Understanding the Benefits of Musical Training

Effects on Oscillatory Brain Activity

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A number of studies suggest that musical training has benefits for other cognitive domains, such as language and mathematics, and studies of children and adults indicate structural as well as functional differences between the brains of musicians and nonmusicians. The induced gamma-band response has been associated with attentional, expectation, memory retrieval, and integration of top-down, bottom-up, and multisensory processes. Here we report data indicating that the induced gamma-band response to musical sounds is larger in adult musicians than in nonmusicians and that it develops in children after 1 year of musical training beginning at age $4^{1}/_{2}$ years, but not in children of this age who are not engaged in musical lessons. We conclude that musical training affects oscillatory networks in the brain associated with executive functions, and that superior executive functioning could enhance learning and performance in many cognitive domains.

Key words: oscillatory brain activity; gamma band; musical experience; musical development

Interest in how music is processed in the brain has increased dramatically over the past decade, in large part because (1) the subject offers a good model to study brain plasticity and the effects of specific experience^{1,2} and (2) formal musical training appears to enhance not only musical processing, but also linguistic and nonlinguistic cognitive processing.^{3,4} A number of studies have shown anatomic and functional differences between musicians and nonmusicians, but the mechanisms by which musical training exerts its domain-general effects are not yet well understood. Here we propose that musical training affects general au-

ditory attention and memory, and that these effects can be studied by observing oscillatory brain activity.

Differences between Musicians and Nonmusicians

At a behavioral level, a number of studies associate musical training with linguistic, spatial reasoning, and mathematical performance.^{3,5–7} In the linguistic domain, it might be predicted that the ability to decode aspects of language that rely on acoustic information would correlate with the ability to perceive musical pitch and rhythm. Phonological awareness is such an aspect, comprising an understanding of the consonant and vowel sound categories of a particular language and how they can be sequenced to form words. Indeed, several studies

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indicate that musical pitch and/or rhythm ability correlates with early phonological awareness.^{8–14} Perhaps more surprising is that musical training is associated with enhanced verbal memory^{15–17} and that early reading ability is correlated with musical pitch and/or rhythm skills.^{8,11–14,18–20} Anvari et al.⁸ tested 50 4-yearolds and 50 5-year-olds on a battery of musical and linguistic tests, and used hierarchical regression to show that musical ability predicts early reading ability even after the variance due to phonological awareness is accounted for. Corrigall and Trainor¹⁶ replicated these findings and demonstrated that the degree of enculturation in preschool children (specifically, ability to detect harmonic violations) predicts phonological awareness, verbal memory, and early reading skills. Even more surprising are the findings that musical training enhances performance on virtually every subtest of the IQ measure.4

At a physiological level, several studies show differences between the brains of adult musicians and nonmusicians. For example, structural MRI studies indicate differences in gray matter between musicians and nonmusicians in motor, auditory, and visual brain regions.²¹ Heschl's gyrus, containing primary auditory cortex, was found to be larger in musicians than nonmusicians, and its size correlated with musical proficiency.²² Furthermore, the left planum temporale, which is important for the processing of complex sounds, is relatively larger than the right planum temporale in professional musicians, especially those with absolute pitch.² With respect to the integrity of directionally organized neural fibers, white-matter tracts also appear to differ between pianists and nonmusicians, particularly in a pathway from primary motor cortex to the spinal cord and in a region near Broca's area, which is important for complex aspects of music and language processing.23,24

At a functional level, the brain responses of adult musicians and nonmusicians also differ as measured by EEG and MEG. For example, some event-related potential responses from au-

ditory cortical areas are larger in musicians compared to nonmusicians, such as N1, occurring about 100 ms after stimulus onset,²⁵ N1c, occurring at about 140 ms and larger in the right hemisphere,²⁶ and P2, occurring about 170 ms after stimulus onset.²⁶ For sequential stimuli, occasional wrong notes in a short melody that is repeated in different keys (i.e., starting on different notes) from trial to trial, elicit a frontally negative event-related potential called mismatch negativity (MMN).²⁷ While MMN to such melodic changes is present in both musicians and nonmusicians, it is much larger in musicians (Fig. 1).²⁸ In terms of polyphonic music, changed notes in either of two simultaneous melodies elicit MMN responses that are larger in musicians than nonmusicians (Fig. 1).²⁹ Errors in one chord of a chord sequence produce an early right anterior negativity that is also larger in musicians than in nonmusicians.³⁰

