

Music training leads to the development of timbre-specific gamma band activity

Antoine J. Shahin,^{a,*} Larry E. Roberts,^{b,c} Wilkin Chau,^d
Laurel J. Trainor,^{b,d} and Lee M. Miller^{a,e}

^aUniversity of California, Davis Center for Mind and Brain, 267 Cousteau Place, Davis, CA 95618, USA

^bDepartment of Psychology, Neuroscience and Behaviour, McMaster University, Hamilton, Ontario, Canada

^cMEG Neuroscience Unit, Down Syndrome Research Foundation, Burnaby, British Columbia, Canada

^dRotman Research Institute of Baycrest, Toronto, Ontario, Canada

^eUniversity of California, Section of Neurobiology, Physiology, and Behavior, Davis, CA, USA

Received 19 November 2007; revised 20 January 2008; accepted 28 January 2008

Available online 21 February 2008

Oscillatory gamma band activity (GBA, 30–100 Hz) has been shown to correlate with perceptual and cognitive phenomena including feature binding, template matching, and learning and memory formation. We hypothesized that if GBA reflects highly learned perceptual template matching, we should observe its development in musicians specific to the timbre of their instrument of practice. EEG was recorded in adult professional violinists and amateur pianists as well as in 4- and 5-year-old children studying piano in the Suzuki method before they commenced music lessons and 1 year later. The adult musicians showed robust enhancement of induced (non-time-locked) GBA, specifically to their instrument of practice, with the strongest effect in professional violinists. Consistent with this result, the children receiving piano lessons exhibited increased power of induced GBA for piano tones with 1 year of training, while children not taking lessons showed no effect. In comparison to induced GBA, evoked (time-locked) gamma band activity (30–90 Hz, ~80 ms latency) was present only in adult groups. Evoked GBA was more pronounced in musicians than non-musicians, with synchronization equally exhibited for violin and piano tones but enhanced for these tones compared to pure tones. Evoked gamma activity may index the physical properties of a sound and is modulated by acoustical training, while induced GBA may reflect higher perceptual learning and is shaped by specific auditory experiences.

© 2008 Elsevier Inc. All rights reserved.

Keywords: Auditory cortex; Development; Gamma band activity; Music training; Plasticity; Timbre-specificity

Musicians possess heightened perceptual abilities, typically acquired through years of practice. As such, musicians represent a good model of how our brains adapt with experience (Münte et al.,

2002). We sought to identify what differentiates the brains of musicians from non-musicians when listening to sounds of their practiced instrument, and whether such attributes are acquired through music training.

Cortical responses to sound occur as early as 19 ms after sound onset and continue at various latencies reflecting activation of serial and parallel stages of processing in the auditory system. Many of these responses, including auditory “middle latency” responses (~19–80 ms) and the longer latency N1/N1m (100 ms, N1m designating the magnetic counterpart of the electrical N1), N1c (140 ms), P2 (180 ms), and N2m (250 ms) responses, have been shown from electromagnetic studies to be enhanced in young and adult musicians compared to non-musicians (middle latency: Schneider et al., 2002; Shahin et al., 2004; N1c: Shahin et al., 2003; N1m: Pantev et al., 1998; N2m: Fujioka et al., 2006; P2: Shahin et al., 2003, 2004, 2005; P2m: Shahin et al., 2005; Kuriki et al., 2006). Enhancement of the middle latency N19m-P30m response in musicians has been shown to parallel an increase of gray matter in Heschl's gyrus, suggesting an enhanced neural population in trained musicians (Schneider et al., 2002, 2005). In principle, these distinct processes in musicians could be inherited and/or learned during the musicians' training history, reflecting improved performance through neural plasticity (Weinberger, 2003). Recent studies revealed that some of these components are enhanced following short term training on auditory discrimination tasks (N1m: Menning et al., 2000; N1c: Bosnyak et al., 2004; P2: Tremblay et al., 2001 and Bosnyak et al., 2004) pointing to their susceptibility to neuroplastic influence.

Brain responses measured in the above studies reflect synchronous neural activity time-locked to the stimulus (“evoked” responses) and may represent specific physical features of the acoustical cues (Näätänen and Picton, 1987). However, acoustic stimulation elicits oscillatory brain responses that are not time-locked to stimulus events (“induced” responses) (Bertrand and

* Corresponding author. Fax: +1 530 297 4603.

E-mail address: ajshahin@ucdavis.edu (A.J. Shahin).

Available online on ScienceDirect (www.sciencedirect.com).

Tallon-Baudry, 2000) and can only be detected in single trial data. Such responses of the gamma frequency band (30–100 Hz) induced by visual stimuli are widely believed to reflect network activity that binds features to form conscious percepts (Singer and Gray, 1995; Tallon-Baudry et al., 1996). The functional significance of induced gamma band activity (GBA) in the auditory domain is less well understood. In one study of the auditory system (Bhattacharya et al., 2001) amateur musicians displayed increased long-range synchrony in the gamma range (30–50 Hz) when listening to a musical piece but not to a novel story, suggesting that synchronous activity may have reflected an advanced ability to bind musical features such as pitch, timbre, and harmony. Induced auditory GBA has also been linked to attention, anticipation and expectation (Sokolov et al., 2004; Snyder and Large, 2005; Zanto et al., 2005). Attentional processing occurs at the time of expected beats in a rhythm pattern, even if the beats are occasionally omitted (Snyder and Large, 2005).

The presence of distinct EEG attributes in musicians invites the hypothesis that musical training modifies a neural system for auditory information processing. If acoustic feature processing expressed in oscillatory activity is a function of auditory learning, we would expect to observe enhanced GBA in musicians specific to the timbre of their instrument of practice. We examined evoked and induced oscillatory gamma band activity recorded in the electroencephalogram (EEG) of professional violinists, amateur pianists, and age-matched non-musicians while passively listening to violin, piano, and pure tones matched in pitch. To establish whether oscillatory activity is affected by musical training (e.g. acquired rather than inherited), we examined GBA in 4- to 5-year-old piano pupils enrolled in a Suzuki music school before they started their musical practice and 1 year after. Age-matched children not undergoing musical training were also measured before and after an interval of 1 year.

Methods

The data used for this study were collected by Shahin et al. (2003, 2004) but subjected to different analyses here.

Participants

The adult musicians' groups consisted of 11 professional violinists (mean age \pm S.D., 24.3 ± 2.2 years; six females) who were members of Canada's National Academy Orchestra and nine amateur pianists (23 ± 2.5 years; eight females) with a grade 10 certification from Canada's Royal Conservatory of Music. The adult non-musicians ($n=14$) were McMaster University students (22.2 ± 3.4 years; eight females) who had no formal musical training. Violinists and pianists had played their instruments for an average of 17 ± 3.7 years and 16.6 ± 4.0 years, respectively, and practiced for 34.7 ± 20.8 and 17.9 ± 11.1 h/week, respectively, at the time of the study. All adult subjects except one pianist and one control reported that they were right-handed. The Suzuki pupils consisted of six pianists from the Suzuki School of Music in Hamilton, Ontario (mean age 4.6 ± 0.4 and 5.6 ± 0.5 years at the first and second measurements, respectively; three females) and six age-matched control children with no musical training (4.8 ± 0.4 and 5.6 ± 0.5 years of age at the first and second measurements, respectively; three females). Normal auditory thresholds were confirmed for all participants by a staircase procedure (<25 dB at 0.25–8.0 kHz). The adult subjects were the same participants involved in Shahin et al. (2003), and the children participants were

the same reported in Shahin et al. (2004). Subjects gave written informed consent in accordance with the Research Ethics Board of McMaster University. For children, consent was also obtained from a parent.

