

available at [www.sciencedirect.com](http://www.sciencedirect.com)journal homepage: [www.elsevier.com/locate/cortex](http://www.elsevier.com/locate/cortex)**Special issue: Research report**

# Early electrophysiological correlates of meter and rhythm processing in music perception

Eveline Geiser<sup>a,b</sup>, Esther Ziegler<sup>a,c</sup>, Lutz Jancke<sup>a</sup> and Martin Meyer<sup>a,\*</sup>

<sup>a</sup>Department of Neuropsychology, University Zurich, Switzerland

<sup>b</sup>Department of Brain and Cognitive Sciences, Massachusetts Institute of Technology, Cambridge, MA, USA

<sup>c</sup>Institute for Behavioral Sciences, Swiss Federal Institute of Technology, Zurich, Switzerland

## ARTICLE INFO

### Article history:

Received 23 February 2007

Reviewed 5 June 2007

Revised 20 July 2007

Accepted 24 September 2007

Published online 7 November 2008

### Keywords:

Rhythm

Brain

Perception

Plasticity

Timing

## ABSTRACT

The two main characteristics of temporal structuring in music are *meter* and *rhythm*. The present experiment investigated the event-related potentials (ERP) of these two structural elements with a focus on differential effects of attended and unattended processing. The stimulus material consisted of an *auditory rhythm* presented repetitively to subjects in which metrical and rhythmical changes as well as pitch changes were inserted. Subjects were to detect and categorize either temporal changes (attended condition) or pitch changes (unattended condition). Furthermore, we compared a group of long-term trained subjects (*musicians*) to non-musicians. As expected, behavioural data revealed that trained subjects performed significantly better than untrained subjects. This effect was mainly due to the better detection of the meter deviants. Rhythm as well as meter changes elicited an early negative deflection compared to standard tones in the attended processing condition, while in the unattended processing condition only the rhythm change elicited this negative deflection. Both effects were found across all experimental subjects with no difference between the two groups. Thus, our data suggest that meter and rhythm perception could differ with respect to the time course of processing and lend credence to the notion of different neurophysiological processes underlying the auditory perception of rhythm and meter in music. Furthermore, the data indicate that non-musicians are as proficient as musicians when it comes to rhythm perception, suggesting that correct rhythm perception is crucial not only for musicians but for every individual.

© 2008 Elsevier Srl. All rights reserved.

## 1. Introduction

Melody and harmonic changes are commonly perceived as the characteristic elements of music. However, just as essential to the perception of music is its temporal structure, that is, meter and rhythm. The reader might recall that a fast rhythm can induce a feeling of excitement or slower rhythms can alleviate feelings of tension. On the other hand,

spontaneous body movements induced by music are most often related to the perceived meter and movement can in fact enhance meter perception in auditory rhythm (Phillips-Silver and Trainor, 2007). In sum, temporal structure crucially affects the specific character of a musical sequence. The present study aims to investigate the correlate of meter and rhythm perception using event-related potentials.

\* Corresponding author. Department of Neuropsychology, University of Zurich, Switzerland.

E-mail address: [mmeyer@access.uzh.ch](mailto:mmeyer@access.uzh.ch) (M. Meyer).

0010-9452/\$ – see front matter © 2008 Elsevier Srl. All rights reserved.

doi:10.1016/j.cortex.2007.09.010

There have been several descriptive approaches taken to define the constituting elements of rhythm and meter. Cooper and Meyer (1960) defined rhythm as the temporal relation between one or several unaccented tones and an accented tone. Schachter describes rhythm as “patterns of durations, emphases and groupings” that do not arise from pitch structure (Schachter, 1986). Lerdahl and Jackendoff (1983) use the term “grouping structure” to mean a hierarchical segmentation of music in motive, phrases and sections based on tone groups belonging to each other according to their temporal relation.

While rhythm is related to the duration of tones, meter is related to the relative accents of tones within their context. Lerdahl and Jackendoff (1983) describe meter as psychological extrapolation of isochronously defined tones perceived through metrical accents. Similarly, Cooper and Meyer (1960) defined meter as the number of pulses between more or less regularly accented tones. One of these authors found that a perceived meter is relatively resistant to deviants, allowing listeners to perceive a syncope within the context of a given meter (Meyer, 1956). This paved the way to Cooper and Meyer focussing on the psychological characteristic of the meter percept, describing it as a Gestalt phenomenon.

Most authors agree that the emergence of a meter percept depends on the perception of accent patterns. However, accents can arise from different characteristics of tones within their musical context. Recent experimental research has tended to focus on temporal, dynamic, and melodic accents. A temporal accent may appear when a tone is relatively isolated, the second of a two-tone cluster, or the initial or final note of a cluster of three or more notes. A dynamic accent is defined as a relative change of intensity on the accentuated tone (Drake and Palmer, 1993), while a melodic accent consists of a higher pitch or a “point of change within the melody” (Trehub and Hannon, 2006). Recent studies showed that the perception of meter is induced by both melodic and temporal accents (Hannon et al., 2004; Povel and Essens, 1985) and that in the absence of melodic accents dynamic accents become important for meter perception (Toivainen and Erola, 2004).

A cognitive approach describing the perception of music has postulated modular or domain-specific processing, thereby assuming different processing mechanisms underlying the perception of structural elements. It has been generally formulated for the processing of pitch as compared to the processing of temporal structure (Lerdahl and Jackendoff, 1983) as well as in association with specific temporal structuring, that is, for meter and rhythm. The latter was embedded in the “two-component model” by Lerdahl and Jackendoff (1981).

The advancement of neurophysiological research methods has enhanced this cognitive approach and led to the suggestion of different neural underpinnings related to the specific processing modules (Peretz, 2006). The neurofunctional differentiation of pitch and temporal processing has found support in a number of lesion and neurofunctional studies and associate temporal processing generally to brain areas of the left hemisphere (Midorikawa et al., 2003; Murayama et al., 2004; Peretz and Kolinsky, 1993; Piccirilli et al., 2000; Liegeois-Chauvel et al., 1998). Empirical evidence in support of the “two-component

model” of temporal processing is, however, still sparse and relates mostly to behavioural research (Essens, 1986; Ibbotson and Morton, 1981; Peretz and Zatorre, 2005; Liegeois-Chauvel et al., 1998). Evidence from lesion studies is ambiguous. Some authors have associated meter reproduction with the right hemisphere (Penhune et al., 1999; Wilson et al., 2002), while rhythm discrimination was associated with the left hemisphere (Di Pietro et al., 2004). In contrast, a study on healthy subjects postulated that memorization of metric rhythm relies on left premotor and parietal cortex areas, while right prefrontal, premotor and parietal cortical areas engage in nonmetrical rhythm processing (Sakai et al., 1999). A similar finding has been observed in a speech production experiment in which the reproduction of rhythmical as compared with isochronous syllables activated fronto-temporal brain areas of the right hemisphere (Riecker et al., 2002). Thus, present neurofunctional evidence about the different neural underpinnings of meter and rhythm processing is inconclusive.

