NeuroImage 124 (2016) 898–905

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Differential processing of melodic, rhythmic and simple tone deviations in musicians -an MEG study

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ARTICLE INFO

Article history:
Received 29 June 2015
Accepted 29 September 2015
Available online 3 October 2015

ABSTRACT

Rhythm and melody are two basic characteristics of music. Performing musicians have to pay attention to both, and avoid errors in either aspect of their performance. To investigate the neural processes involved in detecting melodic and rhythmic errors from auditory input we tested musicians on both kinds of deviations in a mismatch negativity (MMN) design. We found that MMN responses to a rhythmic deviation occurred at shorter latencies than MMN responses to a melodic deviation. Beamformer source analysis showed that the melodic deviation activated superior temporal, inferior frontal and superior frontal areas whereas the activation pattern of the rhythmic deviation focused more strongly on inferior and superior parietal areas, in addition to superior temporal cortex. Activation in the supplementary motor area occurred for both types of deviations. We also recorded responses to similar pitch and tempo deviations in a simple, non-musical repetitive tone pattern. In this case, there was no latency difference between the MMNs and cortical activation was smaller and mostly limited to auditory cortex. The results suggest that prediction and error detection of musical stimuli in trained musicians involve a broad cortical network and that rhythmic and melodic errors are processed in partially different cortical streams.

Introduction

A promising approach to understand music perception holds that the brain generates predictions about upcoming musical events based on previously learned musical regularities (Salimpoor et al., 2015; Schubotz, 2015). Predictive mechanisms in the human brain can be investigated by means of magnetoencephalography using markers for prediction error processing like the mismatch negativity (MMN), (Kujala et al., 2007). The MMN is an event related brain response that occurs automatically when an auditory stimulus is different in pitch, loudness, timbre, or tempo, etc. Previous studies comparing musicians and non-musicians demonstrated that musical experts elicit a larger MMN after melodic and rhythmic deviations (Fujioka et al., 2004; Vuust et al., 2005; Tervaniemi et al., 2014) showing that acquired musical expertise leads to better predictions about upcoming musical events. Expertise dependent increases in the MMN can be observed in musically inept subjects already after a short-term musical training, both for melodic (Lappe et al., 2008) and rhythmic (Lappe et al., 2011) material.

A beamformer source analysis of the MEG data from the latter two training studies with musical novices revealed different neural generators for the processing of melodic and rhythmic components (Lappe et al., 2013a, 2013b). A pitch deviation on the last tone of a musical sequence recruited a neural network comprising auditory cortices, inferior frontal and prefrontal areas. A rhythmic deviation on the last tone of a musical sequence recruited, on the other hand, neural networks involving posterior parts of auditory cortices and the inferior parietal lobule. The involvement of these different brain areas reflect the dual pathway model of auditory processing (Belin and Zatorre, 2000; Rauschecker and Scott, 2009; Bizley and Cohen, 2013). In this model, an antero-ventral pathway processes auditory spectral features and auditory objects while a postero-dorsal stream is responsible for processing spatial and temporal aspects of sound. Arnott et al. (2004) reviewed evidence from several fMRI and PET studies (11 spatial, 27 nonspatial) to examine the reliabilty of this model. They found that all but one of the studies investigating auditory spatial perception identified activation in the inferior parietal lobule as opposed to 41% of the nonspatial studies, and 55% of the spatial studies were reported to have shown activity around the superior frontal sulcus in contrast to only 7% of the nonspatial studies. Inferior frontal activity (Brodmann's area 45 and 47) on the other hand, was found in only 9% of the spatial studies, but in 56% of the nonspatial studies. Regions within the parietal lobe have consistently been associated with temporal processing (for a review see Bueti and Walsh, 2009) and a connection between parietal damage and deficits in temporal processing has been reported in previous lesion studies (DiPietro et al., 2004; Koch et al., 2009).

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http://dx.doi.org/10.1016/j.neuroimage.2015.09.059
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To further investigate the different processing streams for rhythmic and melodic violations, we test in the present study musicians in a within-subject design on both kinds of deviations. A direct, within-subject comparison of the two deviations in musical material has, to our knowledge, not been done so far. We hypothesize that the dual pathway network that processes prediction violation in musical material should be particularly pronounced in musicians since musical sensorimotor training should enhance and strengthen the dorsal and ventral auditory stream.

To investigate furthermore whether prediction violation is processed differently in musical material and in a non-musical context, we presented physically identical tone deviations within a musical sequence and, on the other hand, in a simple, repetitive tone pattern.