Stimuli

The stimuli were the same as Shahin et al. (2003, 2004) and consisted of 2 violin, 2 piano and 2 pure tones each of 500 ms duration. The two violin and piano tones had fundamental frequencies of A3=220 Hz and C3=131 Hz (American notation). The pure tones were matched in frequency to the fundamental frequency of the music tones. The violin tones were taken from Kyma software and the piano tones were obtained from a Korg 01W synthesizer. Pure tones were created with a cosine envelope, with a 20-ms rise and fall time. All tones were presented at 70 dB SPL.

Procedure

Testing was performed in a sound-attenuated and electrically shielded room. The Suzuki students were tested twice, the first time just prior to the commencement of music lessons and the second time 1 year later. The control children measurements matched the time line of the Suzuki children. Adult musicians were tested once. The stimulus procedure was the same for the adults and the children. Tones were presented from a speaker placed at eye level 1 m in front of the subject in a single experimental session that lasted about 45 min. Tones were delivered in a pseudorandomized order using a constant inter-stimulus interval of 2.5 s offset to onset (720 stimuli overall, 120 for each of the six tone types). A passive listening protocol was followed in which adult subjects read a magazine or newspaper and young children watched a silent movie while the tones were presented.

The EEG was recorded using a 10–20 system 32-channel EEG cap (adults) and a 19-channel EEG cap (children). EEG recordings were sampled at 1 kHz (DC to 100 Hz; SynAmps amplifier; Neuroscan, El Paso, TX) and referenced to Cz with a ground at AFz. Channel impedances were reduced to less than 10 k Ω .

Data analysis

Channels with excessive artifacts in any subject were taken out of the analysis across all subjects. The final electrode configuration for children was as follows: frontal FP1, FP2, Fz, F3, F4; anterior-temporal F7, F8; central Cz, C3, C4; temporal T7, T8; parietal Pz, P3, P4, P7, P8. The adults' channel configuration included the above channels as well as the frontal channel FPz, occipital channels Oz, O1, O2; fronto-central channels FC5, FC6; and the posterior channels CB1, CB2, and Iz. Remaining data were high pass filtered at 1 Hz and subjected to further artifact rejection to remove ocular and muscle artifacts. Single trials with shifts of ± 75 μ V at channels FP1, FP2, F7, F8, T7, T8, P7, P8, were rejected in adults. For children, the artifact shift criterion at the above channels was relaxed to ± 100 μ V.

Time–frequency analysis

EEG files were segmented into 1200-ms epochs including a 400-ms pre-stimulus baseline. All channels were re-referenced to an average reference and baseline-corrected to the pre-stimulus interval. Time–frequency analyses of single trial data were

conducted using EEGLAB (Delorme and Makeig, 2004) to extract spectral power with respect to time on each trial [event-related spectral perturbation (ERSP)]. ERSP here represents the spectral power difference between post-stimulus and the pre-stimulus baseline activity. The pre-stimulus baseline was limited to the period from -400 ms to -150 ms before sound onsets to reduce overlap of pre-stimulus and post-stimulus activity due to windowing in spectro-temporal analyses. ERSP is calculated as the log of the ratio of the two activities. This difference is reported in decibel (dB) units. As a guide, if there is a 50% increase of activity for a post-stimulus period compared to the pre-stimulus activity, the spectral power of the post-stimulus period will exhibit a 1.76 dB increase $\{10 \times \log_{10} (\text{post-stimulus power/pre-stimulus power})\}$. The analyses were limited to the gamma bandwidth frequencies of 30 to 100 Hz (1.5-Hz increment) and used a sliding (step size of 5 samples) Hanning-windowed, 3-cycle sinusoidal wavelet transform of the time-domain signals. The sliding window was 128 samples (128 ms) long at the lowest frequency and decreased linearly with frequency reaching 64 samples at the highest frequency. ERSPs contain time-locked (evoked) as well as non-time-locked (induced) oscillatory brain responses on individual trials. To distinguish time-locked activity from the ERSPs, analysis of phase (time) coherence between individual trials [inter-trial phase coherence (ITPC)] was conducted (Tallon-Baudry et al., 1996). ITPC represents the power of phase-locking between single trials and gives a measure of evoked oscillatory activity. Time–frequency spectrograms of ERSPs and ITPCs were averaged according to stimulus type and were analyzed separately.

Statistical analysis

Permutation tests were used to identify regions that showed significant differences in ERSP or ITPC spectrograms between tone types, between control and musician groups within each age cohort (adults or children), and between measurements (before and after musical training in children). Adults and children were not compared directly because the two cohorts differed in several respects including their age, the active tasks they performed (adults: reading; children: watching a silent movie), and the nature and extent of their music training. Comparisons between groups within each age cohort (e.g. adult musicians vs. non-musicians) and measurements were conducted on the ERSPs of music tones normalized to ERSPs of pure tones (e.g. normalized piano ERSP = piano ERSP – pure ERSP) to minimize subject variability. It should be noted that this normalization may be thought of as a difference in spectral power with respect to a pure tone referent, but because the ERSP is a logarithmic measure, the normalization can also be thought of as the log of the ratio of music tones' to pure tones' brain activity. Unlike parametric methods, permutation methods do not assume an explicit parametric form for the population distribution. Instead, they derive the distribution by resampling the data. For example, under the null hypothesis of no group effect, randomly assigning the group label to the subjects would produce a distribution of observations similar to that of the population (chance) distribution. This distribution is referred to as the null distribution. By comparing the null distribution from resamplings against the observations, one can determine whether to accept the null hypothesis for a given Type I error (Good, 2000). To handle the problem of multiple comparisons in neuroimaging data, permutation tests were applied based on the null distributions of the maximum values obtained in repeated resamplings of the data

(Holmes et al., 1996). Maximal null distributions were derived from the pre-stimulus period data to improve statistical power (Chau et al., 2004) and were calculated separately for each comparison of groups, tone types, and measurements (before/after training).

The following steps were conducted for the permutation tests, taking a comparison of groups as an example.

- (1) Compute the mean ERSP or ITPC difference (a time–frequency spectrogram) between control and musician groups.
- (2) Resample. In each resampling step, the subjects are randomly assigned to either the 'control' or 'musician' group. The number of subjects in each group remains unchanged during resampling.
- (3) For each resampling in step (2), determine the ERSP or ITPC spectrogram from the pre-stimulus data for all electrodes and time–frequency points.
- (4) Record the maximum absolute mean ERSP difference between the resampled groups of step (3).
- (5) After all the resamplings, the recorded maximum absolute differences are pooled together to generate the maximal null distribution.
- (6) Determine the threshold value for a given p value (e.g. $p=0.005$ for adult group comparisons) from the maximal null distribution.
- (7) Identify significant group differences in the mean ERSP or ITPC computed in step (1) based on this threshold.