Due to its excellent temporal resolution, we used electro-physiological measures to elucidate the early time course of brain responses during on-line perception of meter and rhythm and to find evidence for or against functional differentiation between rhythm and meter processing. To our knowledge, there are only two studies that recently investigated auditory temporal processing. One study investigated temporal auditory processing in an attended processing task, using DC-potentials of EEG signals (Kuck et al., 2003). Subjects had to perform a same-different task while listening to two subsequent acoustic time sequences. The stimuli differed with respect to either meter or rhythm. Processing of both meter and rhythm produced sustained cortical activation over bilateral frontal and temporal brain regions. Thus, this study speaks against a neurofunctional difference between rhythm and meter processing. However, we believe that the reported activation in the study by Kuck et al. is indeed more related to the comparison of temporal patterns than to the perception of metrical and rhythmical changes as the authors themselves suggest. Especially in the domain of metrical changes, we posit that the comparison of two sequences requires cognitive processes in addition to the mere perception of meter. In another study Vuust et al. (2005) showed an N100 m (the magnet-encephalographic equivalent of the N1, 100–150 ms post stimulus onset) related to the detection of metric deviants, which differ in amplitude depending on the acuteness (sharpness) of metrical change. The early negativity was more pronounced over the left hemisphere for experienced listeners and over the right hemisphere for naive listeners.

On the basis of above mentioned findings we assumed that the perception of temporal deviants is reflected by an ERP in the latency window of an endogenous component, that is, >100 ms after the onset of the deviant tone. Thus, we constructed our stimulus material with the specific aim of analyzing this latency window. Our study investigated processing differences between auditory rhythm and meter perception by presenting subjects with changes in either of the two categories. Our study is novel in several respects. First, subjects are continuously presented with a metrical rhythm. By means of this procedure we are able to induce a strong feeling of meter prior to a deviant stimulus. Secondly, we introduced “processing mode”, that is, an attended and an

unattended processing condition, as an additional experimental factor. The aim of this procedure was to clarify whether correlates of meter and rhythm changes are differentially affected by the processing mode. Finally, we investigated musically long-term trained and untrained individuals under the assumption that long-term training would impact differentially on meter and rhythm and that such training effects could be a strong indicator to differential processing mechanisms.

## 2. Procedure

### 2.1. Stimulus material/experimental conditions

The basis for the stimulus material consisted of an auditory rhythm in 3/4 meter on one note (“g”), which was presented continuously in tempo 100 Hz (=0.6 s per quarter note). The rhythm was devised in such a way that we had a temporal accent at the beginning of each bar. Therefore, the rhythm consisted of a quarter note at the beginning of each bar followed by four eighth notes (Fig. 1).

The stimulus material included *temporal deviants*, that is, two different metric and two different rhythmic changes (Fig. 2). The metric change consisted either of an insertion of one eighth note producing a bar in 7/8 instead of 3/4 meter (condition M7,  $n = 82$ ) or a removal of an eighth note producing bar in 5/8 instead of 3/4 meter (condition M5,  $n = 82$ ). The rhythmic change consisted either of an insertion of two sixteenth notes producing a group of four sixteenths on the third beat (condition R4,  $n = 82$ ) or an insertion of one sixteenth notes producing a group of an eighth note and two sixteenth note on the third beat (condition R2,  $n = 82$ ).

Additionally, pitch manipulations consisting of an “e” or a “b’ flat” on the first eighth of the second beat in a bar were included in the stimulus material and balanced over temporal conditions (Fig. 3).

The stimulus material was designed in such a way that there were two, three, or four bars (4:2:1) between deviant bar and this number of basis bars was randomized over experimental conditions. There was a total number of 82 deviant bars per condition.

Stimuli were constructed using the open-source LilyPond software (<http://lilypond.org/web/>) and exported as midi-files. Then the rhythms were synthesized using a piano-sound on one note (g) using “fruity-loop” software (<http://www.flstudio.com/>) and exported as .wav files. A dynamic accent of 30 percent above the general intensity was induced on the first beat of every bar to reinforce the perceived meter (Hannon et al., 2004). This accent is indicated by a “>” in Figs. 1–3.

### 2.2. Task/experimental design

All subjects were to perform two tasks in two subsequent experimental blocks. In the first block, subjects had to detect and categorize pitch changes. That is, they had to press the



Fig. 1 – Basis of the stimulus material.

right of two buttons when perceiving an “e” and the left button when perceiving a “b’ flat”. This condition is referred to as “unattended” processing condition, since rhythm deviants are perceived inattentively. In the second block, subjects had to detect and categorize temporal changes. That is, they had to press the right button when perceiving a meter change and the left button when perceiving a rhythm change (attended condition). Therefore, the resulting experimental design was a three-factorial design with one between-subject factor (“group”), and two within-subject factors (“processing mode” and “rhythmicity”) as indicated in Table 1.

### 2.3. Experimental groups/subjects

Two groups of male subjects, a musically trained group ( $n = 15$ , mean age = 29.6, std = 4.9) and a musically untrained group ( $n = 15$ , mean age = 31.1, std = 6.2), participated in the experiment. Untrained subjects did not play an instrument and had no musical training at all. Trained subjects were students at the conservatory or musicians. To substantiate the group categorization, an auditory test (Gordon, 1989) was performed. A one-way independent-sampled t-test performed on these data revealed significant group differences between the two groups for the rhythm task ( $t_{(28)} = 3.236$ ;  $p < 0.005$ ) as well as for the tonal task ( $t_{(28)} = 3.322$ ;  $p = 0.001$ ). Musicians performed significantly better than non-musicians in both the rhythm and the tonal task. No subjects had to be excluded on the basis of their rhythm performance with respect to the group performance or with respect to the standardized norm provided by the authors of the test. However, one subject of the musician group had to be excluded from the analysis after EEG-artefact correction. Two further subjects, one from each group, had to be excluded from the analysis due to percent of correct answers below 2 standard deviations of the mean group performance. Thus, we included a total of 13 musicians and 14 non-musicians in our analysis. All subjects were right handed according to the Annett handedness scale (Annett, 1992), with no history of neurological, major medical or psychiatric disorders and with normal audiological status. Furthermore, subjects gave their consent in accordance with guidelines of the Ethical Committee of the local Medical Faculty.