Methods

Subjects

Twenty-one musicians (12 females, between 21 and 27 years of age) participated in the study. Fifteen participants were students from the music conservatory of the University of Münster. Four of them majored in piano or organ, the others had piano as a minor field. The remaining six participants had received private lessons for many years and have been active musicians ever since. Table 1 lists starting age of musical training and years of experience for each participant. All participants were right handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971) and none of the participants had a history of otological or neurological disorders. Pure tone audiometry was used to confirm that the participants had normal audiological status. Subjects were informed about the nature of the study and all of them gave informed consent to take part in the study.

Stimuli

The musical stimuli that were used for the MEG measurement were based on a 6 tone piano sequence that we used in a previous study (Lappe et al., 2008) (Fig. 1). It was composed of a C- major broken chord in root position (C (251.63 Hz), E (329.63 Hz) G(392.00 Hz)) and a G- major broken chord in its first inversion (B (246.94 Hz), D (293.66 Hz), G (392.00 Hz)) representing the two most important chords (tonic and dominant) in the key of C-major. The musical sequence that was used is common in all western musical styles and generally familiar to musicians. Each tone of the six-tone sequence had a duration of 300 ms. For the rhythmic deviant stimulus, the last tone of the sequence was presented 100 ms earlier than in the standard sequence. For the melodic deviant stimulus, the last tone of the sequence was lowered by a minor third to the tone E (329.63). Both deviants were very easy to detect. The lowering of a minor third on the last tone is easily recognised. The advancement of the last tone by 100 ms was, likewise, very detectable. The temporal change was much higher than the perceptual threshold of 50 ms which we found for the same stimuli in a group of musical novices in an earlier study (Lappe et al., 2011).

Table 1
Musical background of the participants of the study. The number of subjects, the starting age of musical training and the duration of practice in years are indicated in the different columns.

Nr.	Age at start of musical training (yrs)	Duration of musical practice (yrs)
1	10	16
2	4	23
3	13	12
4	12	12
5	7	20
6	8	19
7	5	22
8	4	17
9	6	17
10	5	18
11	7	15
12	6	18
13	6	15
14	7	15
15	6	15
16	12	9
17	6	19
18	9	16
19	5	16
20	6	18
21	10	15

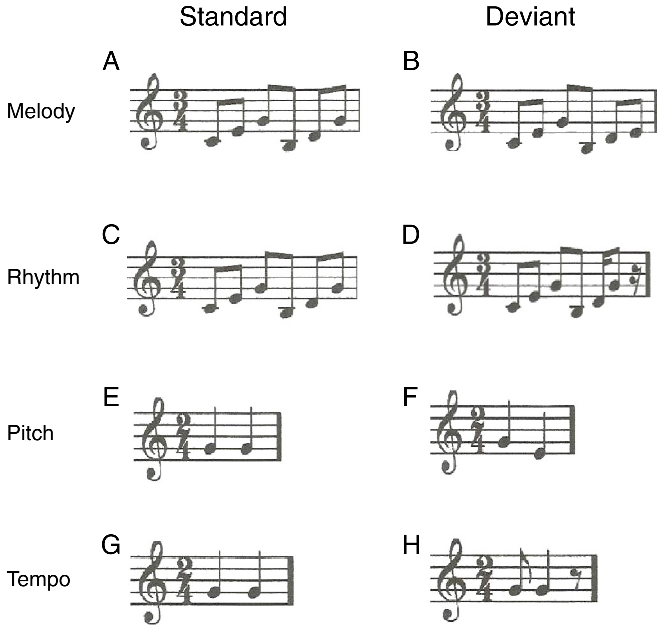

Fig. 1. Stimuli. Standard for the melody condition: Six-tone sequence composed of a C-major followed by a G-major broken chord in first inversion. (B) Melody deviant: Composed like the standard sequence, but the last tone is lowered by a minor third. (C) Same sequence as the standard sequence in the melody condition (see A). (D) Rhythm deviant: the last tone appears 100 ms earlier. (E) The last tone of the standard sequence of the previous conditions (A,C) is repeatedly presented in a row as the standard for the simple tone conditions. (F) The last tone of the melody deviant (A) is used as the pitch deviant in the simple tone condition. Therefore, the tone change in the melody condition presented within a musical sequence is physically identical to the pitch change in the simple tone pattern. (G) The last tone of the standard is repeatedly presented (same as E). (H) In the deviant condition a temporal deviation is produced by presenting the tone 100 ms earlier. Therefore, the tone change in the rhythm condition presented within a musical sequence is physically identical to the temporal change in the simple tone pattern.

The melody and rhythm conditions were presented both within two subsequent runs that were separated by a short break. In each run, the respective deviant stimulus was presented in an oddball paradigm intermixed with the standard stimulus. In each case 320 standards and 80 deviants were presented in a quasi-random order so that at least three standards occurred between two deviants.