Permutation tests were carried out for comparisons between groups, and within groups contrasting tone types or before/after measurements. The number of permutation resamples for each comparison was restricted by the number of subjects or conditions (2^n , where n equals the number of subjects in the comparison; Good, 2000). As such, comparisons of tone types within a group were limited to 512, 2048 and 4096 resamplings for adult pianists ($n=9$), adult violinists ($n=11$) and adult non-musicians ($n=14$), respectively. Comparisons of tone types in children were limited to 64 resamplings. A resampling of 1024 was used for the comparisons between adult groups and a resampling of 512 was used for the comparisons between children groups or between measurements (before and after training). The conditions contrasted by permutation tests are identified herein by the symbol ">". For example, the permutation test "Violin > Piano" conducted within the adult violinist group compares the difference between mean ERSP spectrograms evoked by violin and piano tones. Time–frequency points exceeding significance denote time–frequency points where spectral power induced by the violin tone exceeded that induced by the piano tone (enhancement) or spectral power induced by the piano tone exceeded that induced by the violin tone (suppression). The threshold of significance was set at $p=0.005$ for permutation tests conducted for adult groups, but this was relaxed to $p=0.05$ for tests involving children where fewer subjects were available.

Results

Evoked gamma band (GBA) activity was revealed in the inter-trial phase coherence (ITPC) analysis which indicates the power of phase-locking of activity between single trials (Tallon-Baudry et al., 1996). Induced gamma band activity was revealed in the event-

related spectral perturbation (ERSP) analysis of single trials. Unlike ITPC analysis of the evoked gamma, ERSPs do not depend on the power of inter-trial phase-locking, rather they reveal the spectral power of activity with respect to time and they may include evoked as well as induced activity (Delorme and Makeig, 2004).

Evoked gamma band activity

Evoked GBA occurring between 30 and 100 ms (maximum around 80 ms) was only present in adults. Evoked GBA was distributed across all channels, but it was strongest at the midline channels (Fz, Cz, Pz) with enhanced power at the frontal site Fz, decreasing in power at the vertex (Cz) and more so at Pz. Also, the

evoked gamma exhibited a wide bandwidth (30–90 Hz) with the highest frequencies represented more at the vertex (Cz) and parietal (Pz) sites. Fig. 1A shows the average waveforms at Fz for pure, violin, and piano tones across all adult individuals (musicians and non-musicians) for the wide (0–100 Hz) and narrow (30–60 Hz) bandwidths. The evoked GBA overlapped with the P1 auditory evoked potential (AEP) and terminated at the beginning of the N1 AEP. Fig. 1B (top) shows permutation tests ($p < 0.005$) applied to ITPC plots contrasting music tones to pure tones in musicians (collapsed across violinists and pianists because there were no significant differences between the two groups) and non-musicians. Fig. 1B (bottom) shows the scalp voltage distribution of the evoked gamma band for the above contrasts at 80 ms. Significant evoked

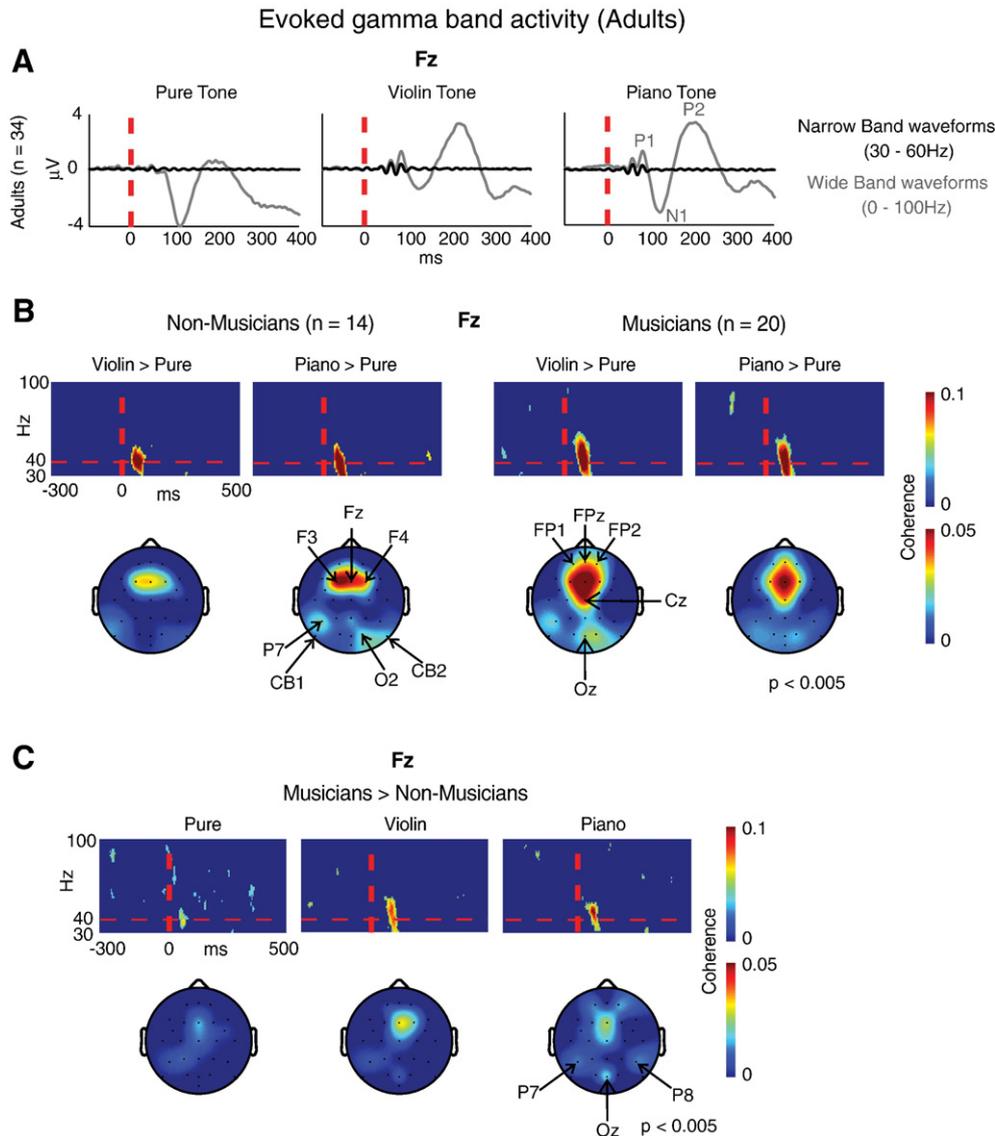


Fig. 1. Evoked gamma band activity in adults. Evoked gamma band activity was present in adults but not in children. (A) Time-averaged narrow band waveforms superimposed on the corresponding wide band waveforms of the Fz channel in adult subjects ($n=34$) for pure, violin and piano tones. The narrow band waveforms were obtained by filtering the wide band waveforms using a zero phase-shift band pass filter with low and high cutoff frequencies of 30 and 60 Hz. The evoked response (narrow band) overlaps with the P1 (wide band) component and terminates at the beginning of the N1 (wide band). (B) Top: Trial-to-trial phase coherence contrasting music tones to pure tones for adult musicians and non-musicians at channel Fz. Bottom: Corresponding evoked GBA scalp distribution at 80 ms. (C) Trial-to-trial phase coherence plots for music tones compared to pure tones contrasting musicians and non-musicians at channel Fz. In all panels, vertical dotted lines indicate sound onset. In panels B and C, horizontal dotted lines indicate the 40-Hz frequency mark. Zero spectral power represents all non-significant differences and not just null differences.

GBA differences were prominent at fronto-central sites (Fz, F3, F3, FPz, FP1, FP2), but also exhibited at posterior sites (P7, P8, Oz, O1, O2, CB1, CB2), indicating the reversal for the evoked auditory generators. The evoked GBA was equally strong for the violin and piano tones but larger for music tones compared to pure tones in all groups. Finally, the musicians expressed enhanced evoked gamma band activity compared to non-musicians, with larger effects occurring for music tones (Fig. 1C).

