

ANNALS OF THE NEW YORK ACADEMY OF SCIENCES

Issue: *The Neurosciences and Music IV: Learning and Memory***Introduction to *The Neurosciences and Music IV: Learning and Memory***

E. Altenmüller,¹ S.M. Demorest,² T. Fujjoka,³ A.R. Halpern,⁴ E.E. Hannon,⁵ P. Loui,⁶
 M. Majno,⁷ M.S. Oechslin,⁸ N. Osborne,⁹ K. Overy,⁹ C. Palmer,¹⁰ I. Peretz,¹¹
 P.Q. Pfordresher,¹² T. Särkämö,¹³ C.Y. Wan,¹⁴ and R.J. Zatorre¹⁵

¹Institute of Music Physiology and Musician's Medicine, Hannover University of Music, Drama and Media, Hannover, Germany. ²School of Music, University of Washington, Seattle, Washington. ³Rotman Research Institute, Baycrest, University of Toronto, Canada. ⁴Department of Psychology, Bucknell University, Lewisburg, Pennsylvania. ⁵Department of Psychology, University of Nevada, Las Vegas, Nevada. ⁶Beth Israel Deaconess Medical Center and Harvard Medical School, Boston, Massachusetts. ⁷Fondazine Pierfranco e Luisa Mariani, Milan, Italy. ⁸Geneva Neuroscience Center, University of Geneva, Geneva, Switzerland. ⁹Institute for Music in Human and Social Development, University of Edinburgh, Edinburgh, United Kingdom. ¹⁰Department of Psychology, McGill University, Montreal, Canada. ¹¹BRAMS, University of Montreal, Canada. ¹²Department of Psychology, University at Buffalo State University of New York, Buffalo, New York. ¹³Institute of Behavioral Sciences, University of Helsinki, Helsinki, Finland. ¹⁴Beth Israel Deaconess Medical Center and Harvard Medical School, Boston, Massachusetts. ¹⁵BRAMS, McGill University, Montreal, Canada

Address for correspondence: Katie Overy, Institute for Music in Human and Social Development (IMHSD), University of Edinburgh, Alison House, 12 Nicolson Square, Edinburgh EH8 9DF, United Kingdom. k.overy@ed.ac.uk

The conference entitled “The Neurosciences and Music-IV: Learning and Memory” was held at the University of Edinburgh from June 9–12, 2011, jointly hosted by the Mariani Foundation and the Institute for Music in Human and Social Development, and involving nearly 500 international delegates. Two opening workshops, three large and vibrant poster sessions, and nine invited symposia introduced a diverse range of recent research findings and discussed current research directions. Here, the proceedings are introduced by the workshop and symposia leaders on topics including working with children, rhythm perception, language processing, cultural learning, memory, musical imagery, neural plasticity, stroke rehabilitation, autism, and amusia. The rich diversity of the interdisciplinary research presented suggests that the future of music neuroscience looks both exciting and promising, and that important implications for music rehabilitation and therapy are being discovered.

Keywords: music; neuroscience; learning; memory; children

Introduction

Music neuroscience research has expanded beyond recognition in recent years, driven not only by increasingly advanced, available, and affordable brain imaging technology and analysis software, but also by a growing interest in musical behavior within the wider disciplines of neuroscience and psychology. The field is diversifying to such an extent that what used to be considered specialized topics can now be considered entire research areas, from specific aspects of music (such as rhythm or imagery) to focused population groups (such as infants or patients), to state-of-the-art techniques (such as EEG,

MEG, TMS, or MRI). Students are entering the field with both undergraduate and postgraduate training in music psychology and music neuroscience, something that could hardly have been imagined ten years ago. There is increasing scientific and public interest in how music neuroscience research can potentially inform, and be informed by, the disciplines of music therapy, music education, and music performance. The future of such research clearly captures the imagination and is not showing any signs of diminishing.

A substantial contributing factor to this successful expansion of the field of music neuroscience is, of course, the long-standing support of the Mariani

Foundation, a charity dedicated to child neurology. The Mariani Foundation's pioneering conferences have created unique opportunities for researchers in the field, attracting students and professors alike from around the globe. Beginning with The Biological Foundations of Music¹ in New York City in 2000, followed by The Neurosciences and Music² in Venice in 2002, The Biological Foundations of Music: From Perception to Performance³ in Leipzig in 2005, and The Neurosciences and Music III: Disorders and Plasticity⁴ in Montreal in 2008, these international conferences have become key events, providing an invaluable opportunity for meeting like-minded scientists, exchanging recent findings, and developing new collaborations. The contribution to the expansion of music neuroscience from some key individuals behind these conferences (Maria Majno, Luisa Lopez, and Giuliano Avanzini), along with the continued support of *Annals of the New York Academy of Sciences* in publishing the proceedings, has been hugely significant.

For the Neurosciences and Music-IV conference, hosted by the Institute for Music in Human and Social Development (IMHSD) at the University of Edinburgh in June 2011, the theme of learning and memory was selected as the central aspect of musical experience. Symposia and posters were invited under four key topics: infants and children, adults: musicians and nonmusicians, disability and aging, and therapy and rehabilitation. Professor Richard Morris gave an opening welcome to nearly 500 international delegates, and, according to tradition, this was followed by an afternoon of methods workshops, this year on the topic of working with children. The following three days included a keynote lecture from Professor Alan Baddeley, "Human Memory;" nine platform symposia; three large and vibrant poster sessions; and a range of concerts in some of Edinburgh's most beautiful university buildings. Here, we introduce the proceedings of *The Neurosciences and Music IV: Learning and Memory*, with each section of the volume introduced by the organizers.

Methods I: Working with children— experimental methods

Katie Overy

Working with children is essential in order to improve our understanding of the development of musical skills and the potential impact of early musi-

cal experiences. Learning and memory are crucial throughout life, but particularly during early development. Noninvasive imaging techniques have been both difficult and rare in research with infants and young children, but technological advances in functional magnetic resonance imaging (fMRI), electroencephalography (EEG), and magnetoencephalography (MEG) are making such research easier. The design of age-appropriate behavioral protocols and measures are also vital, from task and stimuli design to child-friendly environments and procedures to help discourage movement during imaging. This collection of papers outlines current experimental techniques for working with children, from preterm infants to kindergarten children, and includes head-turning techniques, behavioral protocols, fMRI, and EEG.

McMahon and Lahav⁵ begin with a specific discussion of the problematic noise environment of a neonatal intensive care unit (NICU), which has the potential to negatively affect preterm infant auditory development. After a detailed outline of the key milestones of auditory development *in utero*, the authors discuss the nature of auditory plasticity at critical periods, the potential impact of being deprived of maternal sounds after a premature birth, and evidence suggesting that noise exposure in the NICU can negatively influence the neurodevelopment of a child. A range of solutions is offered for reducing high noise levels and increasing exposure to natural sounds, such as offering "kangaroo care" and playing recordings of the mother's voice.

Trainor⁶ continues with an in-depth discussion of current EEG and MEG methods for research with infants and young children. The paper begins by explaining the source of EEG and MEG activity, how they are measured, and the specific advantages of these techniques when working with children. Trainor then describes some of the issues and complexities that can arise, from difficulties with short attention spans and physical movements, to the changing morphology of waveforms with age, to potential artifacts in the data and how to deal with these. A series of research examples are provided, which show how different data analysis techniques have been used to explore specific questions about musical development, such as the effects of exposure to different musical timbres or the development of beat perception.

Trehub⁷ presents a range of behavioral methods for working with infants, alongside key findings regarding infant music perception abilities. Trehub emphasizes that the expansion of neuroimaging technology should not replace good behavioral methods, which can offer important insights into how infants perceive and remember musical information. Trehub explains the advantages and disadvantages of different behavioral methods, regarding issues such as stimuli duration, trial numbers, and attrition rates. Infant attention is identified as the key factor that must be both attracted and observed in experimental procedures, and Trehub points to the benefits of ecologically valid stimuli such as infant-directed singing. In addition, Trehub suggests that ecologically valid infant responses are of potential importance, such as measuring rhythmic movements to music rather than looking behaviors. In conclusion, Trehub advises that future research in this area must use convergent measures and should yield conceptually as well as statistically significant findings.

Finally, Gaab and colleagues provide an extensive and invaluable survey of structural and fMRI techniques and protocols developed for infants and young children over the last 20 years.⁸ Some key challenges are outlined, such as participant anxiety, movement restrictions in the scanner environment, and the availability of child-appropriate equipment and pediatric brain templates. The authors go on to review a wide and detailed range of solutions to such challenges, from preparation sessions with a mock scanner to effective data-acquisition protocols. A strong emphasis is placed on the need for young children to be comfortable, familiar with the environment, and engaged in the tasks presented. The ethical implications of such research are also considered, including the fact that research findings with infants and children can potentially influence public policy, education, and family life.