For comparison, two additional runs (run 3 and 4) tested simple tone deviations, since MMN source strength to pitch deviants depends on context (Brattico et al., 2002). These runs consisted of repetitions of the tone G (392.00 Hz), the last tone of the standard musical sequence intermixed with oddball deviant tones that presented pitch or timing deviations similar to those in the musical sequence. These runs were included in order to contrast expectancy violation within a musical sequence to expectancy violation within a simple tone pattern. In run 3 a pitch deviation was accordingly created by lowering the repeating tone G (392.00 Hz) to E (329.63 Hz). In run 4 a tempo deviation was created by presenting a repeating tone G (392.00 Hz) occasionally 100 ms earlier. Tone stimuli in run 3 and 4 had also a duration of 300 ms.

The entire session, comprising 4 runs (melody MMN, rhythm MMN, pitch MMN, and tempo MMN), was repeated twice on two consecutive days for each subject, and the data were combined accordingly.

MEG data acquisition

The MEG recordings were performed in a magnetically shielded and acoustically silent room. Subjects were seated as comfortably as possible in an upright position, while ensuring that they did not move the head during the measurement. Furthermore, subjects' head position was checked at the beginning and end of each recording block by means of three localization coils fixed to the nasion and the entrances of both ear canals. Subjects were instructed to stay in a relaxed waking state during the measurement, and to not pay attention to the sound stimuli. Alertness and compliance were verified by video monitoring. To control for confounding changes in attention and vigilance, subjects watched a soundless movie of their choice, which was projected on a screen placed in front of them. Participants listened passively to the stimuli, feedback was not required. The silent movie viewing is an established paradigm to distract the subject’s attention. Since the same procedure was used in all conditions, differences between simple and musical conditions and between rhythmic and melodic conditions are not likely to be related to differences in attention.

MEG data analysis

Magnetic field responses were recorded with a 275-channel whole-head magnetometer system (OMEGA 275; CTF Systems). MEG signals were sampled at a rate of 600 Hz after low-pass filtering at 150 Hz and then stored as epochs with a length of 2.1 s including 0.16 s pre-stimulus interval. Data recording was synchronized to the stimulus presentation. Data analysis was performed using FieldTrip software (Oostenveld et al., 2011). The magnetic field data were averaged separately for the standard and deviant stimuli in each run. The averaged field waveforms were 30 Hz low-pass filtered. Baseline correction was performed based on a 100 ms time interval preceding the onset of the piano sequence. Epochs contaminated by muscle or eye blink artifacts containing field amplitudes larger than 2.8 pT in any MEG channel were automatically rejected from the averaging procedure.

For the analysis in sensor space, root mean square (RMS) values were calculated for each subject over all sensor channels for the averaged data sets of the standard, the deviant and the difference (deviant – standard) data sets. The MMN of interest was expected to be evoked in the deviant sequence after the onset of the deviant last tone. Since this tone appeared 100 ms earlier in the rhythm deviation condition, standard and deviant datasets were temporally aligned to the onset of the last tone for the subtraction procedure to generate correct difference waveform data sets for that particular condition. Latencies and amplitudes of the MMN components were subjected to statistical analysis in all conditions.

To investigate whether the two hemispheres contributed differently to the activation, a source space projection onto two equivalent current dipoles (ECD), one in each hemisphere, was applied. Two spatiotemporal dipoles, defined by their dipole moments, orientation, and spatial coordinates, were fitted simultaneously to the data using a 20 ms time window centered on the time of maximum RMS value within a latency window of 100 to 250 ms. This was done separately for each of the four conditions. The dipolar sources were positioned in the anatomical area of the auditory cortex. Locations fulfilling the required anatomical considerations characterizing the human auditory cortex area were included for further analysis. Median values of x, y, and z coordinates of the ECDs as well as of the angles of the dipole orientation were calculated. The median values of the source coordinates and orientations were then used as reference for the source-space projection method (Tesche et al., 1995). To investigate the contribution of the two hemispheres to the brain activation, the individual dipole values were subjected to statistical analysis.

To calculate the neural generators of the mismatch negativity a beamformer source analysis was applied calculating source estimates in the time domain (Linearly Constrained Minimum Variance; LCMV). Beamforming is a method of source analysis in which a spatial filter is used that allows an estimation of the contribution of a given source without the necessity to impose constraints on the source solution by determining the number and positions of the ECDs in advance (Hillebrand et al., 2005; Steinsträter et al., 2005). It supports high localization accuracy, in particular with a high-density setup such as ours (Sekihara et al., 2005; Lin et al., 2008).