Induced gamma band activity

In the analyses to be presented in this section, only spectral powers for frequency/time points exceeding $p=0.005$ in adults and $p=0.05$ in children in any channel (increases or decreases, permutation tests) are reported. Here, we did not segregate the spectral power of evoked and induced GBA in the ERSP analyses. The main differences reported below occurred outside the time locale of the evoked GBA and hence, we can safely conclude that the effects reported below are due to induced and not evoked GBA. Significant spectral powers varied with channel and type of contrast. For example, the minimum positive spectral power that was deemed significant for the violinists in the ‘Violin>Pure’ contrast at channel C4 was 0.5 dB; the minimum positive spectral

value at a 0.05 threshold level for the Suzuki pianists in the ‘Piano>Pure’/‘One year later’ contrast at C4 channel was 0.8 dB. All values between 0 and 0.5 dB in adults and between 0 and 0.8 dB in children were therefore set to zero for C4. Compared to evoked GBA which was detected around 80 ms and at fronto-central channels (Fig. 1B), it will be seen that induced GBA was expressed at other electrode locations and time windows.

Adults

Fig. 2A depicts the mean significant spectral power of induced gamma as a function of time (collapsing over all channels and frequencies of 30–100 Hz) for music tones contrasted to pure tones in violinists, pianists and non-musicians. Violinists exhibited larger gamma band spectral power for both music tones compared to pure tones (Fig. 2A) and this increase was larger for the timbre of their practiced instrument particularly at latencies near 132, 280, and 390 ms. Amateur pianists showed a weak GBA advantage for the ‘Piano>Pure’ contrast near 127 ms. Non-musicians showed mixed enhancement and suppression for the two music tones compared to pure tones, with suppression tending to dominate for piano tones compared to pianists and violinists. Gamma power was maximally exhibited at channels C3 and C4; however, it was distributed at several sites, including the anterior–temporal channels F7, F8,

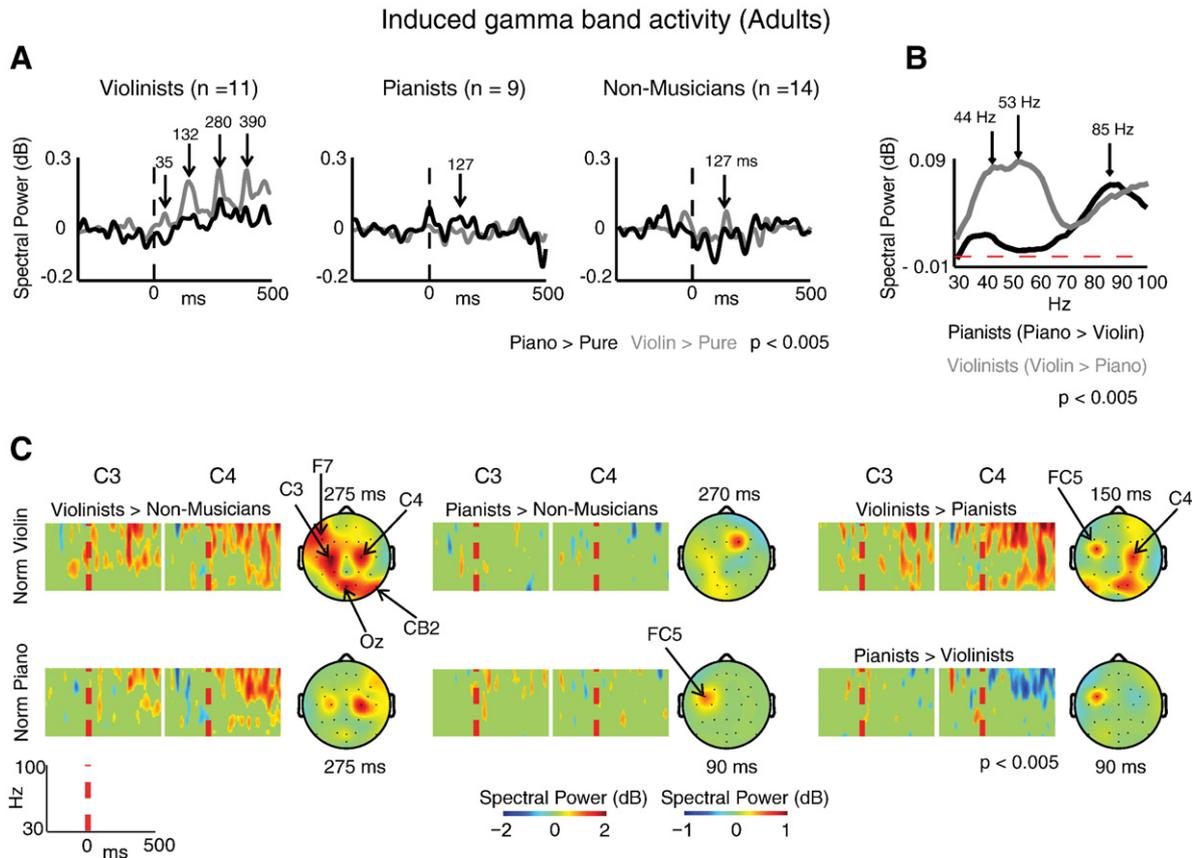


Fig. 2. Induced gamma band activity in adults. (A) Time course of the mean (30–100 Hz) induced gamma band activity (GBA) (collapsing significant activity over 26 channels) for music tones contrasted to pure tones in violinists, pianists and non-musicians. Arrows depict several maximum peaks occurring in each group. (B) Timbre specificity: Frequency response collapsing over all significant time points and channels for GBA induced by the violin tones compared to GBA induced by the piano tones in violinists (top) and GBA induced by the piano tones compared to GBA induced by violin tones in pianists (bottom). (C) Group differences: Spectral power of GBA at channels C3 and C4 and topographies at latencies corresponding to the highest peak values contrasting groups for music tones normalized to pure tones. In panels A and C, the vertical dotted lines indicate sound onset, while in panel B the horizontal dotted lines indicate the zero spectral power mark. Zero spectral power represents all non-significant differences and not just null differences.

lateral fronto-central channels FC5, FC6, and posterior channels Oz, O1, O2, CB1, CB2. Fig. 2B contrasts GBA induced by the violin and piano tones directly (timbre specificity) in musicians. The spectra shown here depict significant spectral power summed

over all time points and channels in the permutation contrasts. The results confirmed timbre specificity for the violin tone in the violinists which is depicted over time for the two musical stimuli separately in Fig. 2A. Timbre-specific enhancement of GBA