### 2.4. Experimental procedure

After receiving written and oral instruction, subjects were made familiar with the task. During the experiment a total number of 328 deviant bars were pseudo-randomly presented using Hifi-headphones. The total number of stimuli was presented twice, each block lasting 32 min. The subjects first performed the pitch detection task in the first block and, after a short break, the attended task (temporal task). The stimuli were presented via headphones in a sound and light attenuated room. Stimulus presentation and answer registration were done using Presentation Software (<http://www.neurobs.com/>).

### 2.5. EEG-recordings

EEGs were recorded continuously using a QuickAmp EEG amplifier (Brain Products GmbH, 2004) and applying



Fig. 2 – Two different types of metric changes (left) and two different types of rhythmic changes (right).

a bandpass filter of 0.1–100 Hz, a notch-filter of 50 Hz. The EEG signal was continuously sampled and digitalized at 500 Hz. EEGs were recorded from 30 electrode sites using a subset of the 10–10 system (Chatrjian et al., 1988) provided by Easy Cap. Vertical and horizontal EOGs were recorded from two bipolar electrodes placed on the infra-orbital ridges of the left and the right eye and the outer canthi of the two eyes. All leads were referenced to a common average reference. The ground electrode was positioned fronto-centrally (AFz). EEG data were scanned off-line for eye movements and other artefacts. When the maximum absolute voltage difference within an interval of 200 ms exceeded 100  $\mu$ V or the electrical activity generally exceeded  $\pm 100 \mu$ V, the signal was excluded from analysis in the time range of 100 ms before and after the rhythmic and metric change, respectively.

### 3. Analysis

#### 3.1. Behavioural data

We analyzed percent correct answers and reaction time for the two conditions. Since we adopted a two-alternative forced choice task, the percentage of correct answers calculated across the meter deviants as well as the rhythm deviants was taken as a measure for task performance. As a measure for discrimination rate,  $d'$  was calculated (Macmillan, 1991). A repeated measure ( $2 \times 2$ ) ANOVA using the within-subject factor “rhythmicity” (meter and rhythm) and the between-subject factor “group” (musicians and non-musicians) was performed for the task performance. Furthermore, a one-way independent sample t-test was performed on the discrimination rate.

#### 3.2. EEG data

EEG data were analyzed using Brainvision Analyzer 1.0 (Brain Products GmbH, Munich). Fig. 4 illustrates the time point within the stream of stimuli from which we calculated the event-related potentials for each stimulus condition. ERPs for deviants were calculated for both processing conditions (attended/unattended) time-locked to the same note. For the meter deviants the ERPs were calculated on the first quarter note of the bar following the 5/8 bar (condition M5) and on the last eighths note of the 7/8 bar (condition M7), respectively. For the rhythm changes the ERPs were calculated on the second sixteenth note of the 4-sixteenths group (condition R2) and on the second sixteenth note of the 2-sixteenths group (condition R4). The ERPs of the rhythm and meter deviants were compared to ERPs evoked by tones which do not constitute a deviant ( $n = 82$ ). This non-deviant tone was

different for each experimental condition. It had to show the same intensity as the deviant tone and had to be preceded by a tone of the same length as the antecedent tone of the deviant. The non-deviant tones are indicated as “control” in Fig. 4. The ratio between deviants and standards was 1:1 in the rhythm condition and approximately 1:3 in the meter condition.

The continuous EEG data were segmented off-line into epochs of 800 ms starting 100 ms before the stimulus of the specific experimental condition. After artefact correction a mean of 65.4 deviants per condition, 71.75 rhythm standards, and 195.5 m standard segments was analyzed per condition and subject. The segments were baselined to the pre-stimulus interval (–100 to 0 ms) and averaged according to stimulus type and processing condition separately for each experimental group. For the attended processing condition only trials which were correctly identified within 3600 ms (3 bars) after the deviant were analyzed.

Analysis of behavioural data revealed, that the performance was better for M5 and R2 as compared to the respective other experimental condition and that this effect was present in both experimental groups (see Section 2.1). Therefore we restricted our analysis of temporal deviants to these two conditions. The N150 peak was determined as the absolute voltage minimum in the time window between 90 and 160 ms after stimulus onset for the rhythm condition and 110–160 ms after stimulus onset for the meter condition occurring at electrode Cz. R2, M5, and their specific control conditions were separately subjected to repeated measures ANOVA using the between-subject factor “group” (musicians–non-musicians), the within-subject factor “processing mode” (unattended–attended), and “rhythmicity” (R2–R2 control)/“metricity” (M5–M5 control), respectively. Interactions in this three-factorial ANOVA were analyzed by three subsequent two-factorial ANOVAs.

### 4. Results

#### 4.1. Behavioural results

One-way independent sample t-test to identify group differences performed on the discrimination rate revealed significant



Fig. 3 – Two pitch manipulations.

**Table 1 – Experimental design with two within-subject factors “processing mode” (attended-unattended) and “temporal manipulation” (rhythm-meter) and one between-subject factor “group” (musicians-non-musicians).**

		Attended	Unattended
Musicians	Meter	M5 (n = 82)	M5 (n = 82)
	Rhythm	R2 (n = 82)	R2 (n = 82)
Non-musicians	Meter	M5 (n = 82)	M5 (n = 82)
	Rhythm	R2 (n = 82)	R2 (n = 82)

group differences ( $t_{(28)} = 3.126; p < 0.05$ ). The repeated measures ANOVA on the percent of correct answers (Table 2) using the within-subject factor “rhythmicity” (meter and rhythm) and the between-subject factor “group” (musicians and non-musicians) revealed a main effect of rhythmicity ( $F_{(1,26)} = 19.948; p < 0.005$ ) and an interaction “group  $\times$  rhythmicity” ( $F_{(1,26)} = 19.648; p < 0.05$ ) as well as a main effect of group ( $F_{(1,26)} = 1379.6; p < 0.05$ ). Two-way independent sample t-tests to resolve the interaction revealed, that the group difference was more pronounced on the meter condition ( $t_{(26)} = 3.304; p < 0.05$ ) as compared to the rhythm condition ( $t_{(26)} = 2.305; p < 0.05$ ). That is, untrained subjects performed worse on the meter as compared to the rhythm condition. This difference was not found in the group of trained subjects.