A number of lines of reasoning suggest that the differences seen between musicians and nonmusicians are due, at least in part, to the intensive musical experience of the former group rather than entirely to initial genetic differences. For example, some plastic changes are specific to the timbre of the instrument of training³¹ and are therefore unlikely to be genetically determined. Furthermore, laboratory training on pitch discrimination can enhance N1,³² P2³³ and N1c³⁴ amplitude, suggesting that the processes underlying these components are particularly plastic, even in adults. Interestingly, musical training in adults that involves sensorimotor practice produces larger changes in auditory cortex than the equivalent experience involving only auditory training.35

In order to fully understand how musical training affects brain development, it is helpful to study children. In terms of the effect of musical training on musical processing, Shahin *et al.*³⁶ showed that 4- and 5-year-old children engaged in music lessons already differ from age-matched controls not engaged in musical practice in terms of an earlier emergence of the

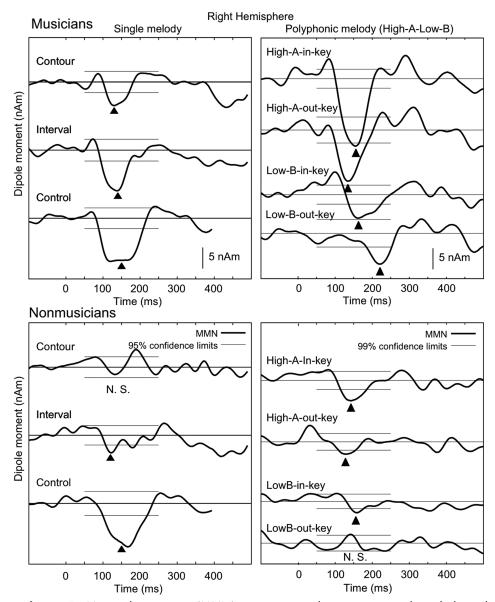


Figure 1. Mismatch negativity (MMN) responses to changes in a single melody and polyphonic melodies in musicians and nonmusicians. Left panels: MEG was used to measure responses to occasional deviant notes in a melody repeated in transposition. Changes involving either a contour or an interval change elicit larger MMN in musicians than in nonmusicians. In the control condition, occasional changes in the pitch of single tones elicit robust MMN in both groups. Right panels: Two simultaneous melodies were presented in transposition from trial to trial. Occasional deviant notes in either the high melody (25% of trials) or in the low melody (25% of trials) elicit MMN. The groups are similar in that deviants in the higher melody elicit larger and earlier MMN than deviants in the lower melody and that MMN is sensitive to the size of the change (in-key deviants were 2 semitones different, and out-of-key deviants were 1 semitone different, from standards) rather than its musical meaning (behaviorally, out-of-key deviants are easier to detect than in-key deviants). However, it can be seen that MMN is larger in the musicians than in the nonmusicians. (Data from Fujioka *et al.*^{28,29})

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N1 and P2 components in response to musical tones. Relations between auditory aspects of musical and linguistic processing are also evident in the brain responses of young children, with the size of response to musical tones correlated with the second language pronunciation accuracy³⁷ and more robust linguistic representations after musical training than after art training.³⁸

The majority of studies on the effects of musical training on brain responses have examined auditory perceptual responses, so it remains largely unknown as to how music influences other cognitive domains. However, in order to understand possible effects of musical training on attention, Fujioka et al.39 measured MEG responses in 4- and 5-year-old children every 3 months for a year. Half of the children were engaged in music lessons and half in other activities, such as sports. They found that the part of the evoked response that changed most over the course of the year, and that developed significantly differently between the musician and nonmusician children, was a negativity around 250 ms after sound onset that is associated with auditory attentional processing.