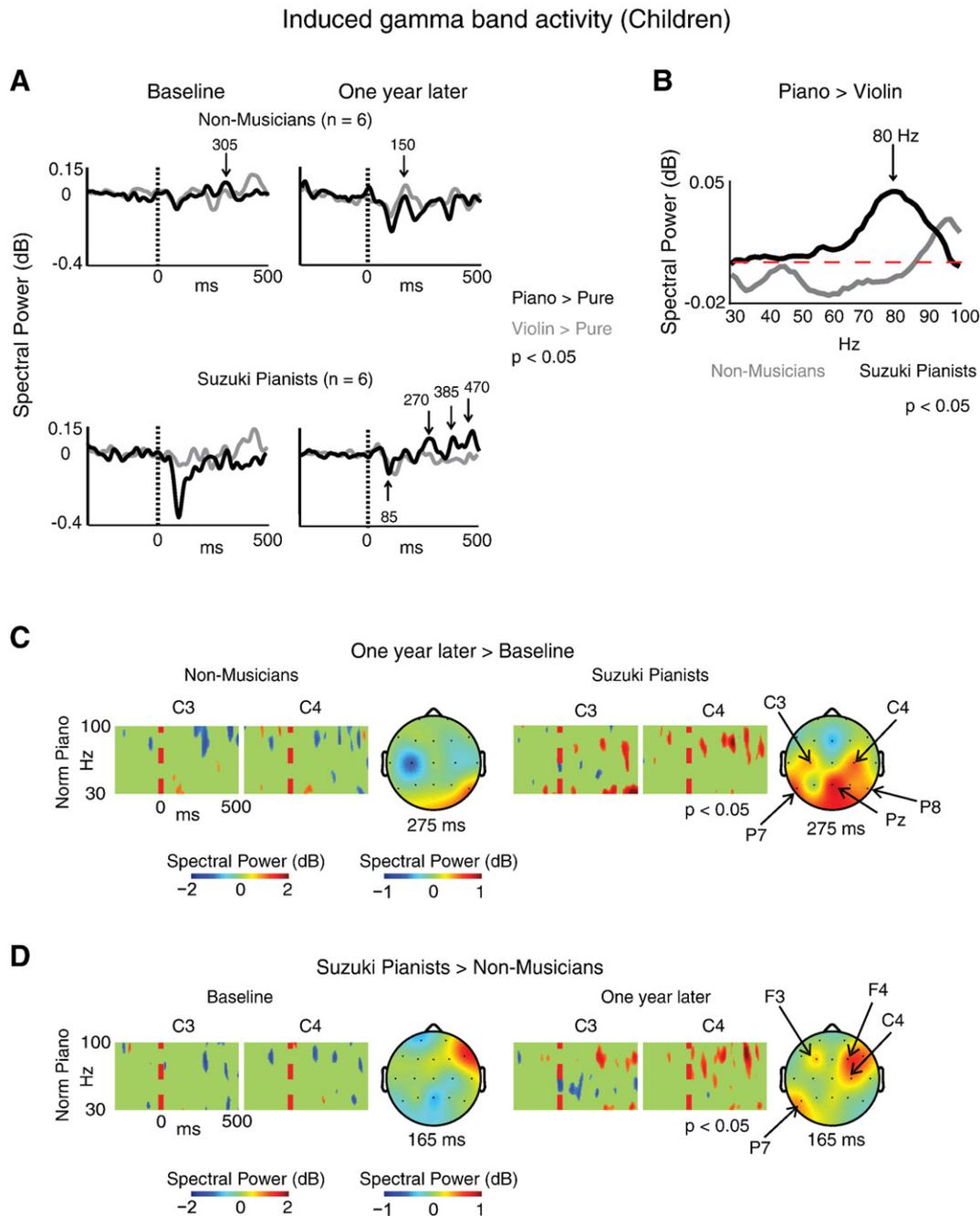


Fig. 3. Induced gamma band activity in children. (A) Time course of the mean (30–100 Hz) induced gamma band activity (GBA) (collapsing significant activity across all channels) for music tones contrasted to pure tones in Suzuki pianists and non-musicians at baseline measurement and 1 year later. The ‘Baseline’ measurement occurred before the commencement of music training in the Suzuki pupils and the ‘One year later’ measurement occurred after 1 year of piano lessons in Suzuki pianists. Arrows depict several GBA extrema for the violin and piano tones. (B) Timbre specificity: Spectral power of the frequency response (collapsing over all significant time points and channels) induced by the piano tones is compared to spectral power induced by the violin tones in control non-musicians and Suzuki pianists for the ‘One year later’ contrast. (C) Training effects: Spectral power of GBA at channels C3/C4 and topographies at latencies corresponding to the highest peaks in the Suzuki pupils contrasting the ‘Baseline’ and ‘One year later’ measurements in non-musicians (left panels) and Suzuki pianists (right panels) for piano tones normalized to pure tones. (D) Group differences: Spectral power of GBA at channels C3/C4 and topographies at latencies corresponding to the highest peaks in the Suzuki pupils contrasting Suzuki pianists compared to age-matched non-musicians at the baseline measurement (left) and 1 year later (right), for piano tones normalized to pure tones.

induced by the violin tone in violinists was particularly prominent for gamma frequency bandwidths of 40 to 60 Hz and >80 Hz. Timbre specificity was also found for the piano tone in pianists at 40 Hz and particularly near 85 Hz. As seen in Fig. 2A, this enhancement occurred predominantly in a time window centered near 127 ms.

Fig. 2C contrasts spectral power between the three adult groups by permutation tests, and shows scalp distributions at the maximum peak latency for each group comparison, for music tones normalized to pure tones. Violinists exhibited larger induced GBA to musical sounds than non-musicians particularly in the right hemisphere (C4 electrode, compare the two left columns of Fig. 2C). The regions of spectral enhancement were prominent around 40 and above 70 Hz. This effect was seen for piano as well as violin tones, but it was more pronounced for the timbre of the instrument of practice. The group difference was most strongly expressed near 275 ms. Pianists showed a small GBA advantage for piano tones particularly around 80 Hz peaking at 90 ms (C3 channel) compared to non-musicians (Fig. 2C, middle panels). When violinists and pianists were compared directly (Fig. 2C, right panels), violinists showed a larger GBA response for violin tones compared to pianists predominantly in the right hemisphere ('Violinists>Pianists') while pianists exhibited suppression in the right hemisphere for piano tones. The relative gamma suppression seen here in the pianists for piano tones reflected enhanced gamma evoked by piano tones in the violinists.

Children

Fig. 3A depicts the significant mean spectral power of induced gamma (collapsed over all channels and frequencies, 30–100 Hz, $p < 0.05$) as a function of time in non-musicians (Fig. 3A, top) and Suzuki pianists (Fig. 3A, bottom) for music tones compared to pure tones at the first measurement ('Baseline') and 1 year later. Suppression of GBA occurred around 85 ms for all comparisons, but especially for the baseline measurement in the Suzuki pianists comparing GBA of piano to pure tones. It is worth noting that suppression at 85 Hz also occurred to a lesser degree in the musically untrained adults (see Fig. 2A) and was mainly exhibited at channels P7 and P8 in adults and similarly at P7 and P8 in Suzuki children. Overall, for the 'Piano>Pure' contrast, suppression dominated for the baseline comparisons as well as for the 'One year later' contrast in control non-musicians. However, for the Suzuki pianists after 1 year of music training, the time course for their timbre of training ('Piano>Pure') commenced with an initial suppression around 85 ms and then resembled that of the professional violinists' response to violin tones (Fig. 2A) with several subsequent enhancements of GBA occurring at later latencies. Gamma enhancement was mainly exhibited at the central C3/C4, fronto-temporal F3/F4/F7/F8 and the posterior-temporal P7/P8 (beyond 85 ms) channels. Control subjects did not show the enhancements found for piano stimuli after 1 year of training in the Suzuki group. A contrast of piano and violin tones after 1 year of piano lessons ('Piano>Violin', Fig. 3B) in Suzuki pianists and control children confirmed that enhancement was larger for the piano sound in the Suzuki pianists and maximally exhibited at the 80 Hz band, resembling the frequency response of adult pianists (see Fig. 2B). The control non-musicians showed less induced gamma for piano than violin for frequencies below 90 Hz and more for piano than violin above 90 Hz.

