

Music and brain plasticity

BARBRO B. JOHANSSON

Wallenberg Neuroscience Center, Experimental Brain Research, BMC A13,
SE 22184 Lund, Sweden. E-mail: Barbro.Johansson@neuro.lu.se

Complex and widespread activation in many brain areas is seen while performing, listening or mentally imaging music, activity that varies with training, previous exposure, personal preference, emotional involvement and many other factors. Playing a musical instrument demands extensive motor and cognitive abilities, and early musical learning results in plastic reorganization of the developing brain – one example being the increased cortical representation area for the left little finger in (right-handed) string-players, which correlates with age at the start of training. Even though the developing brain has the most pronounced changes, the adult healthy brain has a considerable plasticity. Conductors have superior spatial tuning compared with non-musicians and pianists. Attentive listening to music for as little as three hours can temporarily alter the auditory cortex. Interactions between genetic predisposition, environment and training play a role in music as in other areas. It has been proposed that musical training may improve other cognitive functions. There is some evidence that this may be the case but it is an area that needs further exploration.

Introduction

Music is a unique human feature with a powerful capacity of conveying emotion and regulating mood, and it has many social functions. In contrast to the general acceptance of the evolutionary value of language, the evolutionary significance of music is still debated. On one hand, it has been proposed that human musical abilities have played a key role in the evolution of language,^{1–3} while on the other hand music has been grouped together with art and other cultural activities as bi-products of the evolution of the human brain.⁴ Intensely pleasurable responses to music correlate with activities in brain regions involved with emotion, arousal, motivation and reward.⁵ The putative stimulation of endogenous reward systems indicates that music may be of significant benefit to our mental and physical wellbeing. Kuhl⁶ has stressed the importance of the emotional social contact for optimal language acquisition in infants, and infants pay more attention

when their mothers are singing than when they are speaking. In pre-literate societies, singing and music are incorporated in everyday activities like working, dancing and storytelling, and music may enhance the memory capacity in societies with no written records. Listening to and practising music have profound effects not only on the developing but also on the adult brain, and studies on music have provided us with many examples on brain plasticity.⁷⁻¹¹

Brain plasticity

The concept of brain plasticity implies that the brain is adaptable, and includes all the mechanisms responsible for the brain capacity to change in response to incoming stimulation, our activities and thoughts.¹² That neuronal circuits are tuned in close interaction to the environment is evident from the global variations in customs, languages and culture and is in fact an old concept. In *The Principles of Psychology* (1890), William James defined the word plasticity as the possession of a structure weak enough to yield to an influence, but strong enough not to yield all at once, and he wrote ‘we may without hesitation lay down as our first proposition that the phenomena of habit in living beings are due to the plasticity’. Ramón y Cajal, who considered piano playing as the most demanding of all human skills, requiring many years of mental and physical practice, wrote in his book *Textura del Sistema Nervioso* (1904) that in order fully to understand this complex phenomenon it was necessary to admit, in addition to the reinforcement of pre-established organic pathways, the formation of new pathways through ramification and progressive growth of the dendritic arborization and the nervous terminals. In this early era the idea of plasticity was also subject to scientific interest in Italy.¹³ However, it was the Canadian psychologist Donald Hebb who, in the middle of last century, in line with the early idea of Ramón y Cajal, proposed that neuronal cortical connections are strengthened and remodelled by our experience, and he experimentally demonstrated that this is indeed the case.¹⁴ His work inspired many later scientists to study biochemical, behavioural and morphological effects of experience, learning, activities and specific training.¹⁵⁻¹⁸ Another aspect of brain plasticity, first demonstrated in animals in the 1980s, is that cortical representation areas, ‘cortical maps’ can be modified by sensory input and training¹⁹⁻²¹ suggesting that additional neurons can be recruited when needed. Rapid and transient alterations of cortical representation areas are seen during learning tasks.²² Flexible short-term modulations are important in the acquisition of new skills, and can lead to structural changes in the intra-cortical and sub-cortical network as the skill becomes more established and automatic.²³