Methods II: Working with children—social, “real world” methods

Maria Majno and Nigel Osborne

A commonly held view, in many differing world cultures and at many different times, is that the experience of music has both a significant effect on an individual’s mind, body, and relationships with other human beings, and plays a useful role in the social, “real world.” Whereas some societies have

had systems of belief that offer an accounting for this effect (e.g., the neo-Platonists in Europe,⁹ or theorists such as Ibn Sina in the early medieval Islamic world¹⁰), the world of contemporary science has, until recently, struggled somewhat to find convincing explanations and structures for reflection.

More recently, neuroscience has begun to make major contributions in terms of hard evidence and useful understanding—something particularly welcome to educationalists, music therapists, and others who seek to develop reflection on their methodologies and to argue the case for music’s social, real-world usefulness. What has certainly helped is that music is quite “neuroscience friendly.” It is a rich, whole-brain, whole-body information that is highly accountable. Music is communicated mostly, but not exclusively, through sound, which is a relatively slow mechanical energy that may be measured scrupulously in frequencies of pitch and rhythm, precisely to the microsecond in duration, and captured in Fourier transforms, spectrograms, fractals, and other representations of harmonicity, rhythmicity, and turbulence.¹¹ This highly accountable information is processed by the fastest-firing neural system of the brain,¹² while the mechanical energy of sound is perhaps the only energy a human being may “emit” in any consciously controlled, communicative way.

The valuable insights neuroscience offers to music, and music’s “friendliness” to neuroscience, point to important agendas for the future. It may be premature to speak of an “applied music neuroscience,” but it is clear that many areas of social, real-world musical activity exist in which neuroscience may inform practice and where practical experience may inform neuroscience.

In the opening paper,¹³ Majno discusses the psychosocial, and to some extent, political and economic significance of the “Sistema” initiative. The paper traces its progress from its origins in Venezuela, where ubiquitous centers provide irresistible musical opportunities to street children and others (including children with disabilities) as a structured alternative to the temptation of violence and crime, to the implementation of its methods in Italy and other European countries (e.g., the Raploch project in Scotland¹⁴), where community development and social organization have been primary objectives. Sistema is characterized by rigor, deep learning, high standards, joy, and the premise

that music education should become accessible to all at no cost. The psychosocial benefits in terms of social cohesion, sense of identity, and self-respect are predicated upon issues of sense of self, empathy, synchronization, emotional intelligence, memory, cognitive development, and motor skills, all close to the domain of music neuroscience.

Uibel describes the very focused whole-child, educational, and social approach of the Musikkindergarten Berlin,¹⁵ a project initiated by Daniel Barenboim and intended to use music not just as an “addon,” but rather as the central medium for day-to-day learning. The kindergarten provides an education *in* music, including a refreshing range of group creative and developmental activities, and *with* music, including, for example, familiar partners in drama and movement. But most radical is the work *through* music, where music leads interdisciplinary initiatives in areas such as topic-based learning, language development, and numeracy.

Overy¹⁶ raises the thorny issue of negative musical learning experiences and contrasts the human musicality of expert instrumental performance with the more ubiquitous nonexpert human musicality of group singing. Referring to the shared affective motion experience (SAME) model of emotional responses to music,^{17,18} which emphasizes motor and social aspects of musical behavior, Overy proposes that the essential and powerful nature of a musical experience lies not just in the sound, but also in the physical and human origins of the sound, creating a sense of shared experience. Referring to traditional music education methods, Overy suggests alternatives to instrumental training when investigating the nature and impact of musical learning.

Osborne considers the influence of developments in neuroscience on reflection on practice in the use of music to support children who are victims of conflict.¹⁹ This paper locates the work within an enhanced bio-psycho-social framework. Although the standard diagnostic instruments for PTSD (post-traumatic stress disorder) are concerned with issues such as traumatic events, traumatic recall, avoidance, and hypervigilance, there are significant physiological symptoms, such as raised heart rate, respiratory problems, hyperactive or sluggish movement repertoires, and the dysregulation of endocrine systems (including the hypothalamic–pituitary–adrenal axis) and neurotransmission. Osborne further traces a circle around the bio-psycho-

social framework to include aspects of communicative musicality, emotional communication, empathy, self-belief, creativity, and identity, relating each to emerging research in neuroscience. It is important for any music intervention to avoid inappropriate invasion of the physical and mental lives of traumatized children. But evidence from work in neuroscience and related disciplines with nontraumatized populations has been applied to support critical reflection on experimental methodologies seeking to use music to help regulate, for example, motor activity, the autonomic nervous system, and endocrine and respiratory systems.²⁰

Symposium 1: Mechanisms of rhythm and meter learning over the life span

Erin Hannon

Dancing and moving in time with music are universal capacities that constitute a crucial component of human musical experience. Growing evidence suggests that rhythm and beat perception rely on integration of information across multiple sensory modalities and a broad network of brain regions.^{21–23} A fundamental goal of research on rhythm and meter perception is to understand the conditions under which a beat or hierarchical metrical structure can be inferred from a given stimulus, the mechanisms underlying perception of a beat or meter, and the extent to which metrical perception depends on casual listening experience, formal music training, or simply emerges from the interaction between the brain and the stimulus itself. This symposium attempted to tackle these fundamental questions using various methodological approaches and technologies, and testing individuals of different ages and/or abilities.

McAuley²⁴ uses fMRI to examine neural correlates of beat perception. The study uses a sequence-timing paradigm that typically produces large individual differences in sensitivity to the implied beat; however, beat sensitivity declines as the stimulus is presented at slower and slower tempos. By comparing brain responses under conditions of high and low beat sensitivity, the study provides evidence for specific brain networks that are associated with beat- versus interval-based temporal processing. Honing²⁵ tackles the question of whether hierarchical metrical representations arise automatically in the brain or require extensive listening experience or formal music training. The paper

provides a tutorial on developing optimal rhythmic stimuli and tasks that may demonstrate hierarchical beat perception through EEG by measuring a mismatch-negativity (MMN) response to stimulus omissions. It reviews evidence from EEG studies with adults and newborn infants that suggest hierarchical beat perception may be possible with minimal prior experience or training. Hannon, der Nederlanden, and Tichko²⁶ also explore the role of experience in meter and beat perception. They use similarity judgments to examine how well American children and adults detect beat-disrupting changes to familiar (Western) simple-meter and foreign (Balkan) complex-meter folk songs before and after at-home exposure to foreign complex-meter music. The findings indicate that listening exposure dramatically changes how children under age 10 perform in the judgment task, with accuracy improving for complex meters but declining for simple meters. By contrast, adults and older children consistently perform more accurately in the simple- than in the complex-meter conditions, and this trend is virtually unchanged by at-home listening experience. This suggests that at least some of the metrical representations that contribute to beat perception undergo slow developmental change over the course of childhood and that listening experience can fine-tune these representations during early but not late childhood or adulthood.

Together, the three papers raise important questions about the nature of beat-based perception. On the one hand, rhythmic patterns appear to activate beat-based expectancies even in highly inexperienced newborn listeners.²⁵ On the other hand, these expectancies are obviously influenced by listening experience and presumably by the acquisition of culture-specific musical knowledge.²⁶ As research continues to illuminate our understanding of the neural underpinnings of beat-based processing,^{24,25} it may be possible to disentangle the various processes and mechanisms that contribute to our subjective experiences of beat and meter.

Symposium 2: Impact of musical expertise on cerebral language processing

Mathias S. Oechslin

In cognitive neuroscience, the question of whether musical expertise affects or facilitates language processing has been increasingly addressed. In this symposium, we introduced new studies that observe

the influence of musical expertise on various aspects of neural language processing—making use of several brain imaging and cognitive measurements, such as event-related brain potentials (ERP), fMRI, and behavioral performance data. This spectrum of methodological approaches characterized by both time and spatial sensitivity enables a deeper understanding of musicians' neural processing of fine-grained acoustic language properties. Together, the papers in this section provide insight into language processing, ranging from basic auditory segmental speech information to suprasegmental decoding mechanisms at word and sentence level.

Disclosing cortical plasticity by focusing on basal auditory functioning, previous studies have unveiled that musical expertise alters structure and functional mechanisms of various brain areas that are involved in processing of both speech and music.^{27–30} Therefore, it is reasonable to assume that neural encoding in the former domain could benefit from the expertise in the latter—even though percepts of speech and music are phenomenologically completely distinct.