Fig. 3C illustrates the training effects in children. It shows permutation tests contrasting baseline measurements with measure-

ments 1 year later ('One year later>Baseline') for piano tones normalized to pure tones, in non-musician children (left panels) and Suzuki students (right panels) at C3/C4 channels. Also shown are scalp distributions for the normalized piano responses at peak latencies of the Suzuki children. Prior to training ('Baseline') both groups showed mixed activity (GBA suppression and enhancement). However, after training, the Suzuki pupils exhibited more enhancement than suppression for both music tones, but especially for piano tones with the activity mainly concentrated at P7 (around 40 Hz) and C3 and C4 (around 80 Hz). These results were also seen when the two groups were compared directly ('Suzuki Pianists>Non-Musicians', Fig. 3D). Only after 1 year of training did the Suzuki children show greater induced GBA than the non-musician controls for both music tones, but most prominently for piano tones at C4 around the 80 Hz band.

Discussion

We have shown that induced gamma band oscillations are enhanced in adult musicians compared to adult non-musicians. Consistent with the adults' findings, induced GBA was also enhanced in young children after 1 year of piano lessons compared to children who did not study music. In each case, but particularly in the professional violinists, enhancement of induced gamma was largest for the timbre of the instrument of training, suggesting that induced GBA is highly dependent on specific auditory learning. In contrast to induced gamma, evoked GBA displayed functional properties resembling those of the transient P2 response reported by Shahin et al. (2003, 2004) for the same subjects. Like the P2, evoked gamma was larger for music tones compared to pure tones and larger in musicians than non-musicians with no specificity for the timbre of training. Also like the P2, no training effect could be detected for evoked GBA after 1 year of music lessons in the Suzuki group (Shahin et al., 2004). Hence, the evoked and induced gamma band activities appear to reflect different perceptual mechanisms. The different scalp topographies observed for the two types of gamma activity are consistent with this interpretation.

Induced gamma band activity

Induced GBA has been shown to correlate with many perceptual and cognitive phenomena, including feature binding (Singer and Gray, 1995), learning and memory formation (Miltner et al., 1999; Fell et al., 2001; Gruber et al., 2002), attention (Müller et al., 2000; Sokolov et al., 2004; Snyder and Large 2005), and template matching in short- and long-term memory (Herrmann et al., 2004). GBA has also been implicated in rapid learning tasks. Using MEG, van Wassenhove and Nagarajan (2007) found high-frequency-induced gamma band activity (62–98 Hz) following a rapid training (3 days) at auditory discrimination tasks in a subset of their subjects, further suggesting its involvement in a learning system. However, in their study, enhancement was confined to the left inferior frontal cortex. Our results recorded by EEG do not rule out a contribution from frontal sources but are more consistent with activity generated in the primary and non-primary auditory cortices. Induced GBA appearing in a distributed network of brain regions may reflect enhanced binding of musical features in musicians by matching acoustic information to learned templates in musical memory. In our data, induced GBA for the timbre of training showed enhancement at discrete peaks occurring after completion of evoked activity, particularly in professional violinists (Fig. 2A) and after 1 year of

Suzuki music training (Fig. 3A). The presence of these peaks suggests the involvement of a prolonged process involving communication between the auditory cortex and other brain regions, perhaps related to associative memory and attention. Although our subjects were instructed to ignore the tones and concentrate on the reading task (adults) or the silent movie (children), music tones and especially the tones of the instrument of practice may have commanded the attention of musicians to a greater degree than non-musician controls. It is also possible that in trained musicians template matching in memory is an obligatory process that proceeds outside of attention.

GBA induced by piano sounds was somewhat more evident in young children after 1 year of piano lessons than it was in the adult pianists who reported that they had been playing on average for about 16 years. In this respect it may be noteworthy that our Suzuki pianists commenced practice at age 4 years. The majority of our adult amateur pianists, on the other hand, reported that they were on average 1 to 2 years older (and sometimes older) when their music lessons began, and the intensity of their early practice is not known. Hence the group difference, while not large, could be an early learning effect. Auditory cortical responses undergo a prolonged developmental trajectory, with N1 and P2 not reaching adults' levels until the late teenage years (Ponton et al., 2000; Shahin et al., 2004). The weaker GBA enhancement seen in adult pianists could reflect a more highly differentiated network of functional connections and a more sparse representation of piano sounds than was the case in our young musicians. These factors would also have been expected to affect the expression of induced GBA in adult violinists who also reported commencing at an early age. However, the intensity of training and level of musical accomplishment of our violinists were greater than those of our pianists. Our violinists maintained active professional performance schedules at the time of the study and reported that they practiced approximately twice as many hours per week (~35) as did our amateur pianists (~18). It is likely relevant that 6 of our 11 violinists reported that they played piano as a secondary instrument (Shahin et al., 2003). The extent of their violin and piano training may have contributed to the violinists' larger GBA responses for piano as well as violin tones compared to pianists (Fig. 2A). Nevertheless, the current data support the hypothesis that the amount of musical training and type of training (e.g. instrument) induce gamma band activity. It is possible that the amount and type of training have different effects on the induced GBA. Further research is necessary to distinguish these possibilities.

Spectral power of gamma band activity was suppressed for music tones at a time point near 85 ms. This suppression was maximally exhibited at the posterior channels P7 and P8 in adults and children and occurred at approximately the same time evoked GBA for music tones peaked (80 ms) at fronto-central electrodes in adults. The initial suppression of GBA may represent an inhibitory mechanism that sharpens neural responses to sound (Wehr and Zador, 2003), thus increasing the temporal synchrony between consecutive sounds and the magnitude of the evoked response (as in the ITPC analysis) while at the same time decreasing the overall spectral power (as in the ERSP analysis). However, because of their different topographies, it is likely that the evoked and induced gamma activities – including the induced suppression occurring at 85 ms – involved different generators. Alternatively, spectral power suppression may reflect the initial superposition of asynchronized neural activity. Complex tones likely recruited larger populations of neurons including neural populations of sub-regions of the lateral aspects of the auditory

cortex. Initially, these neuronal populations may have acted asynchronously and hence their summed responses at the scalp were diminished compared to what is present in the background (baseline). However, these neural populations may achieve synchrony such that their summed responses become larger and gamma suppression is minimized or enhanced gamma activity (e.g. after musical training) is detected beyond the first 100 ms. The expression of induced GBA at lateral sites (e.g. C3 and C4) as opposed to mid channels in evoked gamma suggests that some of the induced GBA sources originate in the anterolateral aspect of the temporal cortex. This is noteworthy, given that complex sounds are preferentially processed in the lateral belt of the auditory cortex (Rauschecker and Tian, 2000; Shahin et al., 2007) specifically for sounds representing the preferred stimuli (e.g. in rhesus monkeys, the anterolateral temporal lobe shows high selectivity to monkey calls; see Tian et al., 2001).