#### 4.2. EEG results

Fig. 5 shows the ERP waveforms to the deviant tones and to the control tones. Red lines illustrate the ERPs to the attended processing condition and blue lines illustrate the ERPs to the unattended processing condition. Fig. 5 (left) visualizes the ERPs elicited by the meter for all subjects collapsed over both groups and Fig. 5 (right) the ERPs elicited by the rhythm condition for all subjects regardless of group. Results indicate an early negative deflection peaking at 150 ms on average in the rhythm condition. The meter condition elicited a negativity in the same latency window in attended processing only. Thus, a difference between the two temporal manipulations is reflected in a differential effect of the processing mode on the early negative deflection.

Subsequently we report the results revealed by the three-factorial ANOVA (rhythmicity/metricity  $\times$  processing

mode  $\times$  group) calculated on the ERP-amplitude separately for rhythm and for meter manipulations. The ANOVA calculated on the ERPs related to *rhythm manipulation* revealed a main effect of “rhythmicity” ( $F_{(1,25)} = 83.493; p < 0.001$ ). No effect of group or processing mode was observed. That is, rhythm deviants revealed significantly higher amplitudes as compared with control tones in both groups and across experimental conditions. Likewise, the ANOVA calculated on the ERPs related to *meter manipulation* revealed a main effect of “metricity” ( $F_{(1,25)} = 38.553; p < 0.001$ ) as well as an interaction between “metricity” and “processing mode” ( $F_{(1,25)} = 33.316; p < 0.001$ ). No main effect of group was observed. The interaction was due to the significant effect of “metricity” within the attended processing condition only ( $F_{(1,25)} = 53.096; p < 0.001$ ). There were higher amplitudes observed for the meter deviant as compared with the control tone in the attended processing condition. The amplitude related to the meter deviant in the unattended processing condition did not significantly differ from the control tone.

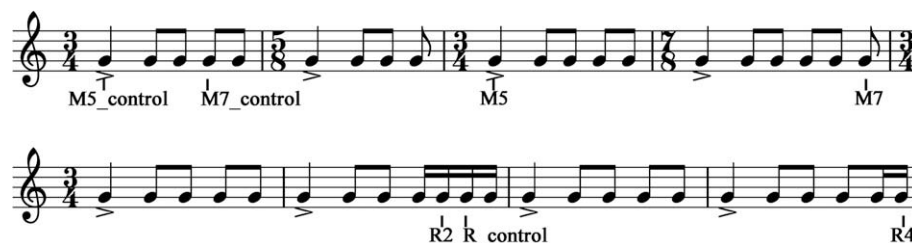
## 5. Discussion

In the following section, we will discuss the behavioural results as well as the early negativity we observed for meter and for rhythm deviants, focussing on the effect the processing mode had on this component. Our discussion will close by reflecting on long-term training effect in auditory temporal processing.

### 5.1. Behavioural data

We found a difference in the discrimination rate between trained and untrained subjects. This result speaks for an effect of expertise in temporal processing due to long-term musical training and is consistent with previously reported behavioural data showing the superiority of musicians over non-musicians in the performance of temporal tasks such as the detection of timing variations (Jones et al., 1995), or the detection of tempo changes (Drake and Botte, 1993; Ehrle and Samson, 2005; Yee et al., 1994).

However, the percentage of correct answers clearly reveals a difference between the perception of meter and rhythm deviants, which is evidenced by a differential effect of



**Fig. 4 – Time point within the stimulus from which the event-related potentials were calculated for each stimulus condition. For the meter changes the ERPs were calculated on the first 1/4 note of the bar following the 5/8 bar (condition M5) and on the last 1/8 note of the 7/8 bar (condition M7), respectively. For the rhythm changes the ERPs were calculated on the second 1/16 of 4/16 (condition R2) and on the second 1/16 of the 2/16 group (condition R4). Control tones for each experimental condition are indicated likewise.**

**Table 2 – Percent correct answers for musicians and non-musicians (left) collapsed over meter and rhythm conditions (right) separately for each condition (standard deviation in brackets).**

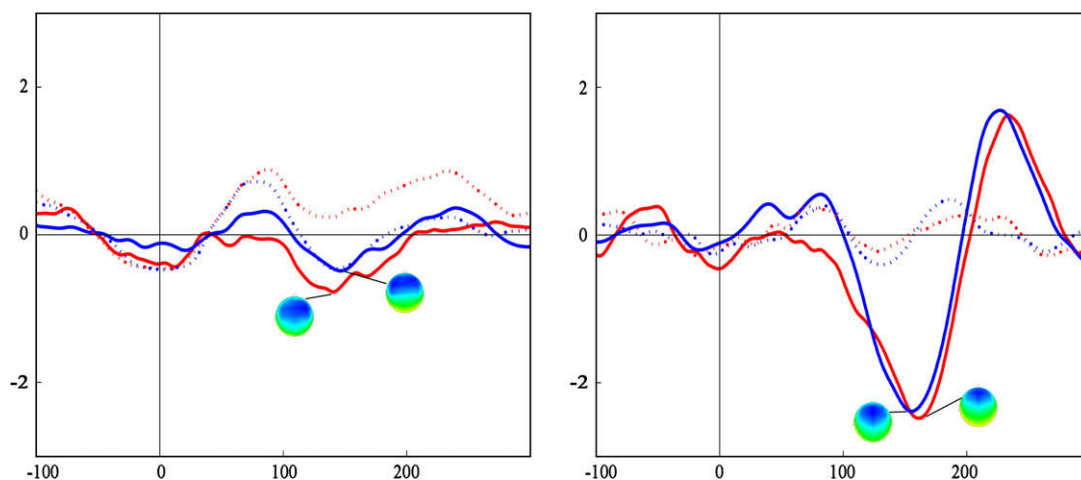
	Meter	Rhythm	M5	M7	R2	R4
Musicians	89.6 (20.9)	94.3 (5.6)	91.1 (17.4)	88.2 (24.6)	95.6 (5.1)	93.0 (6.8)
Non-musicians	75.6 (21.5)	86.1 (12.8)	77.6 (17.8)	73.7 (27.5)	91.9 (8.0)	80.4 (21.7)