Regarding basal auditory functioning, two recent studies^{31,32} have demonstrated preliminary but compelling evidence that musical training induced plasticity in segmental speech processing. Performing an auditory (phoneme discrimination) categorization task, musicians and nonmusicians were asked to identify voiced and unvoiced consonant–vowel (CV) syllables with either natural or broad-band noise acoustic spectra. The fMRI study revealed higher accuracy in identifying CV-syllables with manipulated spectra, flanked by a leftward hemispheric asymmetry and overall enhanced activation of the planum temporale in musicians compared to nonmusicians.³² Moreover, using the same experimental paradigm, electrophysiological data revealed that N1 amplitudes and corresponding topography were identical in voiced and unvoiced stimuli in musicians but not in nonmusicians. Accordingly, in their paper, Meyer *et al.* comprehensively discuss the role of the planum temporale for speech processing as a function of musical expertise.³³ Taken together, these results suggest that musical expertise leads to a honed auditory capacity in spectrotemporal analysis that goes far beyond the domain of music. In this context, Besson *et al.*³⁴ have argued that “enhanced sensitivity to acoustic features that are common to music and speech, and

that imply domain-general processes, allow musicians to construct more elaborated percepts of speech processing than nonmusicians. . . [and] facilitates stages of speech processing that are speech-specific.”

Moving on along this line to the processing of linguistic structures (word segmentation level), the influence or interaction of such sensory plasticity with expertise-dependent top-down modulations (see later) is not yet clear and should be observed in more detail. However, it has been demonstrated that the nature of implicit knowledge in music and language, in general,³⁵ and learning of linguistic structures and musical structures, in particular, are closely related:³⁶ by analyzing behavioral data of a statistical learning paradigm, performance in a linguistic test has been found to be positively correlated with performances in a musical test (based on concatenated results of Refs. 37 and 38). In the latter ERP study,³⁸ musicians and nonmusicians were initially presented with sequences of artificial (sung) language. Then participants were asked to make familiarity ratings of musical and speech sound pairs, indicating whether the first or the second item resembled the previously presented sung sequence. Most interestingly, Francois and Schön found enhanced N400 amplitudes in musicians compared to nonmusicians, elicited by both the linguistic and the music task, concluding for musicians an advantage in stream segmentation or in lexical storage or both. The authors of this paper provide valuable insight into technical details of statistical learning paradigms.³⁹

In a recent publication, Patel⁴⁰ systematically addressed the prerequisites of such possible transfer effects from musical training to neural encoding of speech. In what is formulated as the OPERA hypothesis, Patel concluded that overlapping brain networks processing shared acoustic features in speech and music are the ultimate essentials for possible transfer effects. Furthermore, to end up with a benefit in speech encoding, according to Patel, three additional conditions have to be fulfilled, including aspects of musical processing demands, training intensity, and emotional arousal. Here, Patel presents his most recent view featuring the fundamental aspects of different precision demands in music and speech processing.⁴¹ Originally, the OPERA hypothesis mainly referenced studies that observe musical training-induced subcortical plasticity driven by de-

scending auditory projections.⁴² By analyzing such brainstem responses, it has been revealed that musical expertise yields enhanced auditory frequency representation,⁴³ increased accuracy in encoding linguistic pitch patterns,⁴⁴ and facilitation of hearing speech in noise.⁴⁵ Moreover, the latter acuity is supported by cognitive mechanisms, such as enhanced tonal working memory⁴⁵ and auditory attention⁴⁶ in musicians compared to nonmusicians. Accordingly, topographical ERP analyses confirmed that prefrontal responses are considerably altered (lower prefrontal auditory response variability) as a function of musical expertise during a selective auditory attention task.⁴⁶ In other words, this result signifies advantages for musical experts in situations that require sustained auditory attention. In their paper, Kraus *et al.* specifically focus on musicians' auditory advantages and the mediating role of auditory working memory.⁴⁷ In fact, previous fMRI research found that attention driven top-down modulations facilitate basal auditory speech processing.⁴⁸ This framework lucidly implies that future research is needed to disentangle the potential influence of musical expertise on interactions among structural brain characteristics, cognitive functions, and the architecture of cerebral language processing.

This ensemble of studies that addresses the same topic from different directions is clearly indicative of the increasing relevance of research on transfer effects from music to language mechanisms at several levels of complexity.

Symposium 3: Cultural neuroscience of music

Steven M. Demorest

The goal of the study of the cognitive neuroscience of music is to explain how brain structure and function interact with and shape musical thought and behavior. Research in this area has been dominated by Western thought regarding the nature of music perception and performance, a bias that has the potential to limit the scope of our theories regarding music and brain function. The implicit learning of one's culture or enculturation seems to affect virtually every area of human thought, and the relatively new field of cultural neuroscience⁴⁹ is beginning to document the important influence of culture in shaping brain function. Given that music is one of the primary agents of cultural transmission, it stands to reason that certain aspects of musical thinking are

mediated by culture. This symposium explored current research in the cultural neuroscience of music and how findings in this field might clarify the role of culture in music development, cognition, and learning.

Previous research in infant music perception has identified that encultured responses to music emerge at around 12 months of age.⁵⁰ Here, Trainor *et al.* document how early musical experiences can hasten culturally biased responses in infants.⁵¹ In a series of experiments, they explored the effect of active participation in Kindermusik classes and other formal music exposures that influence infants' behavioral and brain responses to Western rhythm, timbre, and tonality. Vuust *et al.* also present data showing learning-based changes in brain responses, but in adult populations,⁵² they used an innovative MMN paradigm to differentiate the responses of performers from different genres of Western music to acoustic changes in a complex musical stimulus. Tervaniemi and her coworkers extend research on classical musicians' ERP responses to harmonic violations⁵³ to Finnish folk musicians,⁵⁴ whose responses reflect highly specialized sensitization to harmonic violations. Large and Almonte propose a new theory of tonality that seeks to uncover the basic neurodynamic principles that underlie tonal cognition and perception. They provide evidence that auditory neurons respond to tonal relationships in predictable ways and discuss the possibility of general neurodynamic principles that underlie all tonal cognition.⁵⁵

Demorest and Wong both explore how implicit learning of culture influences adults' neurological responses to music of different cultures using ERP and fMRI methodologies, respectively. The first paper explores crosscultural music cognition by tracking ERP responses to melodic expectancy violations in culturally familiar and unfamiliar music.⁵⁶ As in previous research,⁵⁷ Western listeners exhibited a P600 response to scale deviations in Western melodies. They exhibited a smaller P600 when hearing similar deviations in north Indian classical melodies, which may reflect a cultural general sensitivity to statistical properties of tonal sequences or possible areas of overlap between the two tonal systems under study. In the second paper, Wong *et al.* explore fMRI responses to affective judgments across two musical cultures and how they differ between monomusicals and bimusicals.⁵⁸ In addition

to confirming earlier findings of different behavioral responses,⁵⁹ they found significant group differences in the connectivity of a temporal–limbic network. This provides evidence of qualitatively different brain function as a result of exposure to two culturally distinct musical systems. The papers presented here touch on some of the central issues in cultural neuroscience, including the interaction of enculturation, formal training, and development.

Symposium 4: Memory and learning in music performance

Caroline Palmer and Peter Q. Pfordresher

The study of music performance has important implications for understanding basic mechanisms of memory and learning. In contrast to listeners, who acquire vast implicit knowledge resources accumulated during years of perceptual experience, individuals differ greatly in the explicit and implicit knowledge they have acquired for performance. These individual differences in performance knowledge leave open the possibility for studying the development of performance-specific learning and memory in cross-sectional and longitudinal contexts, with child and adult populations. In addition, music performance typically requires the execution of long, rapid sequences typically performed from memory, thus providing a rich context in which to study the development of sensorimotor learning, as performers learn to map auditory and visual feedback to specific actions. Finally, disorders that affect performers offer an excellent venue in which to study music's role in rehabilitation from sensory and motor disorders.

The first paper in this section, by Bailey and Penhune,⁶⁰ explores the acquisition of musical skills at different points in the life span to determine whether this is a “sensitive period” for musical skill acquisition. In keeping with the assumption of a sensitive period for musical development, adult musicians who began training early in life exhibited better synchronization ability than adult non-musicians or musicians who began training later in life. Music performance is fundamentally integrative, involving the online coordination of actions with the perception of feedback from those actions.

The next two papers consider the role of perceptual feedback in performance. Pfordresher addresses how musical training influences the role of

auditory feedback in nonmusicians.⁶¹ Contrary to a purely associationist view, nonmusicians do not approach the novel task of music performance as “blank slates” but instead build on preexisting sensorimotor associations, based on their broader experience of perception/action associations, that are refined through musical training. Zimmerman and Lahav’s review⁶² focuses on the neural underpinnings of multisensory associations that are enhanced by musical training. They argue that the multisensory processing that is enhanced by music listening and performance underlies the success that music-related therapy has had for rehabilitation.

The fourth paper, by Palmer *et al.*,⁶³ discusses the time course of retrieval failures and their sensorimotor consequences during performance. They report the results of an experiment in which pianists practiced and performed novel musical pieces at fast and slow tempi. Both pitch errors and the correctly produced events immediately prior to those errors were produced with lower intensities and reduced tempo from other correctly produced tones, consistent with the view that performers covertly monitor for production errors prior to response selection.