The attentional and memory demands involved in learning to play an instrument are very large. For example, children learning to play the violin must press the strings with one hand while coordinating bow movements with the other. The children need to listen to the sounds that the teacher is making, remember them, and compare them to the sounds they are making, and adjust their body movements so that their sound more closely matches what the teacher is modeling. This learning depends on the integration of top-down and bottomup processes and it may well be that it is the training of this integration that underlies the enhanced attentional and memory processes observed in the musically trained. In order to study these effects, we examined gamma-band responses in adult musicians and nonmusicians and their development in child musicians and nonmusicians.

Gamma-band Activity

As networks of neurons communicate, the brain engages in oscillatory activity that can be measured in EEG and MEG potentials and fields. Oscillations in the 30- to 100-Hz range are termed gamma-band responses. Sound stimuli produce transient evoked gamma-band responses that begin around 30 ms after stimulus onset, and last about 50 ms.⁴⁰ Such evoked responses closely follow the physical characteristics of the sound and are time-locked to its onset, such that when the evoked responses from many presentations of a sound are averaged together (components not time-locked to the stimulus will approach zero in the average), the evoked gamma-band response remains robust. Of more interest to the present discussion, the presentation of sound stimuli also result in *induced* gamma-band responses.^{41,42} These responses are not strictly time-locked to the stimulus as they involve intrinsic (nonstimulusinduced) oscillatory activity that becomes associated with the sound stimulus. Thus, averaging the induced responses of many presentations of a sound stimulus removes the induced gamma-band response because it is at a different phase with respect to stimulus onset in each case. In order to see the induced gamma-band response, it is therefore necessary to analyze the frequency content with respect to time on individual trials before averaging.

Gamma-band activity is thought to reflect a number of integrative functions. In the visual domain, it is believed to be involved in the binding of features, such as location, color, and form, into the conscious percept of an object.^{43,44} In the auditory domain, gamma-band activity likely reflects the binding of features, such as pitch, timbre, and harmony,⁴⁵ and matching of acoustical cues to representations in long-term memory.^{46,47} The gamma band has also been linked to attention, anticipation, and expectation,^{48–51} processes that are thought to be enhanced by music training. For example, Snyder and Large⁴⁹ have shown that rhythmic patterns lead to expectations for sound events at the next beat, and that induced gamma-band activity can be seen at the time point of the expected beat, even when the sound stimulus is omitted.

Methodological Approach

Our interest was in the effects of musical training on gamma-band activity. Accordingly, we measured evoked and induced gamma-band activity in three adult groups: 11 professional violinists, 9 amateur pianists, and 14 nonmusicians (no formal musical training).⁵² We also tested 12 children, initially at $4^{1}/_{2}$ years of age and again at $5^{1}/_{2}$ years of age. Half of the children were just beginning Suzuki piano lessons at the time of the first measurement. The other half of the children were not engaged in musical instruction.

The six stimuli were synthesized 500-ms violin, piano, and pure tones, each presented at two pitches of 220 and 141 Hz. The tones were delivered in a pseudorandom order with an inter-stimulus interval of 2.5 s from a speaker 1 meter in front of the subject, at an intensity of 70 dB SPL. Adults read and the children watched a silent movie in a passive-listening protocol. EEG was recorded from 32 channels in adults and 19 channels in children, artifact rejected, averaged into 1200-ms epochs that included a 400-ms prestimulus period, re-referenced to an average reference, and baseline-corrected to the average amplitude of the prestimulus interval.

In order to measure evoked and induced gamma-band activity, we conducted time-frequency analyses of single-trial data by looking at event-related spectral perturbations (ERSPs).⁵³ Specifically, the baseline spectral power was calculated for the period -400 to -150 ms before stimulus onset to avoid overlap of post-stimulus and prestimulus activity due to windowing. Spectral power differences compared to base line were examined every 5 ms using a sliding Hanning-windowed, 3-cycle sinusoidal wavelet transform. Frequencies between

30 and 100 Hz were examined in 1.5-Hz increments. In Figure 2 the ERSPs are plotted in dB, that is, as the log of the ratio of poststimulus and prestimulus baseline spectral activity (a 50% change in activity corresponds to a 1.76 change in dB). The calculated spectral power differences contain both evoked and induced gamma-band activity. In order to examine the evoked oscillatory gamma-band activity separately, we analyzed the inter-trial phase coherence (ITPC)⁴⁴ as the induced gamma-band activity occurs at different phases on each trial and would therefore not contribute to the ITPC.