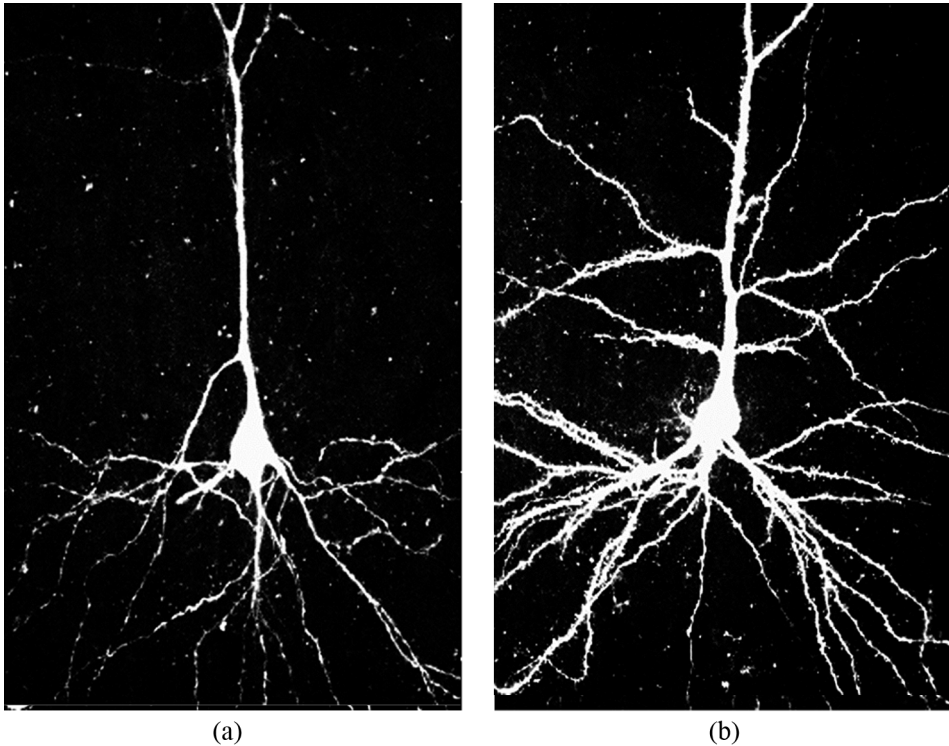


Figure 1. A few weeks exposure to a stimulating environment alters the neurons in the cortex of the brain. To the left (a) is a nerve cell from a rat housed in a standard laboratory cage. The nerve cell to the right (b) demonstrates the effect of 3 weeks housing in a larger cage with more rats and the opportunity for various activities. In addition to more branches there are more small outgrowths, which are where the communication with other neurons take place. From B.B. Johansson and P.V. Belichenko (2001) Environmental influence on neuronal and dendritic spine plasticity after permanent focal brain ischemia, in: N.G. Bazan, U. Ito, V.L. Marcheselli, T. Kuroiwa and I. Klatzo (eds) *Maturation Phenomenon in Cerebral Ischemia IV* (Berlin, Heidelberg: Springer-Verlag), pp. 77–83. Printed with permissions from Springer-Verlag.

Methods applied in studies on music and the brain

In new-born infants, dichotic discrimination and other auditory tests has been evaluated with a sucking response.²⁴ Fluctuations in brain activity can be studied during various test situations with positron emission tomography (PET), and functional magnetic resonance (fMRI).^{25,26} Neuronal activity gives rise to very weak magnetic fields, which after shielding the much stronger magnetic fields of the earth can be registered at many points on the scalp simultaneously with