To obtain individual anatomical data a T1-weighted MR image was recorded from each participant using a three Tesla Scanner (Gyroscan Intera T30, Philips, Amsterdam, Netherlands). Turbo Field acquisition was applied to collect 400 contiguous T1- weighted 0.5 mm thick slices in the sagittal plane. For co-registration with the MEG measurements the positions of the fiducial points (small containers filled with Gadolinium to be visible in the MRI) were used. A realistically shaped head model implemented in the FieldTrip software was fitted to each individual participants’ structural MRI and served as volume conductor model (Nolte, 2003). Individual MRIs were warped to a template MRI in MNI coordinates and divided based on a regular three dimensional grid. The source strength for each grid point was computed for a predefined time window producing a 3D dimensional spatial distribution of the power of the neural generators of the mismatch component. Here, a common spatial filter for the standard and deviant conditions was computed and then applied to each condition to calculate the strength of the source power in each condition. This procedure was done for each run separately and the source power values were then combined from the two runs. Statistical parametric mapping of the source power values was performed with a cluster-based randomization test to control for multiple comparisons. In all statistical tests the alpha level for the cluster analysis was set to 0.05.

The beamformer analysis used the data from 90 ms to 150 ms after the deviant tone onset. This time range contained the onset and peak responses in all conditions and would be short enough so that source localization results would not be contaminated by any later components. To check for the possibility that temporally correlated sources in the two hemispheres reduce the beamformer output, the left and right hemispheres were analysed separately, in addition to the whole head analysis. This hemispheric analysis, however, does not support accurate localization of prefrontal and motor activation, as the cut-off down the midline suppresses contributions from sensors of regions in the unaccounted hemispheric side. The temporal, inferior frontal and parietal activation did not significantly differ between the half- and whole head analysis. Therefore, we report only the whole head analysis.

Results

We first analyzed RMS response strength in each MMN condition. Fig. 2 shows average time courses of the RMS MMN responses (deviant - standard) aligned to deviant tone onsets. There was a clear mismatch negativity component in all conditions. Time courses appeared to differ between conditions with the rhythmic deviation eliciting a faster response than the melodic deviation. To study this more quantitatively, we determined the peak RMS value and its latency for each subject and condition (Fig. 3A).

This analysis confirmed that the latency of the mismatch elicited by the melodic deviation within the musical context was significantly longer compared to the mismatch elicited by the rhythmic deviation (paired t-test, $p < 0.001$). This was not the case for the simple tone deviations. In those conditions, pitch and tempo deviations did not differ in latency (paired t-test, $p = 0.88$). Fig. 3B shows the peak response strengths. In the musical context, the rhythmic deviation produced a larger response than the melodic deviation (paired t-test, $p < 0.001$).