Effects of Musical Training on Evoked Gamma-band Activity

Figure 2 (Panel A) shows the evoked gammaband activity in adults (i.e., ITPC plots). Consistent with previous reports, evoked gammaband activity is centered around 40 Hz, occurs between about 50 and 100 ms after tone onset, and is strongest at fronto-central scalp regions. In order to compare evoked gammaband responses to musical versus pure tones, and to compare responses in musicians and nonmusicians, we used permutation tests,⁵⁴ where the distribution under the null hypothesis of no difference between groups is estimated by repeated sampling from the data. Evoked gamma-band activity was stronger for musical tones, whether violin or piano, than for pure tones for both musicians and nonmusicians. This likely reflects the spectral complexity of the musical tones rather than a specifically musical response. Violinists and pianists did not differ but, as can be seen in Figure 2 (Panel A) musicians showed enhanced phase-locking compared to nonmusicians for all three tone types, suggesting the auditory cortex is better able to represent sound in the musician group.

Interestingly, no significant evoked gammaband response could be measured in children, suggesting that evoked cortical oscillatory responses may take several years to develop.

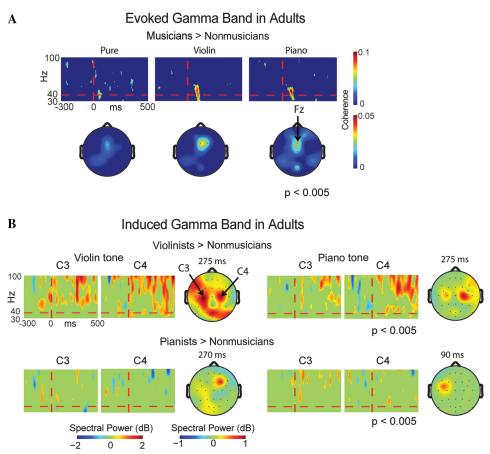
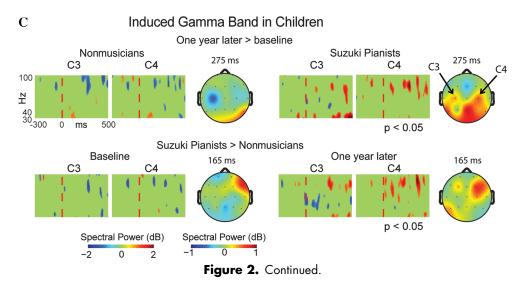


Figure 2. Gamma-band activity. Panel A. Evoked gamma-band activity in adults. Permutation tested inter-trial phase coherence (ITPC) spectrograms at channel Fz contrasting evoked gamma-band activity between musicians and nonmusicians for pure, violin and piano tones, and the scalp distribution at 80 ms. It can be seen that, compared to nonmusicians, musicians show greater ITPC, especially for musical tones. Panel B. Induced gamma-band activity in adults. Permutation tested event-related spectral perturbation (ERSP) spectrograms at left and right central channels C3 and C4 for violin and for piano tones. The upper row shows times and frequencies where violinists show greater activity than nonmusicians. The lower row shows pianists compared to nonmusicians. The corresponding head maps show differences for induced gamma-band activity between groups at peak latencies. The gamma-band activity for musical tones has been normalized to that of pure tones. It can be seen that musicians show increased gamma-band activity compared to nonmusicians. Panel C. Induced gammaband activity in children. The upper row shows differences between induced gamma-band responses at the first measurement and at the second measurement 1 year later for Suzuki music students and nonmusician children. Permutation tested ERSP spectrograms at channels C3 and C4, and corresponding scalp distributions at peak latencies, show that induced gammaband responses increase over the year for the Suzuki children but not for the nonmusician children. The lower row shows differences between Suzuki music students and nonmusician children at the first baseline measurement and at the second measurement 1 year later. Permutation tested ERSP spectrograms at channels C3 and C4, and corresponding scalp maps at peak latencies, show that after 1 year of music lessons, the musician children show increased induced gamma-band activity compared to the nonmusician students, but that the two groups do not differ at the first measurement before the onset of music lessons. Vertical dashed lines indicate sound onset. Horizontal dashed lines indicate the 40 Hz frequency mark. Data from Shahin et al.52



This parallels previous findings showing very long developmental trajectories for maturation of N1 and P2 evoked responses, which are not seen robustly until around age 4 or 5 years. N1 and P2 increase in amplitude and decrease in latency until about 10 to 12 years of age, after which they decrease in amplitude until they reach a steady state near the end of the teenage years.^{36,55} The developmental trajectory of evoked gamma-band activity has not yet been studied extensively, but the present findings suggest a protracted developmental time course.

