifies and categorizes the causes of its sensory inputs. The model postulates a hierarchical organization whereby lower-level brain regions estimate predictions of their expected input based on contextual information through backwards connections from higher-level regions. A comparison between the prediction and actual input produces an error term that, if sufficiently large, will be fed back to call for an update of the model. This generates a recursive process which aims at minimizing the difference between input and prediction. Being related to a mismatch between prediction and input, the ERAN and the MMN both seem to reflect this process. However, the MMN component may solely depend on context (short-term model), whereas the ERAN probably does not (long-term models) (Jääskeläinen et al. 1999; Vuust et al. 2009).

In our source analysis, the grand average sources of the ERAN were located significantly anteriorly to those of the regional sources of the MMN component. Interestingly, ERAN7 showed frontal and temporal regional sources, as well as distributed sources. An explanation for this could be that there is greater expectancy for a long chord and closure in the 7th position than in the other positions. Another explanation could be the fact that the tonality is better established in position 7 than in the other positions, which results in a stronger prediction for position 7. The musical sequence of the present study always contained seven chords; therefore closure by a tonic chord at the 7th position was always expected. In the current design the contribution from closure-effect and tonality are indistinguishable. According to the distributed analysis, the ERAN component was bilaterally distributed over the two hemispheres, in concordance with other studies (Maess et al. 2001; Loui et al. 2005; Leino et al. 2007). This disagrees with the fundamental nomenclature of the ERAN that identifies it as right lateralized, with remarkably similar temporal and mirrored spatial properties as the early left anterior negativity (ELAN) of language (Neville et al. 1991; Friederici et al. 1996; Hahne and Friederici 2002). This has led to comparisons and analogies between the processing of harmony rules and the processing of linguistics syntax. These suggestions remain a matter of debate (Bigand et al. 2006), for, as we have mentioned before, syntax errors may elicit an MMN as well (Menning et al. 2005). In this study the MMN was found to be slightly right-lateralized, in accord with previous studies that also obtained a right-hemispheric predominance of the MMN, especially during the detection of non-phonetic auditory stimuli (Tervaniemi et al. 2000; Opitz et al. 2002; Brattico et al. 2006).

In the behavioral analysis we found that the subjects expressed higher pleasantness and fittingness for the cadences with Sn in the 5th position than in the 3rd and 7th positions, whereas the cadences with Mn were rated sequentially. The findings relate to harmony rules that state that the Sn in the 5th position is harmonically acceptable, whereas the Mn ratings are related to sequence rules that state that errors in a sequence increase as the tonality gets more established.

C. A final word

Our study suggests that the MMN and ERAN are generated by distinct cortical sources. This corresponds with previous studies showing that the ERAN component is related to violations in chord progressions with sources that are localized in the posterior prefrontal cortex (Broca's area and its right homologue), whereas the MMN, related to violations in the sequential aspects of auditory stimuli, is localized in the auditory cortices. However, the spatial resolution of the EEG is in the order of centimeters. A more precise localization of the underlying cortical sources of both signals in the millimeter order would be acquired with fMRI (although loosing on the other hand precision in the temporal dynamics of the brain processes).

CONCLUSION

The present study provides evidence that the ERAN and the MMN components reflect different underlying cognitive processes. The extraction of rules dictating a hierarchical structure of musical events seem to be organized by the prefrontal cortex, whereas for the extraction of sequential music rules determining the frequency ratio between two consecutive sounds, the auditory cortex seem to be sufficient.

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