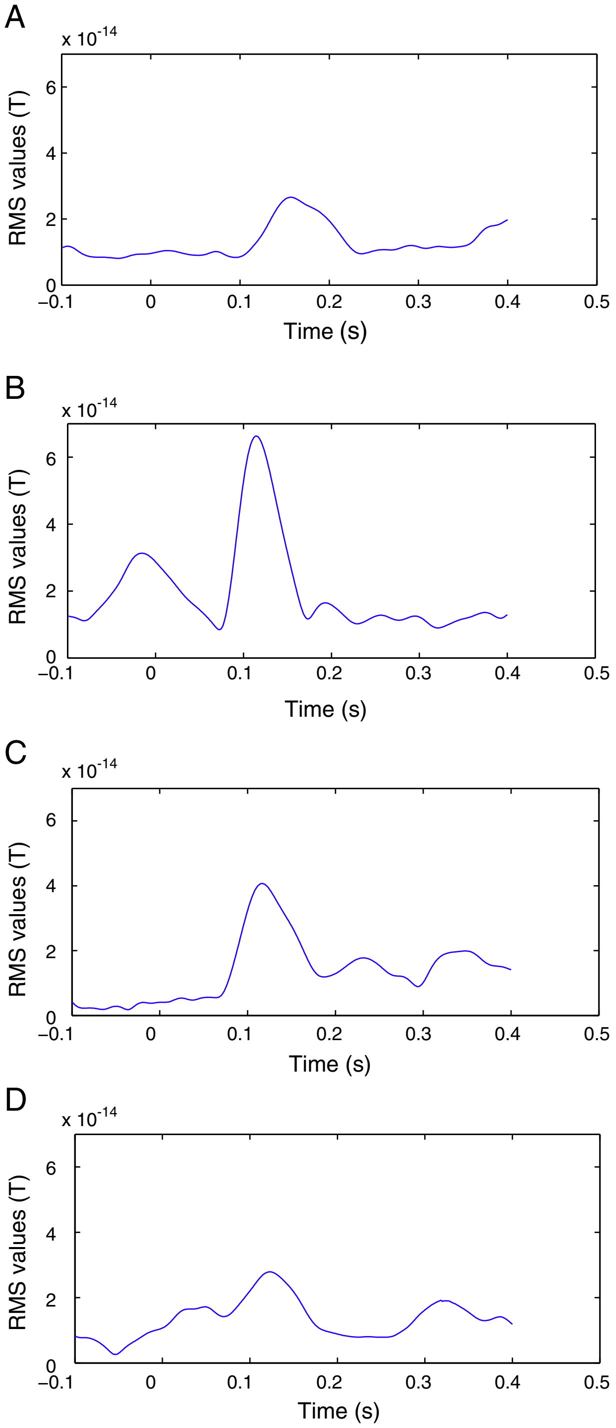

Fig. 2. (A) Time courses of RMS values for the MMN response after a melodic deviation (within a musical context). (B) Peak amplitudes of RMS values for the MMN response after a rhythmic deviation (within a musical context). (C) Peak amplitudes of RMS values for the MMN response after a pitch deviation (not within a musical context). (D) Peak amplitudes of RMS values for the MMN response after a tempo deviation (not within a musical context).

For the simple tone sequences, the results were opposite: the MMN after a pitch deviation within a non musical context was significantly larger than the mismatch elicited after a tempo deviation (paired t-test, $p < 0.001$).

To study any differences in hemispheric contribution to these responses we performed a source space projection onto an equivalent current dipole fitted to the responses at peak RMS for each subject and condition. T-tests of the dipole strength of the individual subjects showed no significant difference in activation between hemispheres for any condition.

The differences in time course between the different conditions could indicate that different cortical response sites contribute to their generation. This would be consistent with earlier findings in musically inept subjects after a short-term musical training (Lappe et al, 2013a, 2013b). To investigate the sources of the elicited mismatch negativity we conducted a whole-head source analysis using LCMV beamforming. For this analysis we selected a time window between 90-150 ms after deviant tone onset, which would encompass the early and peak responses in all conditions but, at the same time, would be brief enough to avoid contamination from any later components in the fast response conditions. This analysis revealed a distributed network of brain areas that contributed to the mismatch negativity (Fig. 4). For the melodic deviation (Fig. 4A) neural activation was found in the left and right auditory cortices, in the pars opercularis and pars triangularis of the inferior frontal gyrus and the superior and medial frontal cortices. Activation spread furthermore bilaterally into the supplementary motor areas.

The rhythmically elicited MMN, likewise, recruited a neural network comprising bilaterally superior, medial and inferior temporal cortices spreading also into supplementary motor areas. However, additional activation occurred in inferior and superior parietal areas in the right hemisphere and in the supramarginal gyrus in the left hemisphere. A direct comparison of the rhythmic deviation minus the melodic deviation revealed stronger rhythmic activation in pre-and postcentral areas, the superior temporal gyrus and in the inferior and superior parietal lobe. In the left hemisphere the direct comparison did not detect any significant differences.

We applied the same analysis to the simple tone conditions (Fig. 5). For pitch deviants not embedded within a musical sequence, neural activation was observed around the right superior temporal and inferior frontal gyri. No activation of the supplementary motor area or the prefrontal cortex was found. For the temporal deviants, which produced on average the smallest responses, neither the whole head beamformer analysis nor separate beamformer analyses for each hemisphere were able to detect any significant activation for deviant stimuli over standard stimuli.

Discussion

To investigate the dissociation of rhythmic and melodic prediction violation networks in a within subject design, musician subjects were tested on a melodic and a rhythmic deviation. To investigate how neural processing of musical and non-musical stimuli differ, both types of deviation were presented within a musical sequence and within a simple tone sequence. We found that melodic and rhythmic deviations within a musical context are processed differently in musicians. MMN responses to a rhythmic deviation occurred at shorter latencies and with higher amplitude than MMN responses to a melodic deviation. The two types of deviations recruited partially different brain networks. The melodic deviation activated areas of the anterior part of the auditory cortex, the inferior and the prefrontal cortices as well as the supplementary motor area. The rhythmic deviation recruited a neural network comprising auditory cortex, the inferior parietal lobule, the superior parietal and postcentral cortices as well as the supplementary motor area. Simple pitch deviations not embedded within a musical context produced no latency difference between the MMNs and the cortical activation was smaller and mostly limited to auditory cortex. In the following we will discuss these findings in detail.

The RMS analysis revealed that the rhythmically elicited MMN within the musical sequence appeared earlier compared to the melodically elicited MMN. A different time course can indicate differential pathways that are used for the processing of the different stimuli. The beamformer source analysis revealed indeed differential processing streams for the two musical deviances. These results support the model of auditory