Effects of Musical Training on Induced Gamma-band Activity

With respect to the question of how musical training affects other cognitive domains, and the effects of musical training on attention and memory processes, the induced gammaband activity is of great interest. Induced gamma-band responses in adults can be seen in the ERSP plots of Figure 2 (Panel B). These spectrograms mainly represent induced responses because most of the activity is after 100 ms and therefore outside the frequencytime locale of the evoked gamma-band activity. In contrast to the evoked gamma band, the induced response covers a broader frequency range and has a more left and right central focus on the scalp in contrast to the frontal central focus of the evoked gamma band. Of great interest is that the induced response is very long-lasting (at least 500 ms after stimulus onset) and comes in quasi-periodic waves of suppression and enhancement. This latter finding suggests that the induced gamma-band response is somehow coupled with, and rides on top of, lower-frequency oscillations in the alpha or beta bands.^{56–58}

As with the evoked gamma-band response, musical training affects the size of the induced gamma-band response. However, extensive training may be needed to see large differences in induced gamma band. As can be seen in Figure 2 (Panel B), the amateur pianists show enhanced induced gamma-band responses compared to those of nonmusicians, but professional violinists showed much larger enhancements. This difference likely reflects the degree of training, although it might also reflect a difference between violin and piano training. Because the violin is not a fixed-pitch instrument, it might promote the allocation of more attentional resources to discriminating fine-pitch differences. In any case, a clear effect of musical training on induced gamma-band responses to musical tones is evident.

The effects of musical training on induced gamma-band development can also be seen in the children (Fig. 2, Panel C). At the first measurement, prior to any music lessons, no significant induced gamma-band responses are evident in either group. However, after 1 year, only those studying piano showed an initial suppression (around 85 ms) and then waves of induced gamma-band enhancement in response to piano tones. A direct comparison of the musician and nonmusician children showed no difference at the initial measurement, but significantly more enhanced induced gamma-band activity in the musician compared to nonmusician children after 1 year of lessons.

Conclusions

Together, the adult and child data show that musical training is associated with enhanced induced gamma-band activity. Although the details of exactly what processes the induced gamma-band activity reflects are unclear, recent studies have associated it with attention, expectation, memory, integration of features into objects, and multisensory integration. For example, induced gamma-band responses occur for omitted stimuli where an expectation for a stimulus at that time is created by the context.⁴⁸ The employment of top-down knowledge in deciphering degraded speech⁴⁶ and accessing memory for environmental sounds⁴⁷ increase gamma-band activity. Interestingly, induced oscillatory activity is also involved in multisensory integration.59

It remains for future research to determine which processes associated with induced gamma-band activity are enhanced by musical training. However, as reviewed by Hannon and Trainor,³ active participation in music lessons gives rise to much larger plasticity effects than passive (listening) exposure to music. Formal lessons engage top-down and attentional processes to a much greater degree than passive listening, leading to the prediction that induced gamma-band responses associated with topdown and attentional processes would be particularly enhanced in musicians. Furthermore, producing music, whether by singing or using an instrument, involves coordination between body movements and auditory perception.⁶⁰ Multisensory connections between movement and auditory areas are present very early in life,⁶¹ but presumably these get refined through musical practice. Interestingly, multisensory processing between auditory and visual areas produces strong induced activity in the 15to 20-Hz beta band.⁶² Given the importance of auditory-movement interactions in musical production, it might be predicted that strong induced oscillations would be present during auditory and motor integration in musicians. Long-range oscillatory activity between far brain regions might be expected to have a lower frequency that the gamma-band activity within a modality. Indeed, Figure 2 (Panels B and C) show periodic increases and decreases in induced gamma-band oscillations, suggesting the presence of beta band activity that is stronger in the musicians compared to the nonmusicians. There is also evidence that children taking music lessons have stronger beta band activity than children not taking lessons.⁶³ In future research we plan to examine induced oscillatory responses in musicians at different frequencies specifically in relation to attentional, memory, and multisensory processing in order to investigate the details of how musical training has widespread benefits for cognitive processing.