The right dominance of induced GBA in adult professional violinists could indicate a right hemisphere specialization for musical memory (Platel et al., 1997; Tervaniemi et al., 2000; Warrier and Zatorre, 2004). In a task relating timbre, pitch, rhythm and familiarity of musical notes, Platel et al. (1997) found a right hemisphere advantage for the timbre task as opposed to pitch, rhythm and familiarity, which weighted toward the left hemisphere. Schneider et al. (2005) reported an enhanced middle latency N19m-P30m auditory-evoked field and gray matter in the right hemisphere of musicians who processed sounds based on spectral content rather than the fundamental pitch. Functional imaging data and anatomical findings summarized by Zatorre and Belin (2001) point to higher synaptic density and less myelination in the primary auditory cortex of the right hemisphere compared to the left hemisphere, which may favor processing of spectral information by this region of the brain. On the other hand, rightward asymmetry of gamma band activity in our violinists might also reflect dominance for the hemisphere contralateral to the most trained (left) ear, or sensorimotor integration related to musical skill. An observation consistent with sensorimotor integration is that the violin is held by the left hand close to the left ear, and violin sounds accompany movement of left fingers when the instrument is played. Enhancement of the cortical representation of the fingering digits in string players has been described (Elbert et al., 1995), and auditory–motor interactions are implicit in the training of musicians (Zatorre et al., 2007). However, while our data do not rule out a sensorimotor contribution to induced GBA, the scalp topographies of induced GBA favor auditory generators as the source of the enhancement. In particular, the existence of activity at posterior sites CB1 and CB2 in the professional violinists and at P7 and P8 in the Suzuki pianists indicates a reversal for generators originating in the auditory but not likely the motor cortex.

Evoked gamma band activity

The evoked gamma band activity (30–90 Hz, 30–100 ms) detected in adults resembles the well-known auditory transient 40-Hz gamma response described by Pantev et al. (1991) originating in the supratemporal plane. Because this response was consistently larger for the complex music tones compared to pure tones, evoked GBA may reflect the physical characteristics of the stimuli. Its enhancement for music tones appears to be driven by the wider bandwidth and/or the spectral complexity of these tones, which may elicit greater neural synchrony (Schreiner et al., 2000). The evoked GBA sensitivity to the spectral attributes of complex tones parallels the N1/N1m and P2 auditory evoked responses which have also been

shown to be augmented for more spectrally and temporally complex tones (Seither-Preisler et al., 2003; Shahin et al., 2005), and specifically for musical tones (Shahin et al., 2005; Lütkenhöner et al., 2006; Meyer et al., 2006). In addition, in the current data, evoked GBA demonstrated a dependence on acoustical training, being larger in adult musicians than in control non-musicians. However, timbre specificity was observed only for induced GBA which appeared later in the stream of auditory information processing. These results extend the report of Pantev et al. (2001) who found that the transient N1m response evoked by trumpet and violin sounds was timbre-specific when contrasted between adult conservatory trumpeters and violinists. Non-overlapping training histories and possibly type of instrument may be essential to the demonstration of timbre specificity in the auditory evoked responses. In our results, induced GBA was more sensitive to the practiced timbres than was evoked GBA.

We did not detect evoked GBA before or after music training in children, despite its robust appearance in adults. This finding implies a developmental trajectory for evoked GBA resembling that of the N1 and P2 auditory evoked responses, which develop later in childhood (Ponton et al., 2000; Shahin et al., 2004) and depend on the emergence of synchronous neural sources in the superficial neocortical laminae between the ages of 5–15 years (Moore and Guan, 2001). Activation of synchronous neural activity underlying evoked GBA does not appear to be strictly dependent on the initial rise time of the temporal envelope of the stimuli. Even though the violin tone had a slower rise time onset than the pure or piano tones, its evoked response was larger than that of the pure tone, and comparable in strength to the evoked response of piano tones.

Conclusion and significance

Timbre specificity of the induced gamma band response in adult musicians, especially professionals, and its development favoring the piano tones in children taking piano lessons over the period of 1 year, indicate that this response is neuroplastic and reflects the specific auditory learning of individuals. Enhanced GBA may indicate receptive field specificity for the preferred musical timbre. However, our finding that the induced gamma band response is sustained during the stimulus suggests that intrinsic top-down processes related to associative memory and attention are likely involved as well, and that music training has profound effects on these systems. It has been suggested that music lessons modify the attentional processing of musical stimuli in children (Fujioka et al., 2006; Hannon and Trainor, 2007). This suggestion is consistent with the view that GBA may represent top-down and bottom-up integration (Herrmann et al., 2004; Polley et al., 2006).

Acknowledgments

This research was supported by the Canadian Institutes of Health Research (CIHR) (L.E.R. and L.J.T.) and the University of California, Davis (L.M.M.).

References

- Bertrand, O., Tallon-Baudry, C., 2000. Oscillatory gamma activity in humans: a possible role for object representation. *Int. J. Psychophysiol.* 38, 211–223.
- Bhattacharya, J., Petsche, H., Pereda, E., 2001. Long-range synchrony in the gamma band: role in music perception. *J. Neurosci.* 21, 6329–6337.
- Bosnyak, D.J., Eaton, R.A., Roberts, L.E., 2004. Distributed auditory cortical representations are modified when non-musicians are trained at pitch discrimination with 40 Hz amplitude modulated tones. *Cereb. Cortex* 14, 1088–1099.
- Chau, W., McIntosh, A.R., Robinson, S.E., Schulz, M., Pantev, C., 2004. Improving permutation test power for group analysis of spatially filtered MEG data. *NeuroImage* 23, 983–996.
- Delorme, A., Makeig, S., 2004. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J. Neurosci. Methods* 134, 9–21.
- Elbert, T., Pantev, C., Wienbruch, C., Rockstroh, B., Taub, E., 1995. Increased cortical representation of the fingers of the left hand in string players. *Science* 270, 305–307.
- Fell, J., Klaver, P., Lehnertz, K., Grunwald, T., Schaller, C., Elger, C.E., Fernandez, G., 2001. Human memory formation is accompanied by rhinal–hippocampal coupling and decoupling. *Nat. Neurosci.* 4, 1259–1264.
- Fujioka, T., Ross, B., Kakigi, R., Pantev, C., Trainor, L.J., 2006. One year of musical training affects development of auditory cortical-evoked fields in young children. *Brain* 129, 2593–2608.
- Good, P., 2000. *Permutation Tests: A Practical Guide to Resampling Methods for Testing Hypotheses*. Springer-Verlag, New York.
- Gruber, T., Müller, M.M., Keil, A., 2002. Modulation of induced gamma band responses in a perceptual learning task in the human EEG. *J. Cogn. Neurosci.* 14, 732–744.
- Hannon, E.E., Trainor, L.J., 2007. Music acquisition: effects of enculturation and formal training on development. *Trends Cogn. Sci.* 11, 466–472.
- Herrmann, C.S., Munk, M.H., Engel, A.K., 2004. Cognitive functions of gamma-band activity: memory match and utilization. *Trends Cogn. Sci.* 8, 347–355.
- Holmes, A.P., Blair, R.C., Watson, J.D.G., Ford, I., 1996. Nonparametric analysis of statistic images from functional mapping experiments. *J. Cereb. Blood Flow Metab.* 16, 7–22.
- Kuriki, S., Kanda, S., Hirata, Y., 2006. Effects of musical experience on different components of MEG responses elicited by sequential piano-tones and chords. *J. Neurosci.* 26, 4046–4053.
- Lütkenhöner, B., Seither-Preisler, A., Seither, S., 2006. Piano tones evoke stronger magnetic fields than pure tones or noise, both in musicians and non-musicians. *NeuroImage* 30, 927–937.
- Menning, H., Roberts, L.E., Pantev, C., 2000. Plastic changes in the auditory cortex induced by intensive frequency discrimination training. *NeuroReport* 11, 817–822.
- Meyer, M., Baumann, S., Jancke, L., 2006. Electrical brain imaging reveals spatio-temporal dynamics of timbre perception in humans. *NeuroImage* 32, 1510–1523.
- Miltner, W.H., Braun, C., Arnold, M., Witte, H., Taub, E., 1999. Coherence of gamma-band EEG activity as a basis for associative learning. *Nature* 397, 434–436.
- Moore, J.K., Guan, Y.L., 2001. Cytoarchitectural and axonal maturation in human auditory cortex. *J. Assoc. Res. Otolaryngol.* 2, 297–311.
- Müller, M.M., Gruber, T., Keil, A., 2000. Modulation of induced gamma band activity in the human EEG by attention and visual information processing. *Int. J. Psychophysiol.* 38, 283–299.
- Münte, T.F., Altenmüller, E., Jäncke, L., 2002. The musician's brain as a model of neuroplasticity. *Nat. Rev. Neurosci.* 3, 473–478.
- Näätänen, R., Picton, T., 1987. The N1 wave of the human electric and magnetic response to sound: a review and an analysis of the component structure. *Psychophysiology* 24, 375–425.
- Pantev, C., Makeig, S., Hoke, M., Galambos, R., Hampson, S., Gallen, C., 1991. Human auditory evoked gamma-band magnetic fields. *Proc. Natl. Acad. Sci. U. S. A.* 88, 8996–9000.
- Pantev, C., Oostenveld, R., Engelien, A., Ross, B., Roberts, L.E., Hoke, M., 1998. Increased auditory cortical representation in musicians. *Nature* 392, 811–814.
- Pantev, C., Roberts, L.E., Schulz, M., Engelien, A., Ross, B., 2001. Timbre-specific enhancement of auditory cortical representations in musicians. *NeuroReport* 12, 169–174.