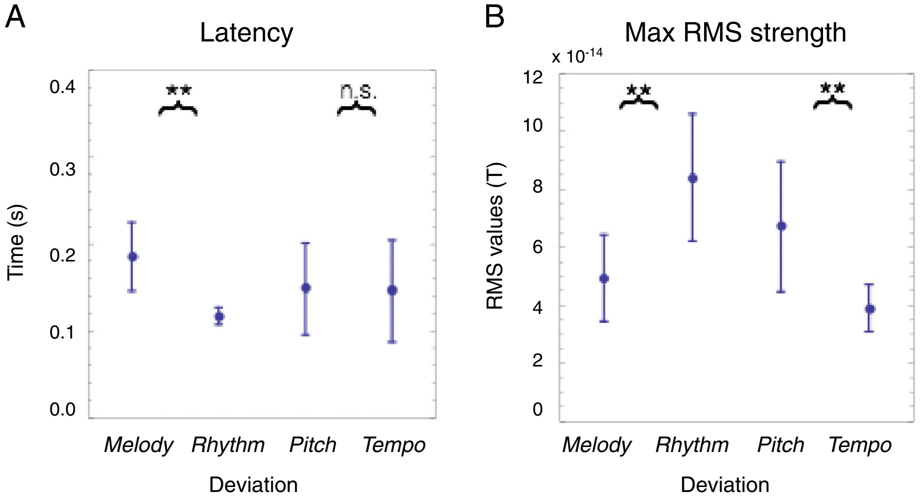

Fig. 3. (A) Latency of the peak amplitudes of RMS values for the melodic deviation within a musical context (Melody), for the rhythmic deviation within a musical context (Rhythm), for the pitch deviation not within a musical context (Pitch) and for the temporal deviation not within a musical context (Tempo). (B) Maximum RMS amplitude values in these conditions.

pathway organization that claims that the processing of time and space related auditory stimuli is dissociated from the processing of spectral acoustic features (Belin and Zatorre, 2000; Rauschecker and Scott, 2009). The model parallels the cortical organization in vision suggesting that a ventral stream is specialized for object recognition while a dorsal stream is responsible for spatial processing (Ungerleider and Haxby, 1994). In analogy, the dual pathway model of auditory processing postulates that auditory spectral features or auditory objects are processed ventral and anterior to primary auditory cortex while temporal and spatial stimuli are processed in posterior-dorsal auditory and parietal areas (Rauschecker and Scott, 2009). Investigations on anatomical connections in auditory cortical areas indicate indeed separate anterior and posterior auditory streams (Hackett et al., 1998; Kaas and Hackett, 2000). Further evidence for a dissociation of the two processing streams and a specific role of parietal regions for processing spatial and temporal auditory stimuli have also been shown in lesion and neuroimaging studies (DiPietro et al., 2004; Koch et al., 2009). Our localization results of the melodically and rhythmically elicited MMN within the musical sequence (c.f. Fig. 4) are in line with our previous findings showing differential neural networks for the processing of rhythmic and melodic deviations after a short-term musical sensorimotor training (Lappe et al., 2013a, 2013b).

The reason why we found such a clear dissociation between the processing of melodic and rhythmic deviation in the present study could be that musician subjects were motorically familiar with the stimuli after long term musical training. Halwani et al. (2011) recently demonstrated higher tract volumes in musicians in the right dorsal and ventral tracts compared to non-musicians. These findings suggest that musical training increases the white matter tracts that are associated with the dual pathway model of auditory processing. The results of the present study also suggest that sensorimotor training strengthens bilaterally the two streams of auditory processing and that predictive mechanisms are coded in these pathways. We hypothesize that sensorimotor training helps to establish a forward model linking a hand movement to a musical tone and, in addition, to a time point when the tone is generated (Novembre and Keller, 2014). Knowledge of when which tone must be generated is indeed crucial in musical performance. During musical training this information is then presumably coded in specialized neural ensembles. When listening to the trained musical stimuli these stimuli are then evaluated by the network that was established through this training process. Internal forward models that are created by sensorimotor training generate precise expectations about upcoming tones. These are essential to detect prediction violations within a musical context and help to process expectation violations more efficiently (Rohrmeier and Koelsch, 2012; Salimpoor et al., 2015). This interpretation gains further support by the source analysis in the musical sequence condition, which showed neural activation within the supplementary motor area (SMA). Previous functional neuroimaging, TMS and animal studies have found the SMA to have an important role in the network that is responsible for learning internal models for sequence performance (Imamizu et al., 2007; White et al., 2013; Padoa-Schioppa et al., 2003).

Several functional magnetic resonance imaging studies have demonstrated that there is a considerable overlap of regions including the SMA implicating perception and production of musical material in musician subjects (Bangert and Altenmüller, 2003; Lahav et al., 2007; Münte et al., 2002). The fact that SMA activation was not visible after a pitch deviation within the simple tone pattern condition, supports this assumption. Here, no musical sequence was present, therefore no action-perception coupling occurred, even though the stimuli generating the tone deviation in the musical sequence and simple tone pattern conditions were identical.