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Conflicts of Interest

The authors declare no conflicts of interest.

References

 Roberts, L.E., D.J. Bosnyak, A. Shahin, *et al.* 2005. Neuroplastic adaptations of the auditory system in musicians and nonmusicians. In *Plasticity and Signal Representation in the Auditory System*. J. Syka & M. Merzenich, Eds.: 387–394. Springer. New York.

- Schlaug, G. 2001. The brain of musicians: a model for functional and structural adaptation. Ann. N. Y. Acad. Sci. 930: 281–299.
- Hannon, E.E. & L.J. Trainor. 2007. Music acquisition: effects of enculturation and formal training on development. *Trends Cogn. Sci.* 11: 466–472.
- Schellenberg, E.G. 2004. Music lessons enhance IQ. Psychol. Sci. 15: 511–514.
- Schellenberg, E.G. 2005. Music and cognitive abilities. *Curr. Directions Psychol. Sci.* 14: 322–325.
- Trehub, S.E. & E.E. Hannon. 2006. Infant music perception: domain-general or domain-specific mechanisms? *Cognition* **100**: 73–99.
- Trainor, L.J. 2005. Are there critical periods for musical development? *Dev. Psychobiol.* 46: 262–278.
- Anvari, S., L.J. Trainor, J. Woodside, *et al.* 2002. Relations among musical skills, phonological processing, and early reading ability in preschool children. *J. Exp. Child Psych.* 83: 111–130.
- Bolduc, J. & I. Montesinos-Gelet. 2005. Pitch processing and phonological awareness. *Psychomusicology* 19: 3–14.
- Gromko, J.E. 2005. The effect of music instruction on phonemic awareness in beginning readers. *J. Res. Music Ed.* 53: 199–209.
- Lamb, S.J. & A.H. Gregory. 1993. The relationship between music and reading in beginning readers. *Ed. Psychol.* 13: 19–27.
- Norton, A., E. Winner, K. Cronin, *et al.* 2005. Are there pre-existing neural, cognitive, or motoric markers for musical ability? *Brain Cogn.* 5: 124–134.
- Overy, K. 2003. Dyslexia and music: from timing deficits to musical intervention. *Ann. N. Y. Acad. Sci.* 999: 497–505.
- Peynircioglu, Z.F., A.Y. Durgunoglu & B. Öney-Kusefoglu. 2002. Phonological awareness and musical aptitude. *J. Res. Reading.* 25: 68–80.
- Chan, A.S., Y. Ho & M. Cheung. 1998. Music training improves verbal memory. *Nature* **396**: 128.
- Corrigall, K.A. & L.J. Trainor. 2009. Sensitivity to key membership and musical harmony predicts reading performance in young children. Presented at Society for Research in Child Development, Denver, Colorado, USA, April.
- Ho, Y., M. Cheung & A.S. Chan. 2003. Music training improves verbal but not visual memory: crosssectional and longitudinal explorations in children. *Neuropsychology* 17: 439–450.
- Atterbury, B.W. 1985. Musical differences in learning-disabled and normal-achieving readers, aged seven, eight and nine. *Psychol. Music.* 13: 114– 123.