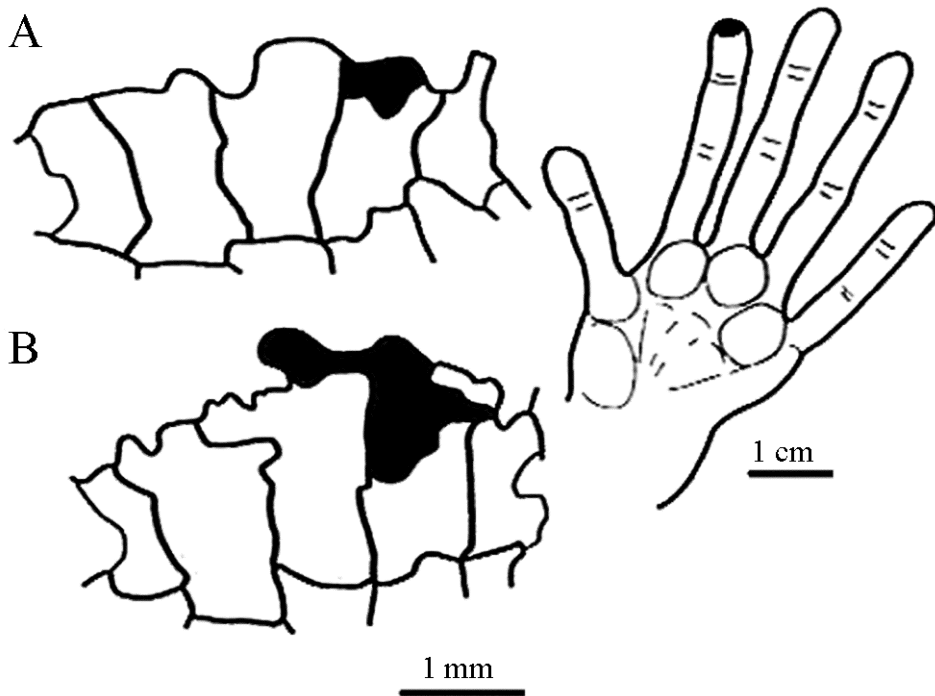


Figure 2. The somatosensory cortex of the hand of a monkey before (A) and after (B) repetitive specific tactile stimulation of the tip of the second finger (black areas). From W.M. Jenkins, M.M. Merzenich, M.T. Ochs, T. Allard and E. Guic-Robles (1990) Functional reorganization of primary somatosensory cortex in adult owl monkeys after behaviorally controlled tactile stimulation. *Journal of Neurophysiology*, **63**, 82–104. Printed with permission from the American Physiological Society.

magneto-encephalography (MEG²⁷). The temporal resolution varies from minutes in PET to seconds in fMRI and milliseconds (ms) in MEG, making MEG an online method capable of measuring the temporal spatial pattern of brain activity – that is, where and when the activation starts – and its temporal spreading to other regions. Similarly, registration of small voltage fluctuations during neuronal activity, event related potentials (ERP), can be performed with multiple electrodes placed on the skull, a method that can be used even in infants.^{6,28} Another online technique that has been applied to language and speech is trans-cranial magnetic stimulation (TMS), in which a pulsed magnetic field can excite or inhibit synaptic efficiency in specific areas and thereby temporarily alter brain function.²⁹ Voxel-based morphometry,^{3,31} a computational technique developed to identify subtle regional differences in grey or white matter between groups of scans, and tensor imaging MRI, used to study the brain white matter³² have substantially

improved our abilities to study the anatomy of the living brain in health and disease and improved the ability to correlate function with anatomy after brain lesions. The design of the studies and the control situations applied are crucial for the interpretation of the data, and individual differences depending on training, previous exposure, personal preference, and emotional involvement have to be considered.³⁵

Music processing in the brain

Based on studies of patients with brain lesions and some very early brain imaging, a right hemisphere dominance was proposed for brain processing of music (relatively independent of musical knowledge and training), and a variable dominance was proposed for musical perception, to be ascribed to the right hemisphere in musically naïve subjects, developing into a left hemisphere dominance in the case of musically sophisticated people.³⁴ The earlier concept of music as predominantly a right hemispheric function has been considerably modified. Music is composed of many components that involve both hemispheres as well as sub-cortical regions and the hindbrain. There is probably no other activity that activates so many neuronal networks as music. It been proposed that cortical asymmetries have been developed as a solution to the need to optimize processing of the acoustic environment in both temporal and frequency domains. The left hemisphere is superior in temporal processing and the right for spectral processing (pitch, prosody) with the left auditory areas preferentially extracting information from short (20–50 ms) integration windows, and the right homologues preferentially from 150–250 ms integration windows.^{35,36} Temporal differences as small as 20 ms may be needed for perception of consonants in language, whereas melodies with note durations shorter than about 160 ms are difficult to identify.³⁷ However, there is disagreement regarding where this takes place, whether in the primary auditory cortex³⁵ or whether processing is roughly the same in the left and the right auditory cortices and the temporal and spectral asymmetry is generated by small differences in the further analysing of the time and spectral domain in the two hemispheres.³⁶

Some workers favour a modular view of music processing with music-specific neuronal networks,^{38,39} an alternative view points to significant overlap between neuronal structures used for language and music processing.^{40–43} Studies with patients with brain lesions have been taken in support of the modular view; several studies in healthy individuals indicate that cortical language networks are also involved in the processing of music, albeit often with a right hemispheric dominance in the musical domain and with a left hemispheric dominance in the language domain.

