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## To musicians, the message is in the meter

### Pre-attentive neuronal responses to incongruent rhythm are left-lateralized in musicians

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**Musicians exchange non-verbal cues as messages when they play together. This is particularly true in music with a sketchy outline. Jazz musicians receive and interpret the cues when performance parts from a regular pattern of rhythm, suggesting that they enjoy a highly developed sensitivity to subtle deviations of rhythm. We demonstrate that pre-attentive brain responses recorded with magnetoencephalography to rhythmic incongruence are left-lateralized in expert jazz musicians and right-lateralized in musically inept non-musicians. The left-lateralization of the pre-attentive responses suggests functional adaptation of the brain to a task of communication, which is much like that of language.**

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#### Introduction

Music is one of the many ways humans communicate with each other. Whether music and verbal language share neuronal networks or music is processed in separate brain modules holds the key to understanding music in an evolutionary perspective (Huron, 2001), as well as music in the context of human communication. Hence, this issue has been hotly debated in the growing field of neurobiological research in music.

In support of neural dissociation between music and language processing, lesion studies and studies of people suffering from acquired and congenital amusia show a double dissociation between aspects of music and language processing (Ayotte et al., 2000; Liegeois-Chauvel et al., 1998; Mendez, 2001; Peretz and Coltheart, 2003; Peretz et al., 1994, 2002) as well as a greater involvement of the right hemisphere in basic music processing of especially pitch-related features (Samson et al., 2002; Tervaniemi and Hugdahl, 2003; Zatorre, 1988; Zatorre et al., 2002). Brain responses to auditory stimuli, however, are not only determined by physical properties of the stimuli, and the nature of cognitive operations involved. In many cases, the listeners' competence and familiarity with the stimuli affect neuronal processing. This has been shown for pre-attentive processing of language at 100–200 ms after stimulus onset as indicated by the mismatch negativity (MMNm), recorded with magnetoencephalography (MEG). Left lateralization of the MMNm occurs to deviating phonemes from subjects' mother tongues only (Näätänen et al., 1997), and deviating Morse code syllables in Morse code trained subjects, only (Kujala et al., 2003), suggesting that left lateralization of sounds occur when they are perceived as meaningful.

Although music—in contrast to verbal language—rarely refers to objects in the real world, musical performance involves communication. When musicians play, they exchange non-verbal signs as messages, and from this interaction, music emerges as a concrete form (Sawyer, 2004). Musical communication, for example, musical humor (Huron, 2004), is often conveyed through violation of musical expectancy. Music theory explains musical expectancy as the motion between opposites as in harmony the tension of the dominant chord resolved by the motion to the tonic. This phenomenon is referred to as an example of musical syntax and violations of the authentic cadence has been shown to activate cortical language areas (Maess et al., 2001). Anticipation of

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rhythmic patterns is another crucial aspect of musical expectancy. It is established by the so-called meter (Sadie et al., 2001) that provides the listener with a grid of strong and weak beats creating expectancy of rhythmic timing as well as strength. This phenomenon is well illustrated as the different feeling of a 3/4 rhythm like waltz and a 4/4 rhythm like in a blues. In jazz, deviations from the well-established rhythmic pattern are a central feature. This has obvious stylistic implications, but importantly, deviations are also means of communicating intentions and ideas in the largely improvised performance. Hence, jazz musicians receive and interpret as cues performances parting from regular rhythm patterns (Berliner, 1994; Monson, 1997; Vuust, 2000). This suggests that skilled jazz musicians may have developed a high sensitivity to subtle deviations of rhythm. To test this, we used MEG to study the strength and lateralization of pre-attentive responses of the central nervous system (MMNm) to deviations from a pattern of rhythm in expert jazz musicians and musically inept non-musicians.

### Materials and methods

To mimic communicative cues in improvised music, we made sequences of increasingly incongruent rhythm, using realistic

broadband drum sounds (Fig. 1a). The stimuli were sI, a simple 4-beat rock rhythm; sII and sID, variations of sI with a last snare drum beat of the sequence tuned up (sII) or down (sID); and sIII and sIII, variations of sI with a weak (sIII) or strong (sIII) departure from the rhythm. sIII may be described as a syncopation breaking the rhythmic expectancy by replacing a weak beat with a strong beat, without interfering with the underlying temporal grid (the meter). This is a well-known stylistic feature in jazz (Kernfeld et al., 2002). In contrast, the violation in sIII constituted a departure from the original musical meter by introducing a beat, which was incongruent with the underlying temporal grid. This is a strong violation of the musical expectancy, and phenomenologically it may be experienced as if the music ‘stumbles’. Both in terms of musical expectancy and communicative valence, sIII can therefore be characterized as a much stronger sign of incongruence, a fact that was substantiated by subjects’ unanimous ratings of sIII as equally or more disturbing than sII.