- Barwick, J., E. Valentine, R. West, *et al.* 1989. Relations between reading and musical abilities. *Br. J. Ed. Psychol.* 59: 253–257.
- Douglas, S. & P. Willatts. 1994. The relationship between musical ability and literacy skills. *J. Res. Reading.* 17: 99–107.
- Gaser, C. & G. Schlaug. 2003. Brain structures differ between musicians and nonmusicians. *J. Neurosci.* 23: 9240–9245.
- Schneider, P., M. Scherg, H.G. Dosch, et al. 2002. Morphology of Heschl's gyrus reflects enhanced activation in the auditory cortex of musicians. *Nat. Neurosci.* 5: 688–694.
- Bengtsson, S.L., Z. Nagy, S. Skare, *et al.* 2005. Extensive piano practicing has regionally specific effects on white matter development. *Nat. Neurosci.* 8: 1148–1150.
- Han, Y., H. Yang, Y. Lv, et al. 2009. Gray matter density and white matter integrity in pianists' brains: a combined structural and diffusion tensor MRI study. *Neurosci. Lett.* In press.
- Pantev, C., R. Oostenveld, A. Engelien, *et al.* 1998. Increased auditory cortical representation in musicians. *Nature* **392**: 811–814.
- Shahin, A.J., D J. Bosnyak, L.J. Trainor, et al. 2003. Enhancement of neuroplastic P2 and N1c auditory evoked potentials in musicians. *J. Neurosci.* 23: 5545– 5552.
- Trainor, L.J., K.L. McDonald & C. Alain. 2002. Automatic and controlled processing of melodic contour and interval information measured by electrical brain activity. *J. Cogn. Neurosci.* 14: 430–442.
- Fujioka, T., L.J. Trainor, B. Ross, *et al.* 2004. Musical training enhances automatic encoding of melodic contour and interval structure. *J. Cogn. Neurosci.* 16: 1010–1021.
- Fujioka, T., L.J. Trainor, B. Ross, *et al.* 2005. Automatic encoding of polyphonic melodies in musicians and nonmusicians. *J. Cogn. Neurosci.* 17: 1578–1592.
- Koelsch, S., T.B. Schmidt & J. Kansok. 2002. Influences of musical expertise on the ERAN: an ERPstudy. *Psychophysiology* **39:** 657–663.
- Pantev, C., L.E. Roberts, M. Schulz, *et al.* 2001. Timbre-specific enhancement of auditory cortical representations in musicians. *Neuroreport* 12: 169– 174.
- Menning, H., L.E. Roberts & C. Pantev. 2000. Plastic changes in the human auditory cortex induced by intensive discrimination training. *Neuroreport* 11: 817– 822.
- Tremblay, K., N. Kraus, T. McGee *et al.* 2001. Central auditory plasticity: changes in the N1-P2 complex after speech-sound training. *Ear Hear.* 22: 79–90.
- Bosnyak, D.J., R.A. Eaton & L.E. Roberts. 2004. Distributed auditory cortical representations are

modified when nonmusicians are trained at pitch discrimination with 40 Hz amplitude modulated tones. *Cereb. Cortex* **14:** 1088–1099.

- Lappe, C., S. Herholz, L.J. Trainor, et al. 2008. Cortical plasticity induced by short-term unimodal and multimodal musical training. *J. Neurosci.* 28: 9632– 9639.
- Shahin, A., L.E. Roberts & L.J. Trainor. 2004. Enhancement of auditory cortical development by musical experience in children. *Neuroreport* 15: 1917–1921.
- Milovanova, R., M. Huotilain, V. Välimäki, et al. 2008. Musical aptitude and second language pronunciation skills in school-aged children: neural and behavioral evidence. *Brain Res.* **1194**: 81–89.
- Besson, M, D. Schön, S. Moreno, *et al.* 2007. Influence of musical expertise and musical training on pitch processing in music and language. *Restor. Neurol. Neurosci.* 25: 1–12.
- Fujioka, T., B. Ross, R. Kakigi *et al.* 2006. One year of musical training affects development of auditory cortical-evoked fields in young children. *Brain* 129: 2593–2608.
- Pantev, C., S. Makeig, M. Hoke *et al.* 1991. Human auditory evoked gamma-band magnetic fields. *Proc. Natl. Acad. Sci. USA* 88: 8996–9000.
- Kaiser, J. & W. Lutzenberger. 2003. Induced gammaband activity and human brain function. *The Neuroscientist* 9: 475–484.
- Pantev, C. 1995. Evoked and induced gamma-band activity of the human cortex. *Brain Topogr.* 7: 321–330.
- Singer, W. & C.M. Gray. 1995. Visual feature integration and the temporal correlation hypothesis. *Annu. Rev. Neurosci.* 18: 555–586.
- Tallon-Baudry, C., O. Bertrand, C. Delpuech & J. Pernier. 1996. Stimulus specificity of phase-locked and non-phase-locked 40 Hz visual responses in human. *J. Neurosci.* 16: 4240–4249.
- Bhattacharya, J., H. Petsche & E. Pereda. 2001. Longrange synchrony in the gamma band: role in music perception. *J. Neurosci.* 21: 6329–6337.
- Hannemann, R., J. Obleser & C. Eulitz. 2007. Topdown knowledge supports the retrieval of lexical information from degraded speech. *Brain Res.* 1153: 134–143.
- Lenz, D., J. Schadow, S. Thaerig, *et al.* 2007. What's that sound? Matches with auditory long-term memory induce gamma band activity in human EEG. *Int. J. Psychophysiol.* 64: 31–38.
- Gurtubay, I.G., M. Alegre, M. Valencia & J. Artieda. 2006. Cortical gamma band activity during auditory tone omission provides evidence for the involvement of oscillatory activity in top-down processing. *Exp. Brain Res.* **175**: 463–470.
- 49. Snyder, J.S. & E.W. Large. 2005. Gamma-band activity reflects the metric structure of rhythmic