There is a constant dynamic interaction that can be either inhibitory or excitatory within a hemisphere and also between the two hemispheres via the bundle of nerve fibres that connect the two hemispheres. Mammalian cortical neurons form behaviour-dependent fluctuations or oscillations across a broad range of frequencies and spatial scales.⁴⁴ Network oscillations temporally link neurons into assemblies and facilitate synaptic plasticity, mechanisms that support temporal representation and long-term consolidation of information. Synchronization in the gamma-band (> 30 Hz) has been shown to play an important role in various higher cognitive functions by binding spatial and temporal information in different cortical areas to achieve a coherent perception. While listening to music, the degrees of gamma band synchrony over distributed cortical areas have been found to be significantly higher in musicians than in non-musicians with no significant difference between the groups for other conditions. The degree of spatial synchrony was also increased and proposed to be a manifestation of a more advanced memory in musicians in binding together several features of the intrinsic complexity of music in a dynamic way.⁴⁵

Developmental plasticity of the brain in infants and children

Sounds in the environment of a pregnant woman can penetrate the tissue and fluid surrounding the head of the foetus and stimulate the inner ear during the last trimester of the pregnancy. This allows the foetus to react to vowels, whereas consonants that are higher in frequency and less intense than vowels are largely unavailable to them. Rhythmic patterns of music are probably detected. New-born babies show a preference for the voice of their mother and to musical pieces that she has been listening to during the late pregnancy, indicating a capacity of implicit learning during foetal life.⁴⁶ Neonates and infants show a right ear (i.e. left hemisphere) advantage for speech and a left ear (right hemisphere) advantage for music.⁴⁷ Infants pay more attention to their mothers when they sing than when they talk to them.^{6,48} Increasing musical exposure attenuates the effects of culture-general factors while amplifying the influence of culture-specific factors.⁴⁹

The effortless learning to talk and to sing while being exposed to language and music is an example of *developmental plasticity*. There is a considerable capacity for cross-modal plasticity in infancy and early childhood. Loss of one sensory modality leads to neural reorganization of the remaining modalities. Early-blind individuals, who cannot get any spatial information from vision, can localize sounds in the peripheral space better than sighted subjects, and their pitch discrimination is superior.^{50–52}

Training induced plasticity

Learning to play an instrument needs practice and is an example of training-induced plasticity, a plasticity that is most pronounced in children but can be induced throughout the life-span in a healthy brain. Musical training involves complex motor and auditory and other cognitive skills, often requiring memorizing long, complex bimanual finger sequences, and translating musical symbols into motor sequences during sight-reading. Continued practice of complicated bimanual motor activity leads to changes in the brain structure and representation of the brain auditory, cortical motor and sensory functional and cortical functional reorganization, 'cortical maps'.

In adult subjects with musical training since early childhood, the brain white matter, consisting of fibres that connect nerve cells in different part of the brain, differs significantly from control subjects in other areas, suggesting the cognitive and motor effects of early musical training.^{54,55} The anterior part of the corpus callosum, consisting of nerve fibres connecting regions crucial for the coordination of bimanual motor activity in the two cerebral hemispheres, is larger in male keyboard and string players who started musical training early, usually before the age of 7 years, than in a musicians who started later, or in non-musicians.^{8,55,56} Male keyboard players in addition have a larger cerebellum than non-musicians.⁵⁷ These anatomical differences are not seen in female musicians, possibly related to basic gender differences with a tendency for a more symmetric organization in the female human brain and the fact that, in relation to their body weight, women have a larger cerebellum than men. Likewise, a few studies have indicated a gender difference in the processing of some musical components. In a pitch memory task, male subjects had greater lateralized activation (left > right) during the perceptual as well as during the memory phase of the test, and the cerebellar activation tended to be higher than in females although there was no gender difference in performance.⁶⁵ A bilateral electrical correlate of music-syntactic processing (response to inappropriate harmonies within a musical sequence) has been observed in females whereas a right hemispheric predominance was seen in males.⁶⁶ When comparing professional male musicians (keyboard players) with matched amateur musicians and non-musicians with the more sensitive voxel-based morphometry method, several differences in regions related to motor, auditory and visuo-spatial functions are noted with a strong association between structural differences, musical status and practice intensity.⁵⁸