Eight inept non-musicians (6 men and 2 women), and nine expert jazz musicians (8 men and 1 woman; educated at the Sibelius Academy of Music, Helsinki, Finland), gave informed consent to participate in the study, approved by The Ethical Committee of Helsinki University Central Hospital. We tested the aptitude for rhythm with a modified version of the imitation task used as part of entry examinations to music conservatories in

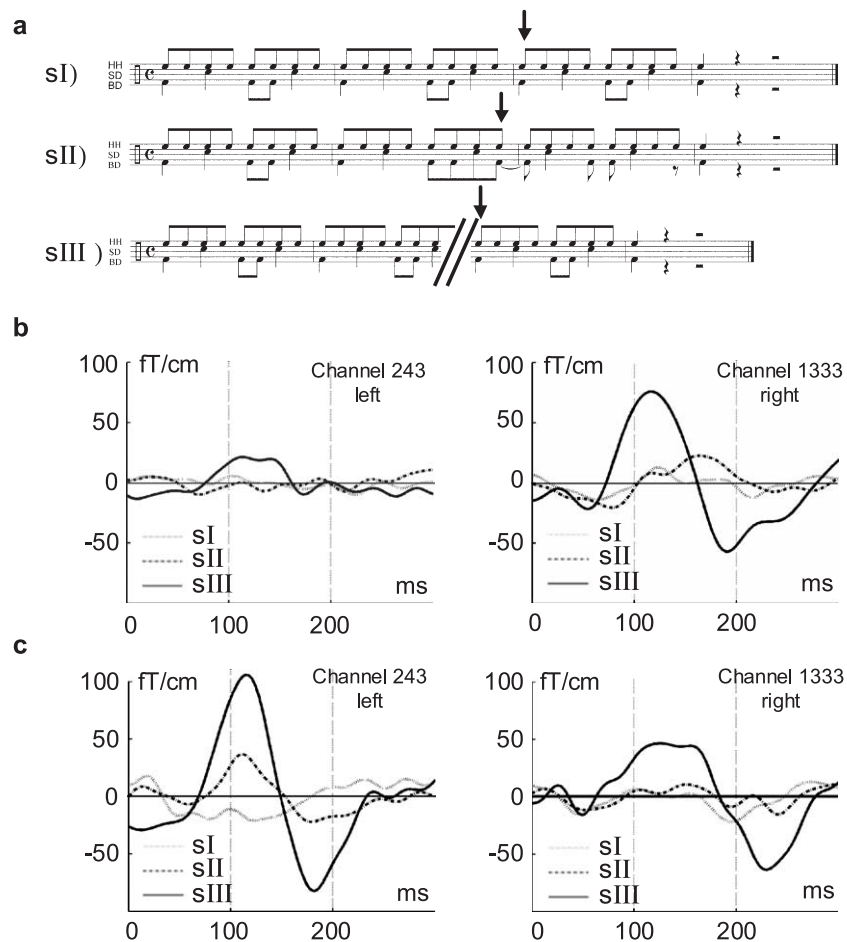


Fig. 1. (a) Note representation of the stimuli; arrow indicates the time of recording. 8th notes interval is 312.5 ms except at the 2nd bar of sIII (105 ms). Typical time courses of averaged magnetic evoked responses from (b) an inept non-musician and (c) an expert musician. Signals are recorded at the auditory cortex and plotted separately for sI, sII and sIII.

Denmark. The scores divided the subjects into three groups according to sense of rhythm subdivision and meter. Inept subjects scored 3 or less, proficient subjects excluded from the study scored between 4 and 13, and expert subjects scored 14 or more.

We used MEG to record the neuronal responses to 600 auditory presentations of rhythm sequences with pseudo-randomized frequencies of 30% (sI–sIII) and 5% (sIu and sId). Instructions to respond to the presence of either sIu or sId directed the attention of the subjects to the intact last part of the rhythm sequences, rather than to the incongruent rhythm in the middle of sII and sIII. Prior to the recordings, subjects trained the task and performed a handedness test (Oldfield, 1971), whereas nothing was mentioned about the rhythmic incongruities. Observed button press responses during recordings showed that subjects were performing the discrimination task adequately. To examine the event-related fields (ERFs) associated with deviation from meter, we realigned and time-locked the recording time window to the drumbeat indicated with an arrow in Fig. 1a, with a 50-ms pre-stimulus baseline.