The final paper, by Felix Strübing and Maria Herrojo Ruiz,⁶⁴ examines how sensorimotor prediction is implemented in healthy and dystonic pianists by recording neural responses to errors using event-related potentials (ERPs). Results suggested degraded error processing among dystonic patients, even preceding error production. Together, these papers intersect with the developmental, skill acquisition, and rehabilitative themes of the other papers in this volume to elucidate the neural foundations of memory for musical experience.

Symposium 5: Mind and brain in musical imagery

Andrea R. Halpern and Robert J. Zatorre

Mental imagery refers to a type of memory representation that is rich in perceptual detail. For instance, when asked to describe one’s living room, most people can report the spatial layout, colors of the walls, and textures of the furniture. Auditory images also contain perceptual information. The reader is invited to imagine a piece of familiar music, perhaps “Happy Birthday.” Musicians and nonmusicians alike can report auditory characteristics of tunes, such as the pitch, rhythm, and tempo.⁶⁵ Thus

the experience can be quite vivid, sometimes so vivid that the auditory experience takes the form of a persistent repetitive memory, colloquially referred to as “earworms.”⁶⁶ In addition to vividness, in several meaningful ways auditory imagery for music can also be said to capture qualities of the actual piece and is thus a veridical representation. For instance, people are willing to set a metronome to the tempo of an imagined familiar tune, or indicate on a keyboard the starting pitch they habitually assign to the tune, which they will replicate reliably over multiple trials.^{67,68} People without absolute pitch abilities can fairly accurately report the opening pitch or key of familiar recorded music.^{69,70}

In addition to behavioral research, a number of studies have documented the similarity of neural mechanisms in imagery and perception. In a prior review,⁷¹ Zatorre and Halpern examined the substantial evidence that the secondary auditory cortex is active when people imagine music, again suggesting that we co-opt perceptual mechanisms when retrieving these vivid and veridical experiences. The review also noted that these experiences are not confusable, and that many studies find additional activation in the frontal cortex during imagery that is absent in perception, suggesting an important moderating influence of executive and memory functions on the auditory cortex.

This symposium at the conference examined new research in auditory imagery that extends earlier studies on basic aspects of auditory imagery. Among the four speakers, a number of methodological approaches were represented: behavioral studies, computer simulations, measurement of electrical activity from the brain surface (ERP), and measurement of relative blood oxygenation as a proxy for neural activity (fMRI). The variety of approaches reminds us of the importance of both “mind” and “brain” in our symposium title.

Three types of extensions to earlier work were evident among our speakers. First, several speakers presented tasks that required experimental participants to make rather fine distinctions during imagery tasks. This is perhaps most evident in Janata’s paper on the accuracy with which people can make in-tune and out-of-tune judgments in imagined tones.⁷² Halpern reports here on the ability to make moment-to-moment judgments on emotional aspects of imagined music using a continuous scale,⁷³ and Zatorre reports on neural correlates of subtle

key-distance effects during mental transformations of music.⁷⁴

Second, many of the studies discussed required fairly complex processing, particularly regarding the extent to which working memory was required for successful completion. As one example, Halpern reports a study in which people learned pairs of tunes and were required to anticipate the second pair member upon presentation of the first.⁷³ Keller reports studies of several aspects of musical performance that need to be maintained in parallel for successful execution.⁷⁵ Arguably, the most difficult study in the set, reported by Zatorre, was asking people to imagine tunes in reverse note order!⁷⁴ This imposes a very high working memory load and was reflected in extensive frontal and parietal activations.

Third, several speakers framed their tasks in the context of the adaptive usefulness of auditory imagery. The most obvious example of this was Keller's exploration of the role of auditory imagery in synchronization of movements among musical performers.⁷⁵ Janata also suggested that auditory imagery actually enhances the fine pitch judgments required in the tasks he presented, and Halpern noted that the ability to extract emotion from imagined music adds to the enjoyment of remembered experience.⁷³

Overall, the talks in the symposium showed that considerable progress has been made in extending the breadth and depth of knowledge about the quality and richness of the musical sounds we hear and manipulate in our minds, despite the essentially private nature of mental imagery.

Symposium 6: Music-induced adaptive and maladaptive brain plasticity in health and disease

Eckart Altenmüller

Emerging research over the last decade has shown that long-term music training and the associated sensorimotor skill learning can be a strong stimulant for neuroplastic changes both in the developing and adult brains, affecting both white and gray matter as well as cortical and subcortical brain structures.⁷⁶ Making music, including singing and dancing, leads to a strong coupling of perception and action mediated by sensory, motor, and multimodal brain regions and affects, either in a top-down or bottom-up fashion, important relay stations in the

brainstem and thalamus.⁷⁷ Furthermore, listening to music and making music provokes motions and emotions, increases between-subject communications and interactions, and is experienced as a joyous and rewarding activity through activity changes in the amygdala, ventral striatum, and other components of the limbic system.⁷⁸ Music is a powerful tool in rehabilitation, providing an alternative entry point into compromised neural circuits due to brain damage.⁷⁹ Music thus can remediate impaired neural processes or neural connections by engaging and linking brain regions with each other that might otherwise not be linked together. The pleasurable power of listening to favorite music can even reverse maladaptive changes in the auditory cortex, causing the torturing tinnitus percept.⁸⁰ On the other hand, music-induced brain plasticity has its dark sides. Prolonged practice, high workload, overuse, and extreme demands on sensorimotor skills in professional musicians may result in a degradation of exactly these fine motor abilities, a condition termed *musician's dystonia*.⁸¹

The aim of this symposium was to summarize the latest research concerning the powerful impact of music on brain plasticity in both directions—adaptive and maladaptive. In the first article, Schulze and Koelsch present a review of behavioral and neuroimaging findings on similarities and differences between verbal and tonal working memory in musicians and nonmusicians.⁸² They demonstrate the impact of musical training on verbal memory and its consequences for verbal learning in children and adolescents. Novel results are discussed that imply the existence of a tonal and a phonological loop in musicians, based on partly differing neural networks underlying verbal and tonal working memory. Finally, the authors propose that both verbal and tonal auditory working memory are based on the knowledge of how to produce the to-be-remembered sounds, and therefore sensorimotor representations are involved in the temporary maintenance of auditory information in working memory.

In the second article, Pantev presents a novel and promising method to reduce chronic tonal tinnitus.⁸³ There is evidence that maladaptive auditory cortex reorganization may contribute to the generation and maintenance of this torturing condition, which can be conceived as a permanent cortical memory trace. Because behavioral training

can modify cortical organization, an approach was chosen to expose chronic tinnitus patients to self-chosen, enjoyable music, which was manipulated to contain no energy in the frequency range of the individual tinnitus, thus promoting lateral inhibition to the brain area generating tinnitus and overwriting the dysfunctional cortical memory.

The third article, authored by Zipse *et al.* from the laboratory of Schlaug, presents an impressive case report on rehabilitation of an adolescent stroke patient suffering from Broca's aphasia.⁸⁴ Using a modified version of melodic intonation therapy (MIT), the behavioral improvements were accompanied by functional MRI changes, demonstrating that the right frontal lobe takes over language functions. This case study not only provides further evidence for the effectiveness of this rehabilitation strategy, but also indicates that intensive treatment can induce functional and structural changes in a right hemisphere frontotemporal network.

Jäncke presents in his article on the dynamic audio-motor system in pianists a pilot study based on the theoretical assumption that continuous closed-loop audio-motor control could be disadvantageous for pianists.⁸⁵ He argues that the functional relationship between the intracerebral electrical activations in the auditory and premotor cortex should be rhythmically decreased and increased. To test this hypothesis, activations and connectivity of the auditory and premotor cortices were estimated using a novel method to analyze EEG time series and their causal relationship, similar to the "dynamic causal modeling" approach used in fMRI. The analysis revealed a "causal relationship" from the auditory cortex to the premotor cortex, which was considerably stronger during piano playing and weaker during rest. Interestingly, this relationship varied rhythmically during the course of piano playing, thus delivering evidence that in professional pianists, the functional coupling between the auditory and premotor cortex is instable, highly dynamic, and extremely adaptive.

Finally, Altenmüller *et al.* focus on musician's dystonia as a syndrome of dysfunctional brain plasticity.⁸⁶ This condition is characterized by a loss of fine motor control of extensively practiced and highly skilled movement patterns in professional musicians. On a neurophysiological level, this phenomenon is due to fusion of sensorimotor receptive fields in the cerebral cortex and to a lack of

lateral inhibition to adjacent body parts. In their paper, the authors demonstrate that behavioral factors can trigger the manifestation of this disabling disorder. The interplay between genetic predisposition, psychological and behavioral factors, such as perfectionism, anxiety, and over-specialization, predominantly in classical reproductive musicians, is elucidated, and its important role in finally causing this neurological condition is convincingly demonstrated.