The SMA is primarily associated with motor control of sequences of movements (Jäncke et al., 2000; Janata and Grafton, 2003; Krings et al., 2000). Sequential auditory information is an inherent feature of music. The C-major chord progression we used aims for the root position which is the tonality defining tonic chord. Therefore, the sequential character of the stimulus was especially strong and expectations about upcoming tones were high.

The sequential character of the stimulus could thus be another reason why SMA and prefrontal activation was observable within the musical material condition but not in the simple tone condition. Moreover, prefrontal activation that is generally associated with top down processes might not have been involved as much when processing the simple tone deviation. The deviations in the simple tone sequence gave smaller and more focal responses. In the pitch deviation condition within the simple tone pattern neural activation focused on the auditory cortex. Inferior frontal cortex activation was, however, observed. This result is in line with previous auditory prediction violation studies showing activation in that region mainly in the right hemisphere with musical and non musical material (Lappe et al., 2013a, 2013b; for an overview see Deouell, 2007). For the temporal deviation in the simple tone pattern condition the beamforming source localization did not yield any significant activations. The question whether inferior frontal activation is related to an unexpected pitch or whether it is a general sign for prediction violation is therefore still an open question. The result of the

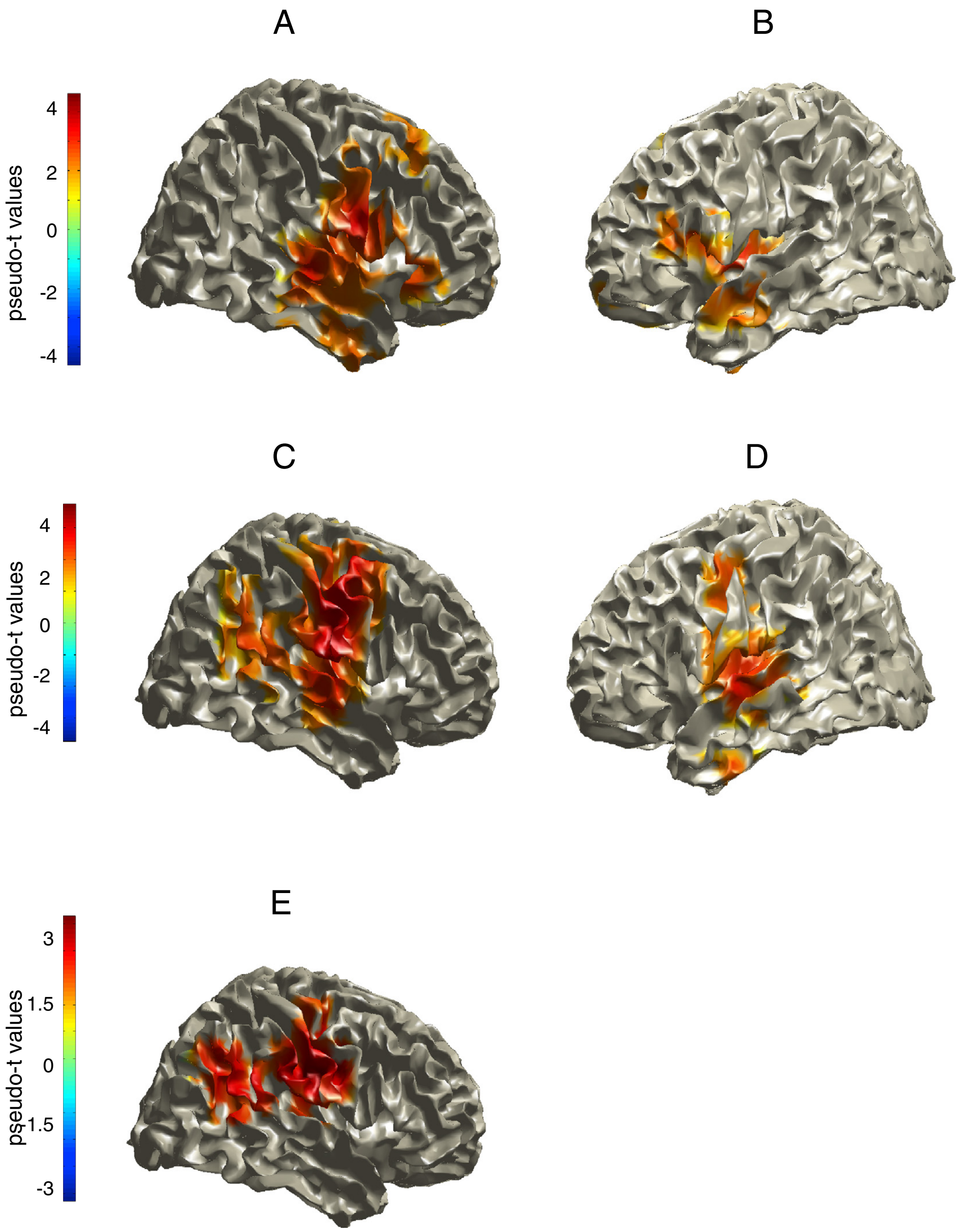

Fig. 4. (A) Right hemispheric neural activation in musicians after a melodic deviation within a musical sequence. (B) Left hemispheric neural activation in musicians after a melodic deviation within a musical sequence. (C) Right hemispheric neural activation in musicians after a rhythmic deviation within a musical sequence. (D) Left hemispheric neural activation network in musicians after a rhythmic deviation within a musical sequence. (E) Direct subtraction between the rhythmic and melodic deviations within a musical sequence.

temporal deviation within the simple tone pattern paradigm might help to answer that question and should be investigated in a future study.