A 306-channel Vector View whole-head MEG device (NeuroMag Ltd., Helsinki, Finland) recorded and band pass-filtered (2–30 Hz) the data. The ERFs were analyzed using two subsets of 31 pairs of orthogonal planar gradiometers—one over each hemisphere. The differential responses to sI, sII and sIII emerged from comparisons of the maximum mean gradient amplitude (MGA) in the interval 100–170 ms for each hemisphere of each subject. We estimated separate equivalent current dipoles (ECD) at the latency of the maximal MGA for each hemisphere with a spherical head model. The amplitudes ( $A$ ) of the dipoles yielded an asymmetry index as the ratio  $(A_{\text{right}} - A_{\text{left}}) / (A_{\text{right}} + A_{\text{left}})$ . Structural magnetic resonance images for one expert and one inept subject were used to anatomically localize the dipoles.

## Results

Total MGA (left + right) to sIII across all subjects significantly exceeded sII ( $P < 0.001$ ,  $T = -15.8$ ), which in turn significantly ( $P = 0.01$ ,  $T = 2.84$ ) exceeded sI (sIII: 74 fT/cm, SE = 6, sII: 28 fT/cm, SE = 4 and sI: 18 fT/cm, SE = 1). Across all subjects, for each hemisphere, MGAs to sIII significantly exceeded sII ( $P < 0.001$ , left:  $T = 10.8$ , right:  $T = 11.9$ ), which in turn significantly [ $P < 0.05$ , left:  $T = 2.17$ , right:  $T = 3.55$ ], exceeded sI (sIII (left) 36.4 fT/cm, SE = 3.9, (left) 14.9 fT/cm, SE = 3.0, sI (left) 8.9 fT/cm, SE = 2.8, sIII (right) 37.7 fT/cm, SE = 2.7, sII (right) 13.3 fT/cm, SE = 1.1, sI (right) 10.1 fT/cm, SE = 0.8]. The difference revealed greater neuronal response to greater rhythmic incongruence. Total MGA of experts to sI, sII and sIII significantly exceeded inept subjects in  $t$ -tests (sI:  $P = 0.02$ ,  $T = 2.5$ , for experts 21 fT/cm, SE = 1.8 vs. inept subjects 16 fT/cm SE = 1.4, sII:  $P = 0.01$ ,  $T = 2.9$ , for experts 37 fT/cm SE = 5.7 vs. inept subjects 19 fT/cm, SE = 1.4, sIII:  $P = 0.03$ ,  $T = 2.43$  for experts 85 fT/cm, SE = 8.0 vs. inept subjects 62 fT/cm, SE = 4.9). Thus aptitude for rhythm appears to be associated with increased pre-attentive neuronal responsiveness.

Responses to sIII had large bilateral peaks at 100–150 and 170–250 ms (Fig. 1) in all subjects. In the interval 100–150 ms of all subjects (goodness of fit 86%, SE = 2, volume = 46 mm<sup>2</sup>, SE = 8), dipolar sources resided in the temporal cortex, specifically the auditory cortex in the two subjects that underwent anatomical imaging. In the left hemisphere, the dipole amplitudes of experts

significantly exceeded those of inept subjects ( $P = 0.004$ ,  $T = 3.53$ , Aleft 63 fT/cm, SE = 10 for experts vs. 26 fT/cm, SE = 2 for inept subjects). Dipole amplitudes did not differ significantly in the right hemisphere ( $P = 0.96$ , Aright 37 fT/cm, SE = 6 for experts vs. 38 fT/cm, SE = 4 for inept subjects).

The neuronal response to sIII was predominant in the left hemisphere ( $P = 0.01$ ,  $T = 3.74$ ) of experts and in the right hemisphere ( $P = 0.03$ ,  $T = -2.61$ ) of inept subjects (Fig. 2b, asymmetry index  $-0.25$ , SE = 0.07 for experts, 0.18, SE = 0.07 for inept subjects). Left hemisphere dipole amplitudes in experts significantly differed from the right hemisphere amplitude in inept subjects ( $P = 0.03$ ,  $T = 2.4$ ), suggesting increased sensitivity to incongruities as distinguished from merely a change in hemispheric dominance. Dipole latency of the groups did not differ ( $P = 0.75$ ,  $T = 0.34$ ) in the right hemisphere (119 ms, SE = 4 for experts vs. 121 ms, SE = 5 for inept subjects). For experts, dipole latency in the left hemisphere (113, SE = 5) was comparable ( $P = 0.30$ ,  $T = 1.07$ ) to that of the right hemisphere. However, for inept subjects, the dipole latency of the left hemisphere exceeded the right hemisphere (139 ms, SE = 4,  $P = 0.02$ ,  $T = 2.79$ ), and also the left hemisphere of experts ( $P = 0.0005$ ,  $T = 4.46$ ) (Fig. 2c).