- Platel, H., Price, C., Baron, J.C., Wise, R., Lambert, J., Frackowiak, R.S., Lechevalier, B., Eustache, F., 1997. The structural components of music perception. A functional anatomical study. *Brain* 12, 229–243.
- Polley, D.B., Steinberg, E.E., Merzenich, M.M., 2006. Perceptual learning directs auditory cortical map reorganization through top–down influences. *J. Neurosci.* 26, 4970–4982.
- Ponton, C.W., Eggermont, J.J., Kwong, B., Don, M., 2000. Maturation of human central auditory system activity: evidence from multi-channel evoked potentials. *Clin. Neurophysiol.* 111, 220–236.
- Rauschecker, J.P., Tian, B., 2000. Mechanisms and streams for processing of “what” and “where” in auditory cortex. *Proc. Natl. Acad. Sci. U. S. A.* 97, 11800–11806.
- Schreiner, C.E., Read, H.L., Sutter, M.L., 2000. Modular organization of frequency integration in primary auditory cortex. *Annu. Rev. Neurosci.* 23, 501–529.
- Schneider, P., Scherg, M., Dosch, H.G., Specht, H.J., Gutschalk, A., Rupp, A., 2002. Morphology of Heschl’s gyrus reflects enhanced activation in the auditory cortex of musicians. *Nat. Neurosci.* 5, 688–694.
- Schneider, P., Sluming, V., Roberts, N., Scherg, M., Goebel, R., Specht, H.J., Dosch, H.G., Bleeck, S., Stippich, C., Rupp, A., 2005. Structural and functional asymmetry of lateral Heschl’s gyrus reflects pitch perception preference. *Nat. Neurosci.* 8, 1241–1247.
- Seither-Preisler, A., Krumbholz, K., Lutkenhoner, B., 2003. Sensitivity of the neuromagnetic N100m deflection to spectral bandwidth: a function of the auditory periphery? *Audiol. Neuro-otol.* 8, 322–337.
- Shahin, A., Bosnyak, D.J., Trainor, L.J., Roberts, L.E., 2003. Enhancement of neuroplastic P2 and N1c auditory evoked potentials in musicians. *J. Neurosci.* 23, 5545–5552.
- Shahin, A., Roberts, L.E., Trainor, L.J., 2004. Enhancement of auditory cortical development by musical experience in children. *Neuroreport* 15, 1917–1921.
- Shahin, A., Roberts, L.E., Pantev, C., Trainor, L.J., Ross, B., 2005. Modulation of P2 auditory-evoked responses by the spectral complexity of musical sounds. *NeuroReport* 16, 1781–1785.
- Shahin, A.J., Roberts, L.E., Pantev, C., Aziz, M., Picton, T.W., 2007. Enhanced anterior–temporal processing for complex tones in musicians. *Clin. Neurophysiol.* 118, 209–220.
- Singer, W., Gray, C.M., 1995. Visual feature integration and the temporal correlation hypothesis. *Annu. Rev. Neurosci.* 18, 555–586.
- Snyder, J.S., Large, E.W., 2005. Gamma-band activity reflects the metric structure of rhythmic tone sequences. *Brain Res. Cogn. Brain Res.* 24, 117–126.
- Sokolov, A., Pavlova, M., Lutzenberger, W., Birbaumer, N., 2004. Reciprocal modulation of neuromagnetic induced gamma activity by attention in the human visual and auditory cortex. *NeuroImage* 22, 521–529.
- Tallon-Baudry, C., Bertrand, O., Delpuech, C., Pernier, J., 1996. Stimulus specificity of phase-locked and non-phase-locked 40 Hz visual responses in human. *J. Neurosci.* 16, 4240–4249.
- Tervaniemi, M., Medvedev, S.V., Alho, K., Pakhomov, S.V., Roudas, M.S., Van Zuijen, T.L., Näätänen, R., 2000. Lateralized automatic auditory processing of phonetic versus musical information: a PET study. *Hum. Brain Mapp.* 10, 74–79.
- Tian, B., Reser, D., Durham, A., Kustov, A., Rauschecker, J.P., 2001. Functional specialization in rhesus monkey auditory cortex. *Science* 292, 290–293.
- Tremblay, K., Kraus, N., McGee, T., Ponton, C., Otis, B., 2001. Central auditory plasticity: changes in the N1–P2 complex after speech–sound training. *Ear Hear.* 22, 79–90.
- van Wassenhove, V., Nagarajan, S.S., 2007. Auditory cortical plasticity in learning to discriminate modulation rate. *J. Neurosci.* 27, 2663–2672.
- Warrier, C.M., Zatorre, R.J., 2004. Right temporal cortex is critical for utilization of melodic contextual cues in a pitch constancy task. *Brain* 127, 1616–1625.
- Wehr, M., Zador, A.M., 2003. Balanced inhibition underlies tuning and sharpens spike timing in auditory cortex. *Nature* 42, 442–446.
- Weinberger, N.M., 2003. The nucleus basalis and memory codes: auditory cortical plasticity and the induction of specific, associative behavioral memory. *Neurobiol. Learn. Mem.* 80, 268–284.
- Zanto, P.Z., Large, E.W., Fuchs, A., Kelso, J.A., 2005. Gamma-band responses to perturbed auditory sequences: evidence for synchronization of perceptual processes. *Music Percept.* 22, 535–552.
- Zatorre, R.J., Belin, P., 2001. Spectral and temporal processing in human auditory cortex. *Cereb. Cortex* 11, 946–953.
- Zatorre, R.J., Chen, J.L., Penhune, V.B., 2007. When the brain plays music: auditory–motor interactions in music perception and production. *Nat. Rev. Neurosci.* 8, 547–558.