In addition to anatomical differences, functional differences in cortical representation areas have been demonstrated in musicians. Examples are the increased representation for the little finger of the left hand in (right-handed) string players that correlates with the age at which the person started training,⁵⁹ and the

increased representation areas in the auditory cortex for tones, pitch and timbre in musicians.^{60,61}

The question of whether the observed differences between musicians and non-musicians are exclusively acquired through training or are at least in part genetically determined has been discussed. To investigate if there are pre-existing neural, cognitive, or motor markers for musical abilities, 5- to 7-year-olds beginning piano or string lessons were compared with children of the same age not beginning musical training. All children received a series of visual-spatial, non-verbal reasoning, verbal, motor and musical tests and fMRI. No neural, cognitive, motor or musical differences were found between the groups, nor any correlation between musical perceptual skills and any brain or visual-spatial measures. However, correlations were found between musical perceptual skills and non-verbal reasoning and phonemic awareness, most likely due to innate abilities or implicit learning during early development. This baseline study is part of an ongoing longitudinal study addressing the effects of intensive musical training on brain and cognitive development.⁶² Electro-physiological changes related to enhanced perception of timbre are specific for the timbre of the instrument played, suggesting that training at least is an important factor. Thus, trumpet players have a specific response to trumpet tones and violinists show larger responses to violin tones.⁶¹ An example of how extensive training can shape cognitive auditory processes also in the adult brain is the superior auditory spatial tuning in conductors, compared to non-musicians and pianists.⁶³ Furthermore, volunteers who began to learn to play a stringed instrument at the age of 20–22 showed changes in activation and representation sites for the left little finger after 6 months.⁶⁴ Even mental practice can change the cortical representation of finger flexors and extensor muscles in adult non-musicians.¹⁰

The difference in activation pattern is seen when comparing professionals and amateurs⁶⁷ and musicians and non-musicians.⁶⁸ In a study comparing activation maps of professional violinists and amateurs during an actual performance and imagery of a Mozart violin concerto, the professions showed higher and more focused activation in several cortical areas.⁶⁸

With MEG, brain activation and life simulating events can be studied online. When trained musicians were presented with visual notes and instructed to image the corresponding sounds, an enhanced activity of left and right occipital area was seen 120–150 ms after the onset of the visual stimulus, then spreading to different parts of the brain implying a complex temporal/spatial activation sequence of multiple cortical areas when musicians recall firmly established audio-visual association.⁶⁹ When individuals with no musical training were listening to authentic piano music characterized by a clearly defined rhythm and melodic structure not earlier known to the subjects (an etude by Liszt), the activity

in motor-related structures correlated with rhythmic components and with distinct laterality depending on the musical expression. Frontal areas generally responded to the music with slow time constants, i.e. a few seconds, reflecting their more integrative mode⁷⁰.

Does music or musical training enhance other cognitive functions?

It has been proposed that musical training, even of listening to music, has a spillover effect on other cognitive functions. Whereas there is little scientific support for a specific ‘Mozart effect’ arousal, mood effects of listening to music may have transient effects on cognitive functions.^{71–73} Whether factors involved in musical training such as bimanual motor coordination, learning to read music, auditory and memory training, attention, concentration, and timing etc can transfer to non-musical domains such as language, mathematics or spatial reasoning is controversial. There is some evidence that it might be the case, and some examples are given below.