tone sequences. Brain Res. Cogn. Brain Res. 24: 117-126.

- Sokolov, A., M. Pavlova, W. Lutzenberger, *et al.* 2004. Reciprocal modulation of neuromagnetic induced gamma activity by attention in the human visual and auditory cortex. *NeuroImage* 22: 521–529.
- Zanto, P.Z., E.W. Large, A. Ruchs, *et al.* 2005. Gamma-band responses to perturbed auditory sequences: evidence for synchronization of perceptual processes. *Music Percept.* 22: 535–552.
- Shahin, A.J., L.E. Roberts, W. Chau, *et al.* 2008. Musical training leads to the development of timbre-specific gamma band activity. *NeuroImage* **41**: 113–122.
- Delorme, A. & S. Makeig. 2004. EEGLAB: and open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J. Neurosci. Methods.* 134: 9–21.
- Chau, W., A.R. McIntosh, S.E. Robinson, *et al.* 2004. Improving permutation test power for group analysis of spatially filtered MEG data. *NeuroImage* 23: 983– 996.
- Ponton, C.W., J.J. Eggermont, B. Kwong, *et al.* 2000. Maturation of human central auditory system activity: evidence from multi-channel evoked potentials. *Clin. Neurophysiol.* 111: 220–236.
- Canolty, R.T., E. Edwards, S.S. Dalal, *et al.* 2006. High gamma power is phase-locked to theta oscillations in human neocortex. *Science* **313**: 1626–1628.
- Lakatos, P., A.S. Shah, K.H. Knuth, *et al.* 2005. An oscillatory hierarchy controlling neuronal excitability and stimulus processing in the auditory cortex. *J. Neurophysiol.* **94**: 1904–1911.
- Fries, P., J.H. Reynolds, A.E. Rorie, *et al.* 2001. Modulation of oscillatory neuronal synchronization by selective visual attention. *Science* **291**: 1560–1563.
- Yuval-Greenberg, S. & L.Y. Deouell. 2007. What you see is not (always) what you hear: induced gamma band responses reflect cross-modal interactions in familiar object recognition. *J. Neurosci.* 27: 1090–1096.
- Zatorre, R.J., J.L. Chen & V.B. Penhune. 2007. When the brain plays music: auditory-motor interactions in music perception and production. *Nat. Rev. Neurosci.* 8: 547–558.
- Phillips-Silver, J. & L.J. Trainor. 2005. Feeling the beat in music: movement influences rhythm perception in infants. *Science* **308**: 1430.
- Senkowski D., M. Gomez-Ramirez, P. Lakatos, *et al.* 2007. Multisensory processing and oscillatory activity: analyzing non-linear electrophysiological measures in humans and simians. *Exp. Brain Res.* 177: 184–195.
- Fujioka, T. & B. Ross. 2008. Auditory processing indexed by stimulus-induced alpha desynchronization in children. *Int. J. Psychophysiol.* 68: 130–140.