expertise on the detection of the two temporal characteristics. This effect was more pronounced on the meter condition than on the rhythm condition. Since this group difference was observed for the rhythm condition as well, although to a lesser extent, a ceiling effect on rhythm perception can be excluded. In other words in untrained subjects rhythm perception performance is better than meter perception performance, while experts perform significantly better on both and bring meter perception to an equivalent level of performance as rhythm perception. We interpret this data in the sense that the ability to perceive meter is specifically necessary in music performance, whereas the ability to process rhythm seems to be also most relevant for untrained subjects, presumably in other perceptual domains of the auditory modality such as speech perception (Geiser et al., 2008; Ramus et al., 2000; van Zuijlen et al., 2005). There is evidence indicating that the perception of rhythmic aspects of speech highly facilitates speech comprehension (Friedrich et al., 2004; Goswami et al., 2003). In addition, to the frequent exposure to speech rhythm, there is evidence in the literature for rhythm perception as an “ancestral skill” of the auditory system with which to group incoming events. For example, primate research shows that tamarins are able to discriminate languages of different rhythm classes (Tincoff et al., 2005). While our data cannot disentangle the question of nature or nurture on temporal perception, it speaks for a clear proficiency of musically trained subjects in temporal perception. Our data may further implicate a categorical difference between rhythm and meter in that superior perception of one element does not automatically allow for a good perception of the other.

## 5.2. Electrophysiological data

The electrophysiological analysis revealed a negative fronto-central deflection peaking at 150 ms time-locked to the onset of the deviant tone. The main purpose of this study was to identify differences between the perception of rhythm and meter deviants by manipulating the factors training and processing mode. After a general discussion of the event-related potential observed, we address the differences between meter and rhythm with respect to processing mode. Then we discuss the fact that we did not find any group differences in the negative deflection.

Negative deflections in the time window between 100 and 200 ms have been reported formerly in auditory experiments, e.g., experiments related to pitch deviants within a melody (Nittono et al., 2000), to timbre discrimination (Meyer et al., 2006), or changes of pitch and intensity (Snyder and Hillyard, 1976). Likewise, a negativity has been observed in the perception of auditory temporal deviants reported as an N1/P2 complex with a negativity peaking at 130 ms (Ford and Hillyard, 1981). An N2b component was reported in auditory omission conditions with a peak amplitude at 145–195 ms elicited by an auditory temporal omission condition (Raij et al., 1997). These authors reported strong sensitivity of this component to attention, showing enhanced amplitudes in an attended processing condition as compared to an unattended processing condition. Similarly, another recent study reported an N150 related to temporal omission in an attended processing condition (Jongsma et al., 2005). The authors relate this component to the earlier reported N2b component and interpret this effect as an orienting reaction due to temporal



**Fig. 5 – ERPs related to deviant and standard stimuli in the explicit and implicit processing condition. Left, meter processing; right, rhythm processing; red, attended processing; blue, unattended processing; solid line, deviant stimulus; dotted line, control stimulus. ERPs are collapsed over experimental groups. Scalp distributions relate to the deviant peaks.**

omission. Thus, in all of the above-mentioned studies the negativity peaking between 100 and 200 ms time-locked to the stimulus onset was related to the perception of a temporal deviant. It was elicited in attended and unattended processing conditions and sometimes differentially manipulated by attention (Raj et al., 1997). Given the latency window of our component we are inclined to relate this finding to the N2b component associated with the perception of temporal deviants (Jongasma et al., 2005). However, this interpretation should be considered with caution since the scalp distributions of these components are slightly different to our findings. Our component displayed fronto-central negativity while the component reported by Jongasma and colleagues was centro-parietally localized.

One might alternatively interpret the N150 we observed as a mismatch negativity (MMN)-like component. It is well known that the mismatch negativity in the auditory modality is evoked in a specific pre-attentive oddball paradigm involving participants in the performance of a task such as reading a book or watching a silent movie (Gottselig et al., 2004; Naatanen et al., 2004; Restuccia et al., 2005; Ritter et al., 2006). However, an MMN-like component was recently reported when subjects focussed on another acoustic aspect of the stimulus material (Rinne et al., 2006). In this experiment subjects were listening to pitch differences while the MMN was elicited by intensity deviants. The observed component was described as MMN-like on the basis of its latency window as well as due to its characteristic scalp distribution displaying a fronto-central negativity. This distribution is clearly distinct from the central negativity commonly observed for the N1 component. Similarly, Sabri et al. (2006) have reported an MMN in the time range of 110–170 ms elicited by pitch deviants while subjects performed an auditory duration task.

The paradigm adopted in our experiment was comparable with the paradigm used in those studies. Furthermore, the component elicited in the unattended processing condition showed a scalp distribution similar to that of the MMN (Ritter et al., 2006; Shalgi and Deouell, 2007).<sup>1</sup> Thus, the latency of the negativity as well as the scalp distribution observed in our experiment might speak for an MMN-like component. However, since we did not use the standard MMN-paradigm we choose to refer to our component as a N150. The N150 was found for the temporal deviants compared to the standard tones. This finding indicates that the perception of temporal changes induces a more extensive neuronal activity and, furthermore, that this effect is possibly due to an orienting reaction. In the following section we discuss the observed between meter and rhythm deviants' differences in this component.

### 5.3. Differences between meter and rhythm processing

Most evident is the difference in negativity observed between rhythm and meter deviants. The rhythm deviants elicited an N150 with higher amplitudes compared to the N150 elicited by the meter deviant. However, this difference in amplitude

cannot be attributed to the temporal characteristic of our experimental stimuli solely but could be influenced by the difference in intensity of the tones. A meter change was always time-locked to an accented tone, while a rhythm change was unaccented. The most relevant difference between meter and rhythm-related ERPs is to be found within the differential effects that the processing mode had on the observed component.

The rhythm deviants elicited an N150 independent of processing mode. However, the meter deviant only elicited a negative deflection in the attended processing condition. One might argue that this effect is due to a greater salience of rhythm as compared with meter changes. However, musicians performed just as well in the meter condition as compared to the rhythm condition in both groups. Since this group difference did not show in the electrophysiological data, we are of the opinion that this attention related difference could speak for the existence of different neurofunctional mechanisms underlying the processing of meter and rhythm. More precisely, the meter perception might differ from the rhythm percept in the time course of its perception. Early theoretical models have already suggested that meter perception relies on Gestalt phenomena and hence requires the integration of several sequential auditory cues and subsequent reinterpretation (Cooper and Meyer, 1960). Therefore, it is plausible that the perception of meter in the unattended processing condition takes place later than 150 ms after the stimulus onset. Contrarily, in the attended processing condition, when listeners focussed on temporal changes, we observed a clear N150 for meter changes. One must therefore infer that this attention dependent negativity in the context of the present study reflects a percept of meter. This poses a question on the suggested difference between meter and rhythm processing.