Symposium 7: The role of music in stroke rehabilitation—neural mechanisms and therapeutic techniques

Takako Fujioka and Teppo Särkämö

Neuroplasticity is a key mechanism underlying learning new skills and relearning lost skills during rehabilitation. Recent cognitive neuroscience research has shown that training in music making can enhance neural processing in sensory, motor, executive, and affective brain systems and facilitate interactions between those brain systems in healthy children and adults.^{87–90} This is likely due to the fact that the massed practice associated with music making requires enormous resources within each specific brain system as well as extensive coordination between the systems. Importantly, music making also involves social interaction and induces strong emotional experiences. Even simply listening to music can have a short-term positive effect on arousal, attention, memory, and mood.^{91–93}

The next question is how these findings can be incorporated and translated into the rehabilitation of the damaged brain. One of our strong allies in answering this question is the music therapy community, which has accumulated and practiced theories on how music can be used to help neurological, psychological, and functional recovery in various clinical populations, including stroke patients. Another guiding principle is the knowledge obtained from rehabilitation sciences that meaningful and relevant tasks and motivated participation in activities enhance rehabilitation outcomes in everyday life, compared to mere repetition of rote exercises. Thus, it seems that we have reached the crucial point at which each discipline can help inform the others in ascertaining how music can be used for improving the lives of patients.

How can music-related activities fit into rehabilitation? Within the framework of the International Classification of Functioning, Disability and Health (ICF) of the World Health Organization (WHO),⁹⁴ we propose that music making and/or music listening activities can be understood as an activity that influences a stroke patient's environment, which in turn interacts with behavioral activity and participation, as well at the level of brain function. For example, a music-making exercise demands not only sensorimotor but also auditory memory functions incorporated with motor planning and execution. Increasing complexity and challenge can easily be built into musical exercises, such that they are in line with the principles of effective motor learning. Also, the goal-oriented approach of music making resonates with the importance of meaningful tasks in rehabilitation. Compared with many traditional motor and cognitive rehabilitation methods, music-based activities have the advantage of being intrinsically motivating and fun as well as providing direct and natural feedback, which can be crucial for engaging patients in their rehabilitation process. At the same time, engagement in music making can become an important emotional event, often providing solace and comfort and relieving stress and anxiety, and can therefore have an important additional positive impact on quality of life.

In this section, we synthesize recent studies of musical interventions for stroke survivors. The interventions are based on existing evidence regarding underlying brain mechanisms, and outcome measures are demonstrated as functional changes at the level of behavior and the brain. These give us important insights into how the human brain in both the healthy and damaged state processes music, with its multimodal interactions. In the first article,⁹⁵ Särkämö and Soto review current evidence of the effects of music listening on emotion, cognition, and the brain; present two bodies of experimental studies showing that listening to pleasant music after a stroke can temporarily enhance visual awareness in patients suffering from unilateral spatial neglect as well as improve the recovery of memory, attention, and mood; and discuss the potential neural mechanisms underlying the rehabilitative effect of music listening. In the second article,⁹⁶ Rodríguez-Fornells, Rojo, Amengual, Ripolles, Altenmüller, and Münte review the literature concerning the

application of music-supported therapy (MST) (a new motor rehabilitation method that uses musical instruments) and present experimental results indicating that MST is effective for improving the recovery of motor skills and mood after a stroke, with a direct impact on the activity and functional connectivity of the frontotemporal auditory–motor networks. MST is also discussed in the third article⁹⁷ by Fujioka, Ween, Jamali, Stuss, and Ross, which demonstrates, using MEG, that listening and tapping to a beat are both associated with the periodic modulation of beta oscillations in the brain that are typically linked to motor functions, and that MST can induce changes in the contribution of auditory and motor brain areas to the beta activity after chronic stroke. Their data also give some insight into how rhythmic auditory stimulation (RAS) using music or metronome sounds may successfully enhance rehabilitation exercises through activating the sensorimotor beta-band network.^{98,99}

In the fourth article,¹⁰⁰ van Wijck *et al.* introduce the rationale and methodological basis of a novel, innovative motor intervention for stroke patients, which integrates the patient's preferred music with game technology in a rhythmic auditory cueing task for training upper limb function. Finally, Tomaino¹⁰¹ describes various singing-related techniques used in clinical music therapy to enhance speech ability in nonfluent aphasic patients. Although MIT has been known as an effective singing exercise,^{84,102} the paper documents how diverse the symptoms of aphasic patients can be and how emphasizing different musical features and social/motor cues in the practice can help with treating them differently.

In summary, this section highlights recent advances in the field of music therapy for stroke and provides steps toward integrating musical activities into the neurological rehabilitation of stroke patients and toward understanding how music can work in the damaged brain. Although the findings are encouraging, the field is still new, and more research is clearly needed for building a solid evidence base through randomized control trials that compare musical interventions against adequate control interventions. Through this synthesis, our hope is to inspire and stimulate future research directions with joint efforts among neuroscientists, therapists, psychologists, and engineers.

Symposium 8: Autism and music

Catherine Y. Wan

Autism spectrum disorder (ASD) is a developmental condition that affects one in 110 children, and as many as one in 70 boys.¹⁰³ In addition to social abnormalities and the presence of repetitive and stereotyped behaviors, one of the core diagnostic features of ASD is impairment of language and communication.¹⁰⁴ Severe deficits in communication not only diminish quality of life for affected individuals but also present a lifelong challenge for their families.

Despite their social and communication deficits, children with ASD can enjoy auditory–motor activities, such as making music, through singing or playing an instrument. In addition, such children often display enhanced music and auditory-perception abilities.¹⁰⁵ In the first published report of autism, Kanner¹⁰⁶ described the exceptional musical skills of several children, including one notable example of an 18-month-old boy who was able to discriminate among many symphonic pieces of music. Recent investigations have provided further evidence for enhanced music-perception abilities in individuals with ASD. Often described as emotionally unreachable or in their own world, these individuals are nevertheless often able to express typical affective responses to music and to derive enjoyment from music.

The paper entitled “Music: a unique window into the world of autism” presents recent advances in research examining neurobiological underpinnings of musical processing in ASD and the therapeutic potential of music making in ameliorating some of the associated deficits. Molnar-Szakacs and Heaton summarize research on the dissociation between emotional communication abilities in the musical and social domains in individuals with ASD.¹⁰⁷ Although individuals with ASD are often impaired in their ability to understand nonverbal expression of emotions, they can nevertheless understand simple and complex musical emotions.¹⁷ Potential explanations for such uneven development across functional domains, as well as future directions for the study of music in autism, are discussed.

Hyde and colleagues review the behavioral and neuroimaging literature on auditory pitch and time processing in ASD.¹⁰⁸ Individuals with ASD generally show enhanced perceptual skills in a musical context but not in a linguistic context. These

observations may be related to the locally oriented or highly focused behaviors that are common in ASD.¹⁰⁹ Identifying the brain–behavior relationships of auditory processing in ASD may help to identify neurobiological markers and enhanced treatment potential in ASD.

Wan *et al.* present diffusion tensor imaging data collected from a group of completely nonverbal children with ASD.¹¹⁰ Abnormalities in a language-related white matter tract, the arcuate fasciculus, were investigated. This tract connects auditory and motor brain regions and is important in the mapping of sounds to articulatory actions during speech. The preliminary imaging findings reported here may explain why children with ASD fail to develop speech naturally. Furthermore, the findings complement the laboratory’s ongoing treatment study of a novel intonation-based intervention (auditory–motor mapping training, AMMT), which aims to facilitate speech output in nonverbal children with ASD.¹¹¹ It is suggested that interventions that are designed to engage abnormal auditory–motor connections (such as AMMT) have the potential to effectively facilitate the development of expressive language skills.

Taken together, the three papers on music and autism review current knowledge in this emerging field, which will hopefully stimulate further research and the development of interventions for a disorder that affects the lives of a great many individuals.

Symposium 9: Learning and memory in musical disorders

Psyche Loui and Isabelle Peretz

Although music is ubiquitous across human cultures, a subset of the normal population appears to have an abnormal lack of musical ability. Increasing evidence from behavioral, neuroimaging, and genetic studies has documented difficulties in pitch perception as well as production, also known as congenital amusia or tone deafness.^{112,113} Although these substantial deviations from the musical norm are fascinating to the general public, they can also be informative as a window into the psychological and neural capacities necessary for musical functioning. Furthermore, they can provide us with a model system through which to investigate capacities that, like music, might be uniquely human, such as speech and language, expectation for future events, and consciousness.