The incongruent rhythm of sIII strongly and rapidly stimulated the left hemisphere of experts. In contrast, in inept subjects, the protracted dipole latency in the left hemisphere and the significant asymmetry both indicate processing of incongruent rhythm in the right hemisphere.

For the more weakly incongruent sII sequence, robust dipolar field patterns appeared in the left hemisphere in six out of the nine experts and in the right hemisphere of the remaining three experts. No such field patterns were observed in the hemispheres of inept subjects. Furthermore, left MGAs of the experts to sII significantly exceeded the right MGA in inept subjects ( $P = 0.05$ ,  $T = 2.22$ ). Thus, experts appear to be more sensitive to subtle rhythm cues. The asymmetry of MGA to sII [ $(MGA_{\text{right}} - MGA_{\text{left}}) / (MGA_{\text{left}} + MGA_{\text{right}})$ ] indicated stronger left hemisphere activity in experts than in inept subjects ( $P = 0.005$ ,  $T = 4.47$  asymmetry index  $-0.14$ , SE = 0.09 of experts vs. 0.24, SE = 0.07 of inept subjects). Furthermore, a two-way ANOVA, performed for the asymmetry index, showed a significant effect ( $P = 0.005$ ,  $F = 9.25$ ) of competence adjusted for type of incongruence (sII and sIII), but no effect of type of incongruence.

## Discussion and conclusion

In the right hemisphere, the rhythm cues elicited responses of similar strength in expert and inept subjects. In the left hemisphere, the expert subjects responded with greater strength than in the right hemisphere, while inept subjects responded less rapidly and with less strength. In addition, experts responded with greater strength in the left hemisphere than inept subjects in the right hemisphere did. These competence-related differential activation patterns are strikingly similar to the competence-related patterns of activity found in studies of phonetic perception. Näätänen et al. (1997) demonstrated left-lateralized MMN to deviant vowels in a native language while other deviant vowels in a closely related but foreign language elicited very little response and no clear lateralization. This finding was confirmed by Rinne et al. (1999) who found left lateralization of phonemes only when they contained enough formant structure to be categorized appropriately by subjects. Shtyrov et al. (2000) found that syllables of a native

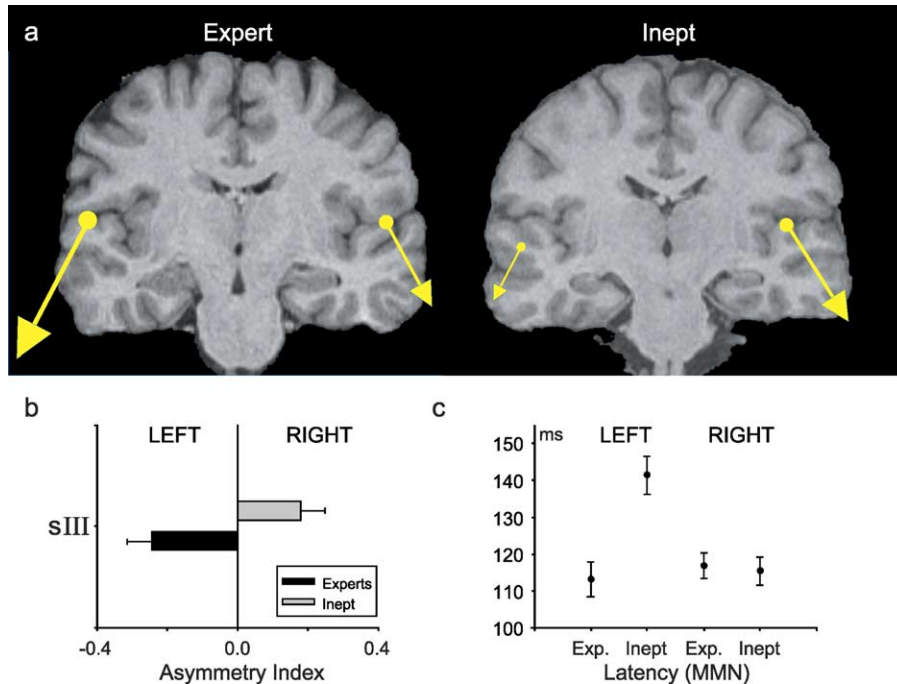


Fig. 2. (a) Location of dipoles (MMN) to sIII in one expert and one inept subject. Direction of the dipoles are projected onto the individual coronal MR slice. The relative amplitude (left expert: 60 nAm) represented by size of arrows. (b) Asymmetry index calculated on the basis of dipole amplitudes. (c) Latency of the MMNs in experts and inept subjects.

language elicit MMN-response in the left hemisphere, while non-syllabic sounds activated the right hemisphere or the midline. Thus, prior to attention, expert jazz musicians process rhythmic signs in the auditory cortex of the left hemisphere where also phonemes are processed in brains of highly competent users of a language.