Interestingly, Vuust et al. (2005) found an effect of meter perception reflected by a negativity between 100 and 150 ms after stimulus onset in an unattended processing condition. This negativity was elicited by two different temporal deviants and displayed increased amplitudes for the stronger, as compared to the weaker, deviant. We are of the opinion that our finding is only at first sight contradictory to the finding reported by Vuust et al. Rather, this difference is due to the specific construction of the stimuli in that study. The weaker manipulation in the study by Vuust et al. was a syncope, which can be described as a rhythm change without affecting the underlying metric pattern. It is specific for the meter percept that it is not affected by short irregularity, such as a syncope (Meyer, 1956). We suggest that the component observed by Vuust et al. could be comparable to the negativity we observed in the rhythm condition. With reference to the reported strong violation, Vuust et al. (2005, p. 561) mention the introduction of a beat which is incongruent with the underlying metrical grid, making it seem as if the music were to “stumble”. This violation, however, strongly differs from our metric manipulation. Vuust et al. delayed an expected beat, a manipulation which could also be considered a cesura. This is a musical terminus for a small delay of an expected tone used as an effect in musical interpretation. Thus, one would expect that this effect does not affect the percept of the underlying meter. In our study, we took a different approach by removing a tone. The deviant tone appeared exactly at the

<sup>1</sup> An illustration of scalp potential distribution maps at the N1 latency is available as supplementary material on <http://www.neurowissenschaft.ch/mmeyer/COR-08/>.

time expected, while the dynamic characteristic of this tone was unexpected (Toivainen and Eerola, 2004). Thus, the two metrical manipulations are crucially different in their nature, which most likely causes the observed electrophysiological differences. In sum, the fact that the metrical manipulation in our data failed to elicit an N150 in the unattended processing condition even in high performing trained subjects, while the rhythm manipulation elicited an N150 might sustain the notion of a difference between meter and rhythm processing. However, this effect of processing mode on the processing of the meter needs to be further investigated.

#### 5.4. No differences between trained and untrained subjects

Interestingly, we did not find differences in the N150 component between musicians and non-musicians. This electrophysiological finding suggests that musicians and non-musicians perceive meter and rhythm changes in the same way.

Several authors investigated training effects on auditory processing. There is evidence of short-term training effects in components of 100–200 ms latency which were elicited by melodic changes, different voice-onset times, or frequency changes (Bosnyak et al., 2004; Tervaniemi et al., 2001; Tremblay et al., 2001). Long-term training effects have been found by comparing musicians and non-musicians in the perception of pure tones and pitch grouping (Shahin et al., 2003; van Zuijen et al., 2004). More specifically, a long-term training effect on temporal processing has been found by Jongasma et al. (2005) reporting higher N150 amplitudes time-locked to an auditory temporal omission.

Yet, there are studies that do not find training effects in auditory processing of pure tones, familiar or unfamiliar chords, or the violation of temporal irregularity (Lutkenhoner et al., 2006; Neuloh and Curio, 2004; van Zuijen et al., 2005). Thus, it appears that the literature on this matter is yet inconclusive and that possible training differences might occur, although not in every aspect of temporal processing. In accordance with van Zuijen et al., we argue that the unobserved group differences on the N150 in either the unattended or attended temporal processing clearly speaks for a functional relevance of these perceptive processes, not only pertinent to musically trained subjects. This relevance is possibly related to the perception of speech that highly relies on temporal segmentation processes.

Contrary to this electrophysiological finding, behavioural results of our study clearly show differences in the performance rate between the two groups. Musicians performed significantly better on the detection task, particularly in the detection of meter deviants. These findings seem conflicting. That musicians are more proficient in meter perception as compared with non-musicians has been documented earlier (Ehrle and Samson, 2005). In our opinion, this discrepancy between our electrophysiological and our behavioural data could be an indication that the electrophysiological correlate of the meter percept is not reflected in the early latency window we analyzed. This hypothesis is in line with research reporting short-term training effects reflected in late ERP, for example, an enhanced P2-amplitude or P2m dipole moment (Atienza et al., 2002; Kuriki et al., 2006; Reinke et al., 2003; Shahin et al., 2005).

On the basis of these findings we speculate that the behavioural differences observed in the present experiment might be reflected in electrophysiological processes within a later latency window. However, this issue needs further investigation.

One difference we observed between musicians and non-musicians lies in the scalp potential distributions related to the attended processing of meter deviants. While musicians showed centro-frontal negativity, the negativity was more lateralized to right frontal regions in non-musicians.<sup>2</sup> Although this lateralization difference is not sustained statistically in a source estimation analysis, we may speculate that this differential effect relates to a well described difference between trained and untrained subjects. There is increasing evidence that one of the main characteristics of the musically trained brain lies within a more distributed network underlying the processing of acoustic stimuli in musicians, specifically the interaction between the hemispheres. Anatomical as well as functional evidence supports this concept (Gaser and Schlaug, 2003; Jancke, 2002; Schlaug et al., 1995a, 1995b).

## 6. Summary

Our study reveals an electrophysiological correlate of auditory rhythm perception in the form of a negative deflection in the latency window of 100–200 ms. This deflection is present in both attended and unattended processing. Meter deviants only elicit a similar negative deflection in the attended processing condition of our study.

Our data provide evidence on one hand of a categorical difference between rhythm and meter, as evidenced by this effect of processing mode as well as by a differential effect of expertise on the perception of meter and rhythm. On the other hand, this data might be interpreted as evidence for rhythm perception as an “ancestral skill” of the auditory system with which to group incoming events.

## Acknowledgments

During the preparation of this manuscript E.G. was supported by the Swiss National Sciences Foundation (SNF) 3200B0-105877 and the “Fonds zur Förderung des Akademischen Nachwuchses”. We thank Elsa Sägerser and Marcus Cheetham for very helpful comments on former versions of this manuscript.

## REFERENCES

- Annett M. Five tests of hand skill. *Cortex*, 28: 583–600, 1992.  
 Atienza M, Cantero JL, and Dominguez-Marin E. The time course of neural changes underlying auditory perceptual learning. *Learning and Memory*, 9: 138–150, 2002.