Given that musical disorders may have important implications for a broader scientific community, there is a need to have a solid understanding of their underlying cognitive processes and mechanisms. How do musical disorders inform our model of the human capacity for music? To date, tested theories of the causes of musical disorders include difficulties in fine-grained pitch discrimination,¹¹⁴ spatial processing¹¹⁵ (see also Ref. 116), pitch awareness,¹¹⁷ disconnection of neural pathways,¹¹⁸ and short-term memory limitations in pitch.¹¹⁹ Despite these theories, we know relatively little about how cognitive constraints might limit musical performance. In particular, limitations on memory are only recently becoming addressed as possible explanations for musical disorders. Given that persons with congenital amusia have pitch-specific limitations on their short-term memory resources that are independent of perceptual difficulties,¹²⁰ it remains to be seen whether and to what extent these memory limitations could give rise to learning difficulties. If learning is indeed affected in people with musical disorders, then to characterize these learning deficits, and possibly to design rehabilitation strategies, we need to know about the types of information learning that are affected: whether these learning difficulties are circumscribed to music, and whether related modalities such as language learning might be affected as well.

The last section in this volume aims to address precisely these questions concerning the cognitive underpinnings of musical disorders. The section begins by exploring memory limitations in persons with congenital amusia, a topic introduced by Dalla Bella *et al.*, who outline a model of vocal production and its impairment in amusia and suggest that memory can be a source of disorders in musical production.¹²¹ Stewart, in collaboration with Susan Anderson *et al.*, describe and present preliminary results from a musical intervention with five individuals diagnosed with congenital amusia.¹²² Loui explores further the notion of learning in musical disabilities by reporting a novel investigation of rapid statistical learning abilities and its disruption in tone-deaf individuals.¹²³ This statistical learning approach is followed up in the last chapter by Peretz *et al.*, who report five novel experiments showing that persons with amusia can learn novel words as easily as controls, whereas they systematically fail on musical materials.¹²⁴

Taken together, the aim of this section is to provide a comprehensive review of musical disorders, bring novel results to light regarding learning and memory and their interactions in normal and disordered brains, and ultimately to offer new perspectives toward the fundamental questions regarding neuroplasticity and the domain generality versus domain specificity of music.

Conclusion

It is evident from this introduction that the field of music neuroscience is rich and varied in ideas, approaches, implications, and potential applications. Much of the work is interdisciplinary in nature, including strong links with psychology, neurology, and clinical practice, and growing links with music performance, education, and therapy. Although the papers included here certainly reflect the current state of the art, it must also be emphasized that they represent only a small fraction of ongoing research internationally and only hint at the research being planned and prepared. The future of our understanding of the underlying neurobiology of human musical ability and behavior looks healthy, exciting, and promising, from the first milliseconds of auditory perception in infants to long-term training, individual musical preferences, and cultural diversity. We look forward with anticipation to *The Neurosciences and Music V*, planned for France in 2014.

Conflicts of interest

The authors declare no conflicts of interest.

References

1. Zatorre, R.J. & I. Peretz, Eds. 2001. The Biological Foundations of Music. *Ann. N.Y. Acad. Sci.* **930**.
2. Avanzini, G., C. Faienza, M. Majno & D. Miniacchi, Eds. 2003. The Neurosciences and Music. *Ann. N.Y. Acad. Sci.* **999**.
3. Avanzini, G., L. Lopez, S. Koelsch & M. Majno, Eds. 2006. The Neurosciences and Music II: From Perception to Performance. *Ann. N.Y. Acad. Sci.* **1060**.
4. Dalla Bella, S., N. Kraus, K. Overy, *et al.*, Eds. 2009. The Neurosciences and Music III: Disorders and Plasticity. *Ann. N.Y. Acad. Sci.* **1169**.
5. McMahon, E., P. Wintermark & A. Lahav. 2012. Auditory brain development in premature infants: the importance of early experience. *Ann. N.Y. Acad. Sci.* **1252**: 17–24. This volume.
6. Trehub, S.E. 2012. Behavioral methods in infancy: pitfalls of single measures. *Ann. N.Y. Acad. Sci.* **1252**: 37–42. This volume.

7. Trainor, L.J. 2012. Musical experience, plasticity, and maturation: issues in measuring developmental change using EEG and MEG. *Ann. N.Y. Acad. Sci.* **1252**: 25–36. This volume.
8. Raschle, N., J. Zuk, S. Ortiz-Mantilla, *et al.* 2012. Pediatric neuroimaging in early childhood and infancy: challenges and practical guidelines. *Ann. N.Y. Acad. Sci.* **1252**: 43–50. This volume.
9. Marenbon, J.A., Ed. 2003. *Boethius*. Oxford University Press. New York.
10. Shehadi, F. 1995. *Philosophies of Music in Medieval Islam*. Brill. Leiden, The Netherlands.
11. Katznelson, Y. 2004. *An Introduction to Harmonic Analysis*. Cambridge University Press. Cambridge, UK.
12. Bear, M.F., B.W. Connors & M.A. Paradiso. 2006. *Neuroscience: Exploring the Brain*. 3rd ed. Lippincott. Philadelphia.
13. Majno, M. 2012. From the model of *El Sistema* in Venezuela to current applications: learning and integration through collective music education. *Ann. N.Y. Acad. Sci.* **1252**: 56–64. This volume.
14. The Scottish Government. 2011. *Evaluation of the Big Noise, Sistema Scotland*. Scottish Government Social Research. ISBN 978-1-78045-099-5.
15. Uibel, S. 2012. Education through music—the model of the Musikkindergarten Berlin. *Ann. N.Y. Acad. Sci.* **1252**: 51–55. This volume.
16. Overy, K. 2012. Making music in a group: synchronization and shared experience. *Ann. N.Y. Acad. Sci.* **1252**: 65–68. This volume.
17. Molnar-Szakacs, I. & K. Overy. 2006. Music and mirror neurons: from motion to ‘e’motion. *Soc. Cogn. Affect. Neurosci.* **1**: 235–241.
18. Overy, K. & I. Molnar-Szakacs. 2009. Being together in time: musical experience and the mirror neuron system. *Music Percep.* **26**: 489–503.
19. Osborne, N. 2012. Neuroscience and “real world” practice: music as a therapeutic resource for children in zones of conflict. *Ann. N.Y. Acad. Sci.* **1252**: 69–76. This volume.
20. Osborne, N. 2009. Music for children in zones of conflict and post-conflict: a psychological approach. In *Communicative Musicality*. S. Malloch & C. Trevarthen, Eds.: 331–356. Oxford University Press. Oxford, UK.
21. Sakai, K., O. Hikosaka, S. Miyauchi, *et al.* 1999. Neural representation of a rhythm depends on its interval ratio. *J. Neurosci.* **19**: 10074–10081.
22. Grahn, J.A. & M. Brett. 2007. Rhythm and beat perception in motor areas of the brain. *J. Cogn. Neurosci.* **19**: 893–906.
23. Penhune, V.B., R.J. Zatorre & A.C. Evans. 1998. Cerebellar contributions to motor timing: a PET study of auditory and visual rhythm discrimination. *J. Cogn. Neurosci.* **10**: 752–765.
24. McAuley, J.D., M.J. Henry & J. Tkach. 2012. Tempo mediates the involvement of motor areas in beat perception. *Ann. N.Y. Acad. Sci.* **1252**: 77–84. This volume.
25. Honing, H. 2012. Without it no music: beat induction as a fundamental musical trait. *Ann. N.Y. Acad. Sci.* **1252**: 85–91. This volume.
26. Hannon, E.E., C.M.V.B. der Nederlanden & P. Tichko. 2012. Effects of perceptual experience on children’s and adults’ perception of unfamiliar rhythms. *Ann. N.Y. Acad. Sci.* **1252**: 92–99. This volume.
27. Oechslin, M.S., M. Meyer & L. Jäncke. 2010. Absolute pitch—functional evidence of speech-relevant auditory acuity. *Cereb. Cortex* **20**: 447–455.
28. Schlaug, G. *et al.* 1995. In vivo evidence of structural brain asymmetry in musicians. *Science* **267**: 699–701.
29. Schön, D. *et al.* 2010. Similar cerebral networks in language, music and song perception. *NeuroImage* **51**: 450–461.
30. Schneider, P. *et al.* 2002. Morphology of Heschl’s gyrus reflects enhanced activation in the auditory cortex of musicians. *Nat. Neurosci.* **5**: 688–694.
31. Ott, C.G. *et al.* 2011. Processing of voiced and unvoiced acoustic stimuli in musicians. *Front. Psychol.* **2**: 195.
32. Elmer, S., M. Meyer & L. Jäncke. 2012. Neurofunctional and behavioral correlates of phonetic and temporal categorization in musically trained and untrained subjects. *Cereb. Cortex* **22**: 650–658.
33. Meyer, M., S. Elmer & L. Jäncke. 2012. Musical expertise induces neuroplasticity of the planum temporale. *Ann. N.Y. Acad. Sci.* **1252**: 116–123. This volume.
34. Besson, M., J. Chobert & C. Marie. 2011. Transfer of training between music and speech: common processing, attention, and memory. *Front. Psychol.* **2**: 94.
35. Ettliger, M., E.H. Margulis & P.C. Wong. 2011. Implicit memory in music and language. *Front. Psychol.* **2**: 211.
36. Schön, D. & C. Francois. 2011. Musical expertise and statistical learning of musical and linguistic structures. *Front. Psychol.* **2**: 167.
37. Francois, C. & D. Schon. 2010. Learning of musical and linguistic structures: comparing event-related potentials and behavior. *NeuroReport* **21**: 928–932.
38. Francois, C. & D. Schon. 2011. Musical expertise boosts implicit learning of both musical and linguistic structures. *Cereb. Cortex* **21**: 2357–2365.
39. François, C., B. Tillmann & D. Schön. 2012. Cognitive and methodological considerations on the effects of musical expertise on speech segmentation. *Ann. N.Y. Acad. Sci.* **1252**: 108–115. This volume.
40. Patel, A.D. 2011. Why would musical training benefit the neural encoding of speech? The OPERA hypothesis. *Front. Psychol.* **2**: 142.
41. Patel, A.D. 2012. The OPERA hypothesis: assumptions and clarifications. *Ann. N.Y. Acad. Sci.* **1252**: 124–128. This volume.
42. Kraus, N. & B. Chandrasekaran. 2010. Music training for the development of auditory skills. *Nat. Rev. Neurosci.* **11**: 599–605.
43. Musacchia, G. *et al.* 2007. Musicians have enhanced subcortical auditory and audiovisual processing of speech and music. *Proc. Natl. Acad. Sci. USA* **104**: 15894–15898.
44. Wong, P.C. *et al.* 2007. Musical experience shapes human brainstem encoding of linguistic pitch patterns. *Nat. Neurosci.* **10**: 420–422.
45. Parbery-Clark, A. *et al.* 2011. Musical experience and the aging auditory system: implications for cognitive abilities and hearing speech in noise. *PLoS ONE* **6**: e18082.
46. Strait, D.L. & N. Kraus. 2011. Can you hear me now? Musical training shapes functional brain networks for selective auditory attention and hearing speech in noise. *Front. Psychol.* **2**: 113.