The comparatively weak MMN elicited by the temporal deviation in the simple tone sequence in comparison to the rhythmic deviation in the musical material suggests that expectations for the timing of events build-up during the musical sequence. The number and timing of the deviants was the same in both conditions. However, in the rhythm condition the deviant tone occurred at the end of a sequence of six tones. Thus, there was always a sequence of five equally spaced intervals before any temporal deviant. This supports a build-up of temporal expectation, which is a characteristic of rhythm. In the tempo condition, in contrast, there is a variable number of standard intervals before any deviant. This variability does not support a consistent percept of rhythm during the stimulation, and, hence, does not allow to build up a rhythmic expectation.

The melody condition and the rhythm condition differ in that the melodic difference requires reference beyond the directly preceding tones while the rhythmic deviation, in principle, can be detected from the difference of the current interval to the preceding interval. If the perceptual system relies on the sequential buildup of expectation in the rhythm condition, then the situation in the rhythm condition is comparable to the melodic condition, which also leads to expectation of the last tone based on the sequence of the five preceding tones. If the perceptual system would not take the extended sequence into account

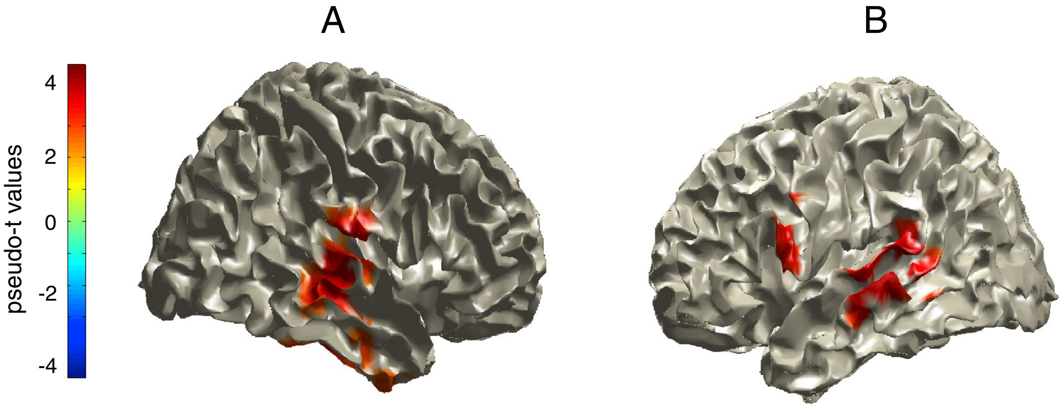

Fig. 5. (A) Right hemispheric neural activation in musicians after a pitch deviation not within a musical sequence (tone deviation within a row of repeating tones). (B) Left hemispheric neural activation in musicians after a pitch deviation not within a musical sequence (tone deviation within a row of repeating tones).

then the rhythm condition would be similar to the tempo condition, characterised by reliance on only the immediately preceding interval. The results we observed show a difference between the rhythm and tempo conditions, suggesting a reliance on rhythmic structure beyond the preceding interval. Moreover, from the difference in response strength between the rhythm condition and the tempo condition it is clear that the rhythm condition supports a much larger MMN than the tempo condition.

The rhythmic and melodic conditions differ with respect to expectation also in another way: When subjects experienced the rhythmic deviation, they did not expect the tone to appear already at that point in time. In the melody condition, in contrast, the deviation occurred at an expected point in time. One may wonder whether this difference could explain the difference in time course. However, since the same conditions occur in the pitch and temporal deviation of the simple tone pattern but do not lead to a time course difference, this explanation appears unlikely.

The faster time course of the rhythmically elicited MMN indicates that a rhythmical deviation within a musical context is processed faster. Different time courses of a melodically elicited and rhythmically elicited MMN were also observed in our previous training studies showing that the pitch MMN occurred 50 ms later (Lappe et al., 2008, 2011). We find the same time difference in the present study in a within subject design. It is therefore reasonable to believe that a rhythmic deviation in a musical context is especially noticeable and striking.

Acknowledgements

The present work has been funded by the German Research Foundation DFG LA 3080/1-1.

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