<sup>2</sup> See supplementary material on [http://www.psychologie.unizh.ch/neuroopsy/home\\_mmeyer/COR-08/index.html](http://www.psychologie.unizh.ch/neuroopsy/home_mmeyer/COR-08/index.html).



- Bosnyak DJ, Eaton RA, and Roberts LE. Distributed auditory cortical representations are modified when non-musicians are trained at pitch discrimination with 40 Hz amplitude modulated tones. *Cerebral Cortex*, 14: 1088–1099, 2004.
- Chatrian GE, Lettich E, and Nelson PL. Modified nomenclature for the “10%” electrode system. *Journal of Clinical Neurophysiology*, 5: 183–186, 1988.
- Cooper GW and Meyer LB. *The Rhythmic Structure of Music*. Chicago: University of Chicago Press, 1960.
- Di Pietro M, Laganaro M, Leemann B, and Schnider A. Receptive amusia: temporal auditory processing deficit in a professional musician following a left temporo-parietal lesion. *Neuropsychologia*, 42: 868–877, 2004.
- Drake C and Botte MC. Tempo sensitivity in auditory sequences – evidence for a multiple-look model. *Perception and Psychophysics*, 54: 277–286, 1993.
- Drake C and Palmer C. Accent structures in music performance. *Music Perception*, 10: 343–378, 1993.
- Ehrle N and Samson S. Auditory discrimination of anisochrony: influence of the tempo and musical backgrounds of listeners. *Brain and Cognition*, 58: 133–147, 2005.
- Essens PJ. Hierarchical organization of temporal patterns. *Perception and Psychophysics*, 40: 69–73, 1986.
- Ford JM and Hillyard SA. Event-related potentials (ERPs) to interruptions of a steady rhythm. *Psychophysiology*, 18: 322–330, 1981.
- Friedrich CK, Kotz SA, Friederici AD, and Gunter TC. ERPs reflect lexical identification in word fragment priming. *Journal of Cognitive Neuroscience*, 16: 541–552, 2004.
- Gaser C and Schlaug G. Brain structures differ between musicians and non-musicians. *The Journal of Neuroscience*, 23: 9240–9245, 2003.
- Geiser E, Zaehle T, Jancke L, and Meyer M. The neural correlate of speech rhythm as evidenced by meter processing: an fMRI study. *Journal of Cognitive Neuroscience*, 20: 541–552, 2008.
- Gordon EE. *Advanced Measures of Music Audiation*. Chicago: Publications Inc., 1989.
- Goswami U. How to beat dyslexia: the Broadbent Lecture 2003. *The Psychologist*, 16: 462–465, 2003.
- Gottselig JM, Brandeis D, Hofer-Tinguely G, Borbely AA, and Achermann P. Human central auditory plasticity associated with tone sequence learning. *Learning and Memory*, 11: 162–171, 2004.
- Hannon EE, Snyder JS, Eerola T, and Krumhansl CL. The role of melodic and temporal cues in perceiving musical meter. *Journal of Experimental Psychology – Human Perception and Performance*, 30: 956–974, 2004.
- Ibbotson NR and Morton J. Rhythm and dominance. *Cognition*, 9: 135, 1981.
- Jancke L. What is special about the brains of musicians? *Neuroreport*, 13: 741–742, 2002.
- Jones MR, Jagacinski RJ, Yee W, Floyd RL, and Klapp ST. Tests of attentional flexibility in listening to polyrhythmic patterns. *Journal of Experimental Psychology – Human Perception and Performance*, 21: 293–307, 1995.
- Jongsma ML, Eichele T, Quian QR, Jenks KM, Desain P, Honing H, et al. Expectancy effects on omission evoked potentials in musicians and non-musicians. *Psychophysiology*, 42: 191–201, 2005.
- Kuck H, Grossbach M, Bangert M, and Altenmüller E. Brain processing of meter and rhythm in music. Electrophysiological evidence of a common network. *Annals of the New York Academy of Sciences*, 999: 244–253, 2003.
- Kuriki S, Kanda S, and Hirata Y. Effects of musical experience on different components of MEG responses elicited by sequential piano-tones and chords. *The Journal of Neuroscience*, 26: 4046–4053, 2006.
- Lerdahl F and Jackendoff R. On the theory of grouping and meter. *The Musical Quarterly*, 67: 479–506, 1981.
- Lerdahl F and Jackendoff R. An overview of hierarchical structure in music. *Music Perception*, 1: 229–252, 1983.
- Liegeois-Chauvel C, Peretz I, Babai M, Laguitton V, and Chauvel P. Contribution of different cortical areas in the temporal lobes to music processing. *Brain*, 121: 1853–1867, 1998.
- Lutkenhoner B, Seither-Preisler A, and Seither S. Piano tones evoke stronger magnetic fields than pure tones or noise, both in musicians and non-musicians. *Neuroimage*, 30: 927–937, 2006.
- Macmillan NA. *Detection Theory: A Users’ Guide*. Cambridge: Cambridge University Press, 1991. 1–407.
- Meyer LB. *Emotion and Meaning in Music*. Chicago: University of Chicago Press, 1956.
- Meyer M, Baumann S, and Jancke L. Electrical brain imaging reveals spatio-temporal dynamics of timbre perception in humans. *Neuroimage*, 32: 1510–1523, 2006.
- Midorikawa A, Kawamura M, and Kezuka M. Musical alexia for rhythm notation: a discrepancy between pitch and rhythm. *Neurocase*, 9: 232–238, 2003.
- Murayama J, Kashiwagi T, Kashiwagi A, and Mimura M. Impaired pitch production and preserved rhythm production in a right brain-damaged patient with amusia. *Brain and Cognition*, 56: 36–42, 2004.
- Naatanen R, Pakarinen S, Rinne T, and Takegata R. The mismatch negativity (MMN): towards the optimal paradigm. *Clinical Neurophysiology*, 115: 140–144, 2004.
- Neuloh G and Curio G. Does familiarity facilitate the cortical processing of music sounds? *Neuroreport*, 15: 2471–2475, 2004.
- Nittono H, Bito T, Hayashi M, Sakata S, and Hori T. Event-related potentials elicited by wrong terminal notes: effects of temporal disruption. *Biological Psychology*, 52: 1–16, 2000.
- Penhune VB, Zatorre RJ, and Feindel WH. The role of auditory cortex in retention of rhythmic patterns as studied in patients with temporal lobe removals including Heschl’s gyrus. *Neuropsychologia*, 37: 315–331, 1999.
- Peretz I. The nature of music from a biological perspective. *Cognition*, 100: 1–32, 2006.
- Peretz I and Kolinsky R. Boundaries of separability between melody and rhythm in music discrimination: a neuropsychological perspective. *Quarterly Journal of Experimental Psychology*, 46: 301–325, 1993.
- Peretz I and Zatorre RJ. Brain organization for music processing. *Annual Review of Psychology*, 56: 89–114, 2005.
- Phillips-Silver J and Trainor LJ. Hearing what the body feels: auditory encoding of rhythmic movement. *Cognition*, 105: 533–546, 2007.
- Piccirilli M, Sciarra T, and Luzzi S. Modularity of music: evidence from a case of pure amusia. *Journal of Neurology, Neurosurgery, and Psychiatry*, 69: 541–545, 2000.
- Povel D and Essens P. Perception of temporal patterns. *Music Perception*, 2: 411–440, 1985.
- Raij T, McEvoy L, Makela JP, and Hari R. Human auditory cortex is activated by omissions of auditory stimuli. *Brain Research*, 745: 134–143, 1997.
- Ramus F, Hauser MD, Miller C, Morris D, and Mehler J. Language discrimination by human newborns and by cotton-top tamarin monkeys. *Science*, 288: 349–351, 2000.
- Reinke KS, He Y, Wang CH, and Alain C. Perceptual learning modulates sensory evoked response during vowel segregation. *Cognitive Brain Research*, 17: 781–791, 2003.
- Restuccia D, Della Marca G, Marra C, Rubino M, and Valeriani M. Attentional load of the primary task influences the frontal but not the temporal generators of mismatch negativity. *Cognitive Brain Research*, 25: 891–899, 2005.
- Riecker A, Wildgruber D, Dogil G, Grodd W, and Ackermann H. Hemispheric lateralization effects of rhythm implementation during syllable repetitions: an fMRI study. *Neuroimage*, 16: 169–176, 2002.