47. Kraus, N., D.L. Strait & A. Parbery-Clark. 2012. Cognitive factors shape brain networks for auditory skills: spotlight on auditory working memory. *Ann. N.Y. Acad. Sci.* **1252**: 100–107. This volume.
48. Jäncke, L., S. Mirzazade & N.J. Shah. 1999. Attention modulates activity in the primary and the secondary auditory cortex: a functional magnetic resonance imaging study in human subjects. *Neurosci. Lett.* **266**: 125–128.
49. Chiao, J. & N. Ambady. 2007. Cultural neuroscience: parsing universality and diversity across levels of analysis. In *Handbook of Cultural Psychology*. S. Kitayama & D. Cohen, Eds.: 237–254. Guilford, New York.
50. Hannon, E.E. & S.E. Trehub. 2005. Metrical categories in infancy and adulthood. *Psychol. Sci.* **16**: 48–55.
51. Trainor, L.J., C. Marie, D. Gerry, *et al.* 2012. Becoming musically enculturated: effects of music classes for infants on brain and behavior. *Ann. N.Y. Acad. Sci.* **1252**: 129–138. This volume.
52. Vuust, P., E. Brattico, M. Seppänen, *et al.* 2012. Practiced musical style shapes auditory skills. *Ann. N.Y. Acad. Sci.* **1252**: 139–146. This volume.
53. Koelsch, S., B.-H. Schmidt & J. Kansok. 2002. Effects of musical expertise on the early right anterior negativity: an event-related brain potential study. *Psychophysiology* **39**: 657–663.
54. Tervaniemi, M., T. Tupala & E. Brattico. 2012. Expertise in folk music alters the brain processing of Western harmony. *Ann. N.Y. Acad. Sci.* **1252**: 147–151. This volume.
55. Large, E.W. & F.V. Almonte. 2012. Neurodynamics, tonality, and the auditory brainstem response. *Ann. N.Y. Acad. Sci.* Online only. In press.
56. Demorest, S.M. & L. Osterhout. 2012. ERP responses to cross-cultural melodic expectancy violations. *Ann. N.Y. Acad. Sci.* **1252**: 152–157. This volume.
57. Brattico E., M. Tervaniemi, R. Näätänen & I. Peretz. 2006. Musical scale properties are automatically processed in the human auditory cortex. *Brain Res.* **1117**: 162–174.
58. Wong, P.C.M., A.H.D. Chan & E.H. Margulis. 2012. Effects of mono- and bicultural experiences on auditory perception. *Ann. N.Y. Acad. Sci.* **1252**: 158–162. This volume.
59. Wong, P.C.M., A.K. Roy & E.H. Margulis. 2009. Bimusicalism: the implicit dual enculturation of cognitive and affective systems. *Music Percept.* **27**: 81–88.
60. Bailey, J.A. & V.B. Penhune. 2012. A sensitive period for musical training: contributions of age of onset and cognitive abilities. *Ann. N.Y. Acad. Sci.* **1252**: 163–170. This volume.
61. Pfordresher, P.Q. 2012. Musical training and the role of auditory feedback during performance. *Ann. N.Y. Acad. Sci.* **1252**: 171–178. This volume.
62. Zimmerman, E. & A. Lahav. 2012. The multisensory brain and its ability to learn music. *Ann. N.Y. Acad. Sci.* **1252**: 179–184. This volume.
63. Palmer, C., B. Mathias & M. Anderson. 2012. Sensorimotor mechanisms in music performance: actions that go partially wrong. *Ann. N.Y. Acad. Sci.* **1252**: 185–191. This volume.
64. Strübing, F., M. Herrojo Ruiz, H.C. Jabusch & E. Altenmüller. 2012. Error monitoring is altered in musician's dystonia: evidence from ERP-based studies. *Ann. N.Y. Acad. Sci.* **1252**: 192–199. This volume.
65. Hubbard, T.L. 2010. Auditory imagery: empirical findings. *Psychol. Bull.* **136**: 302–329.
66. Halpern, A.R. & J.C. Bartlett. 2010. Memory for melodies. In *Music Perception*. M.R. Jones, A.N. Popper & R.R. Fay, Eds. Springer-Verlag, New York.
67. Halpern, A.R. 1989. Memory for the absolute pitch of familiar songs. *Mem. Cogn.* **17**: 572–581.
68. Halpern, A.R. 1988. Perceived and imagined tempos of familiar songs. *Music Percept.* **6**: 193–202.
69. Levitin, D.J. 1994. Absolute memory for musical pitch: evidence from the production of learned melodies. *Percept. Psychophys.* **56**: 414–423.
70. Schellenberg, E.G. & S.E. Trehub. 2003. Good pitch memory is widespread. *Psychol. Sci.* **22**: 262–266.
71. Zatorre, R.J. & A.R. Halpern. 2005. Mental concerts: musical imagery and auditory cortex. *Neuron* **47**: 9–12.
72. Janata, P. 2012. Acuity of mental representations of pitch. *Ann. N.Y. Acad. Sci.* **1252**: 214–221. This volume.
73. Halpern, A.R. 2012. Dynamic aspects of musical imagery. *Ann. N.Y. Acad. Sci.* **1252**: 200–205. This volume.
74. Zatorre, R.J. 2012. Beyond auditory cortex: working with musical thoughts. *Ann. N.Y. Acad. Sci.* **1252**: 222–228. This volume.
75. Keller, P.E. 2012. Mental imagery in music performance: underlying mechanisms and potential benefits. *Ann. N.Y. Acad. Sci.* **1252**: 206–213. This volume.
76. Münte, T.F., E. Altenmüller & L. Jäncke. 2002. The musician's brain as a model of neuroplasticity. *Nat. Rev. Neurosci.* **3**: 473–478.
77. Wan, C.Y. & G. Schlaug. 2010. Music making as a tool for promoting brain plasticity across the life span. *Neuroscientist* **16**: 566–577.
78. Blood A.J. & R.J. Zatorre. 2001. Intensely pleasurable responses to music correlate with activity in brain regions implicated in reward and emotion. *Proc. Natl. Acad. Sci. USA* **98**: 11818–11823.
79. Altenmüller, E., J. Marco-Pallares, T.F. Münte & S. Schneider. 2009. Neural reorganization underlies improvement in stroke-induced motor dysfunction by music-supported therapy. *Ann. N.Y. Acad. Sci.* **1169**: 395–405.
80. Okamoto, H., H. Stracke, W. Stoll & C. Pantev. 2010. Listening to tailor-made notched music reduces tinnitus loudness and tinnitus-related auditory cortex activity. *Proc. Natl. Acad. Sci. USA* **107**: 1207–1210.
81. Altenmüller, E. & H.C. Jabusch. 2010. Focal dystonia in musicians: phenomenology, pathophysiology and triggering factors. *Eur. J. Neurol.* **17**(Suppl 1): 31–66.
82. Schulze, K. & S. Koelsch. 2012. Working memory for speech and music. *Ann. N.Y. Acad. Sci.* **1252**: 229–236. This volume.
83. Pantev, C., H. Okamoto & H. Teismann. 2012. Tinnitus: the dark side of the auditory cortex plasticity. *Ann. N.Y. Acad. Sci.* **1252**: 253–258. This volume.
84. Zipse, L., A. Norton, S. Marchina & G. Schlaug. 2012. When right is all that is left: plasticity of right-hemisphere tracts in a young aphasic patient. *Ann. N.Y. Acad. Sci.* **1252**: 237–245. This volume.
85. Jäncke, L. 2012. The dynamic audio-motor system in pianists. *Ann. N.Y. Acad. Sci.* **1252**: 246–252. This volume.
86. Altenmüller, E., V. Baur, A. Hofmann, *et al.* 2012. Musician's cramp as manifestation of maladaptive brain plasticity: arguments from instrumental differences. *Ann. N.Y. Acad. Sci.* **1252**: 259–265. This volume.