It is widely held that music and language employ separate neuronal networks (modules) especially for the spectral aspects of music whereas less is known about the temporal aspects of music (Peretz and Coltheart, 2003). At the level of the auditory cortex, the left hemisphere appears to be specialized for the processing of fine-grained temporal stimuli necessary for language comprehension. The auditory cortex of the right hemisphere, on the other hand, has a higher spectral resolution, suitable for processing of musical elements such as pitch (accuracy) (Zatorre and Belin, 2001; Zatorre et al., 2002). In a comparative study of chords and vowels, Tervaniemi et al. (1999) found right lateralization of the MMNm to chords in contrast to left lateralized processing of acoustically matching vowels, indicating that hemispheric lateralization in the auditory cortex depends not only on acoustical features but also on the type of stimuli even at the pre-attentive level. Lateralization of the temporal aspects of music is more unclear. Many studies report left lateralization of rhythm, but right lateralization of meter (Kester et al., 1991; Polk and Kertesz, 1993; Samson et al., 2001; Schuppert et al., 2000). Meter and rhythm, however, are not easily dividable musical components as any rhythm induces a sense of meter. In the present study, we find that lateralization of MMNm to incongruent rhythms is lateralized differently in experts and inept subjects. Notably, the processing of rhythm in this study is indistinguishable from processing of meter as indicated by asymmetry indices for sII and sIII, respectively. The result indicates that the lateralization of pre-attentive brain responses to rhythm and meter is determined mainly by the rhythmical competence of the listener. In a recent

study, Kujala et al. (2003) showed that the amplitude of the MMNm to Morse code reversed lateralization from the hemisphere opposite to the one dominant for the MMN to native language sounds to the speech hemisphere after 3 months of intensive training. This result indicates that once a rhythmic pattern conveys meaning it is pre-attentively processed by the left hemisphere. In the present study, we demonstrate that there is a correlation between musical competence and left lateralization of pre-attentive brain responses to rhythmic cues. We propose that this may be functionally linked to the left lateralization of MMN to vowels and syllables, as shown in previous language studies. The shift in hemispheric dominance arises from a large increase in the left hemisphere response of the experts. Thus expert jazz musicians are neurally more sensitive to the rhythmic cues in music than inept non-musicians. The increase in sensitivity appears mainly to be localized in the left hemisphere. This suggests that the intense musical training has shifted the pre-attentive processing of rhythmic cues towards the left hemisphere, just as linguistic training shifted the pre-attentive processing of native language phonemes towards the left hemisphere.

We propose that the processing of relevant rhythm in the left hemisphere is a functional adaptation of the brains of expert musicians to rhythmic cues in music. This suggests that pre-attentive, left-lateralized processing of significant features of a message, be that phonemes or rhythmic and metric patterns, is a feature of highly developed competence in both music and language. We observe this left lateralization in expert jazz musicians as opposed to inept non-musicians, both in the processing of strong metric expectancy and weaker rhythmic expectancy. Both rhythmic and metric violations are only meaningful seen against the overall temporal grid of the music. We therefore propose that to these musicians, the message is in the meter.

An interesting question, which the present study leaves unsolved, is whether the observed brain response is a feature exclusive to musicians in improvisational styles of music or whether it develops with any kind of musical training. In this study, we decided to include expert jazz musicians only since creating and grasping violation in rhythmic expectancy is a crucial element in their musical performance. We therefore hypothesized that these musicians would be ideal candidates for differential neuronal activity to rhythmic and metric violations, when compared with inexpert non-musicians. In recent study, Tervaniemi et al. (2001) found that musicians who primarily perform music without a score are better at detecting changes in a melodic pattern than musicians performing with a score, and these differences are reflected in the patterns of the MMNm response. Jazz musicians mainly play and learn to play by ear. They use challenging rhythmic material in their musical communication, under the constraint of a steady tempo. Thus, we hypothesize that jazz musicians on average would respond stronger to rhythmic and metric violations than would musicians trained in musical styles where the musical score is used for learning and performance. However, further studies need to be conducted in order to decide whether the observed lateralization is special to improvised music or could be generalized to expert musicians in all genres.

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