- Rinne T, Sarkka A, Degerman A, Schroger E, and Alho K. Two separate mechanisms underlie auditory change detection and involuntary control of attention. *Brain Research*, 1077: 135–143, 2006.
- Ritter W, De Sanctis P, Molholm S, Javitt DC, and Foxe JJ. Preattentively grouped tones do not elicit MMN with respect to each other. *Psychophysiology*, 43: 423–430, 2006.
- Sabri M, Liebenthal E, Waldron EJ, Medler DA, and Binder JR. Attentional modulation in the detection of irrelevant deviance: a simultaneous ERP/fMRI study. *Journal of Cognitive Neuroscience*, 18: 689–700, 2006.
- Sakai K, Hikosaka O, Miyauchi S, Takino R, Tamada T, Iwata NK, et al. Neural representation of a rhythm depends on its interval ratio. *The Journal of Neuroscience*, 19: 10074–10081, 1999.
- Schachter C. Aspects of meter. *Music Forum*, 6: 1–59, 1986.
- Schlaug G, Jancke L, Huang Y, Staiger JF, and Steinmetz H. Increased corpus callosum size in musicians. *Neuropsychologia*, 33: 1047–1055, 1995a.
- Schlaug G, Jancke L, Huang Y, and Steinmetz H. In vivo evidence of structural brain asymmetry in musicians. *Science*, 267: 699–701, 1995b.
- Shahin A, Bosnyak DJ, Trainor LJ, and Roberts LE. Enhancement of neuroplastic P2 and N1c auditory evoked potentials in musicians. *The Journal of Neuroscience*, 23: 5545–5552, 2003.
- Shahin A, Roberts LE, Pantev C, Trainor LJ, and Ross B. Modulation of P2 auditory-evoked responses by the spectral complexity of musical sounds. *Neuroreport*, 16: 1781–1785, 2005.
- Shalgi S and Deouell LY. Direct evidence for differential roles of temporal and frontal components of auditory change detection. *Neuropsychologia*, 2007.
- Snyder E and Hillyard SA. Long-latency evoked-potentials to irrelevant, deviant stimuli. *Behavioral Biology*, 16: 319–331, 1976.
- Tervaniemi M, Rytönen M, Schroger E, Ilmoniemi RJ, and Naatanen R. Superior formation of cortical memory traces for melodic patterns in musicians. *Learning and Memory*, 8: 295–300, 2001.
- Tincoff R, Hauser M, Tsao F, Spaepen G, Ramus F, and Mehler J. The role of speech rhythm in language discrimination: further tests with a non-human primate. *Developmental Science*, 8: 26–35, 2005.
- Toivainen P and Eerola T. The role of accent periodicities in meter induction: a classification study. In *Proceedings of the Eighth International Conference on Music Perception and Cognition*, 2004: 422–425.
- Trehub SE and Hannon EE. Infant music perception: domain-general or domain-specific mechanisms? *Cognition*, 100: 73–99, 2006.
- Tremblay K, Kraus N, McGee T, Ponton C, and Otis B. Central auditory plasticity: changes in the N1–P2 complex after speech-sound training. *Ear and Hearing*, 22: 79–90, 2001.
- Vuust P, Pallesen KJ, Bailey C, van Zuijlen TL, Gjedde A, Roepstorff A, et al. To musicians, the message is in the meter pre-attentive neuronal responses to incongruent rhythm are left-lateralized in musicians. *Neuroimage*, 24: 560–564, 2005.
- Wilson SJ, Pressing JL, and Wales RJ. Modelling rhythmic function in a musician post-stroke. *Neuropsychologia*, 40: 1494–1505, 2002.
- Yee W, Holleran S, and Jones MR. Sensitivity to event timing in regular and irregular sequences – influences of musical skill. *Perception and Psychophysics*, 56: 461–471, 1994.
- van Zuijlen TL, Sussman E, Winkler I, Naatanen R, and Tervaniemi M. Grouping of sequential sounds – an event-related potential study comparing musicians and nonmusicians. *Journal of Cognitive Neuroscience*, 16: 331–338, 2004.
- van Zuijlen TL, Sussman E, Winkler I, Naatanen R, and Tervaniemi M. Auditory organization of sound sequences by a temporal or numerical regularity – a mismatch negativity study comparing musicians and non-musicians. *Cognitive Brain Research*, 23: 270–276, 2005.