87. Jäncke, L. 2009. The plastic human brain. *Restor. Neurol. Neurosci.* **27**: 521–538.
88. Hannon, E.E. & L.J. Trainor. 2007. Music acquisition: effects of enculturation and formal training on development. *Trends Cogn. Sci.* **11**: 466–472.
89. Ruiz, M.H., H.C. Jabusch & E. Altenmüller. 2009. Detecting wrong notes in advance: neuronal correlates of error monitoring in pianists. *Cereb. Cortex* **19**: 2625–2639.
90. Thompson, W.F., E.G. Schellenberg & G. Husain. 2004. Decoding speech prosody: do music lessons help? *Emotion* **4**: 46–64.
91. Thompson, W.F., E.G. Schellenberg & G. Husain. 2001. Arousal, mood, and the Mozart effect. *Psychol. Sci.* **12**: 248–251.
92. Schellenberg, E.G., T. Nakata, P.G. Hunter, *et al.* 2007. Exposure to music and cognitive performance: tests of children and adults. *Psychol. Music* **35**: 5–19.
93. Greene, C.M., P. Bahri & D. Soto. 2010. Interplay between affect and arousal in recognition memory. *PLoS ONE* **5**: e11739.
94. World Health Organization (WHO). 2001. International Classification of Functioning, Disability and Health (ICF). URL <http://www.who.int/classification/icf/en/> [accessed on 8 November 2011].
95. Särkämö, T. & D. Soto. 2012. Music listening after stroke: beneficial effects and potential neural mechanisms. *Ann. N.Y. Acad. Sci.* **1252**: 266–281. This volume.
96. Rodriguez-Fornells, A. *et al.* 2012. The involvement of audio–motor coupling in the music-supported therapy applied to stroke patients. *Ann. N.Y. Acad. Sci.* **1252**: 282–293. This volume.
97. Fujioka, T. *et al.* 2012. Changes in neuromagnetic beta-band oscillation after music-supported stroke rehabilitation. *Ann. N.Y. Acad. Sci.* **1252**: 294–304. This volume.
98. Thaut, M.H., G.P. Kenyon, C.P. Hurt, *et al.* 2002. Kinematic optimization of spatiotemporal patterns in paretic arm training with stroke patients. *Neuropsychologia* **40**: 1073–1081.
99. Thaut, M.H., A.K. Leins, R.R. Rice, *et al.* 2007. Rhythmic auditory stimulation improves gait more than NDT/Bobath training in near-ambulatory patients early poststroke: a single-blind, randomized trial. *Neurorehabil. Neural Repair* **21**: 455–459.
100. van Wijck, F. *et al.* 2012. Making music after stroke: using musical activities to enhance arm function. *Ann. N.Y. Acad. Sci.* **1252**: 305–311. This volume.
101. Tomaino, C.M. 2012. Effective music therapy techniques in the treatment of nonfluent aphasia. *Ann. N.Y. Acad. Sci.* **1252**: 312–317. This volume.
102. Sparks, R., N. Helm & M. Albert. 1974. Aphasia rehabilitation resulting from melodic intonation therapy. *Cortex* **10**: 303–316.
103. Autism Speaks. URL www.autismspeaks.org [accessed on 8 March 2012].
104. Tager-Flusberg, H. 2003. Language impairments in children with complex neurodevelopmental disorders: the case of autism. In *Language Competence across Populations: Toward a Definition of Specific Language Impairment*. Y. Levy & J.C. Schaeffer, Eds.: 297–321. Lawrence Erlbaum Associates, Mahway, NJ.
105. Heaton, P., L. Pring & B. Hermelin. 2001. Musical processing in high functioning children with autism. *Ann. N.Y. Acad. Sci.* **930**: 443–444.
106. Kanner, L. 1968. Autistic disturbances of affective contact. *Acta Paedopsychiatr.* **35**: 100–136.
107. Molnar-Szakacs, I. & P. Heaton. 2012. Music: a unique window into the world of autism. *Ann. N.Y. Acad. Sci.* **1252**: 318–324. This volume.
108. Ouimet, T., N.E.V. Foster, A. Tryfon & K.L. Hyde. 2012. Auditory-musical pitch processing in autism spectrum disorders: a review of behavioral and brain imaging studies. *Ann. N.Y. Acad. Sci.* **1252**: 325–331. This volume.
109. Samson, F., K.L. Hyde, A. Bertone, *et al.* 2011. Atypical processing of auditory temporal complexity in autistics. *Neuropsychologia* **49**: 546–555.
110. Wan, C.Y., S. Marchina, A. Norton & G. Schlaug. 2012. Atypical hemispheric asymmetry in the arcuate fasciculus of completely nonverbal children with autism. *Ann. N.Y. Acad. Sci.* **1252**: 332–337. This volume.
111. Wan, C.Y., L. Bazen, R. Baars, *et al.* 2011. Auditory-motor mapping training as an intervention to facilitate speech output in non-verbal children with autism: a proof of concept study. *PLoS ONE* **6**: e25505.
112. Peretz, I. 2008. Musical disorders: from behavior to genes. *Curr. Directions Psychol. Sci.* **17**: 329–333.
113. Stewart, L. 2008. Fractionating the musical mind: insights from congenital amusia. *Curr. Opin. Neurobiol.* **18**: 127–130.
114. Peretz, I. *et al.* 2002. Congenital amusia: a disorder of fine-grained pitch discrimination. *Neuron* **33**: 185–191.
115. Douglas, K.M. & D.K. Bilkey. 2007. Amusia is associated with deficits in spatial processing. *Nat. Neurosci.* **10**: 915–921.
116. Tillmann, B. *et al.* 2010. The amusic brain: lost in music, but not in space. *PLoS ONE* **5**: e10173.
117. Peretz, I. *et al.* 2009. The amusic brain: in tune, out of key, and unaware. *Brain* **132**: 1277–1286.
118. Loui, P., D. Alsop & G. Schlaug. 2009. Tone deafness: a new disconnection syndrome? *J. Neurosci.* **29**: 10215–10220.
119. Tillmann, B., K. Schulze & J.M. Foxtan. 2009. Congenital amusia: a short-term memory deficit for non-verbal, but not verbal sounds. *Brain Cogn.* **71**: 259–264.
120. Williamson, V.J. & L. Stewart. 2010. Memory for pitch in congenital amusia: beyond a fine-grained pitch discrimination problem. *Memory* **18**: 657–669.
121. Dalla Bella, S., A. Tremblay-Champoux, M. Berkowska & I. Peretz. 2012. Memory disorders and vocal performance. *Ann. N.Y. Acad. Sci.* **1252**: 338–344. This volume.
122. Anderson, S., E. Himonides, K. Wise, *et al.* 2012. Is there potential for learning in amusia? A study of the effect of singing intervention in congenital amusia. *Ann. N.Y. Acad. Sci.* **1252**: 345–353. This volume.
123. Loui, P. & G. Schlaug. 2012. Impaired learning of event frequencies in tone deafness. *Ann. N.Y. Acad. Sci.* **1252**: 354–360. This volume.
124. Peretz, I., J. Saffran, D. Schön & N. Gosselin. 2012. Statistical learning of speech, not music, in congenital amusia. *Ann. N.Y. Acad. Sci.* **1252**: 361–367. This volume.