In a study on early reading ability in 50 four-year-old and 50 five-year-old Canadian children, music skills were found to correlate significantly with both phonological awareness and reading development. Regression analyses indicated that music perception skills were a contribution in predicting reading ability, even when variance due to phonological awareness and other cognitive abilities (mathematics, digit span, and vocabulary) had been accounted for.⁷⁴ Music training facilitates pitch processing in both music and language⁷⁵ and is associated with enhanced ability to perceive prosody in speech.^{76,77} Formal music training has been shown to enhance verbal memory.^{78–80}

Professional pianists after long-lasting practising have a superior tactile spatial discrimination performance than non-musicians. In addition, in the musicians the individual discrimination thresholds were linearly correlated with the daily training duration. Despite an already high level of performance in pianists, after three hours of training with a tactile co-activation protocol known to improve spatial tactile acuity, the training gain in pianists was significantly larger than in control subjects. The enhanced learning ability in pianists was proposed to implicate a form of meta-plasticity in professional pianists.⁸¹ Likewise, studies on trumpet players and controls have indicated that early training-induced reorganization of the brains leads to a qualitatively different way of processing multi-sensory information.⁸² Evidence that musical training improves proficiency in mathematics^{83,84} and enhances IQ⁸⁵ is so far modest and inconclusive. Many of the above studies are based on a few individuals under specific test situations and further studies are needed to evaluate to what extent the data can be generalized.

Maladaptive brain plasticity

Not all training-induced plasticity is beneficial. Some musicians develop a disabling condition, focal hand dystonia or musicians cramp. A recent long-term outcome study on 21 violin and viola players with focal dystonia, an average 13.8 years after onset of symptoms, showed that only 38% had been able to maintain their professional careers.⁸⁶ Based on experimental data in animals^{87,88} and confirming studies in musicians with this condition, it is now considered to be a disorder of maladaptive plasticity.^{89–92} Frequent very rapid time-synchronous movements during vigorous practising can cause a degradation of the sensory feedback controlling fine motor movements, with the result that the distinct cortical representation of the individual fingers may be fused. The aberrant sensory representation interferes with motor control, and abnormal motor control strengthens the sensory abnormality reinforcing the dystonic condition. The sensory representation abnormalities parallel focal hand dystonia. Methods based on relearning principles aimed at restoring the normal representation areas of sensory feedback from the hand have been developed. Substantial improvement has been reported from three centres including a one-year follow-up study^{93–96}; there is some evidence that a hereditary component may be predisposing.⁹⁷

A corresponding disorder has been observed in professional brass and woodwind players involving abnormal non-coordinated movements and involuntary muscle contraction of lip, jaw, and tongue muscles used to control the flow of air into a mouthpiece while playing.⁹⁸ There is evidence that abnormal somatosensory reorganization contributes to the disorder,⁹⁹ which often is so disabling that the musicians have to limit or give up their occupation.

Concluding remarks

Playing an instrument is a very demanding task for the human brain and engages many cognitive processes. We are still in an early stage of knowledge but the discipline of neuroscience of music is progressing rapidly. It is evident that musical activities have an extensive effects on the human brain. By studying music we can learn much about human cognition and underlying brain mechanisms. However, because music is a very personal experience influenced by a combination of genetic and environmental factors, such as training, previous exposure, personal preference, and emotional involvement there are obvious limits to what neuroscience can achieve in understanding or explaining the individual musical experience.

References

1. N. L. Wallin, B. Merker and S. Brown (2000) *The Origins of Music* (Cambridge, Massachusetts, USA: The MIT Press).
2. R. J. Zatorre and I. Peretz (2003) *The Cognitive Neuroscience of Music* (Oxford University Press).
3. S. E. Trehub (2003) The developmental origins of musicality. *Nature Neuroscience*, **6**, 669–673.
4. S. Pinker (1997) *How the Mind Works* (New York: W.W. Norton).
5. A. J. Blood and R. J. Zatorre (2000) Intensive pleasurable responses to music correlate with activity in brain regions implicated in reward-emotion. *Proceedings of the Academy of Science*, **98**, 11818–11823.
6. P. K. Kuhl (2004) Early language acquisition: cracking the speech code. *Nature Reviews Neuroscience*, **5**, 831–843.
7. T. E. Münte, E. Altenmüller and L. Jäncke (2002) The musician's brain as a model of neuroplasticity. *Nature Reviews Neuroscience*, **3**, 473–478.
8. A. G. Schlaug (2001) The brain of musicians. A model for functional and structural adaptation. *Annals of the New York Academy of Sciences*, **930**, 281–299.
9. R. Zatorre and J. McGill (2005) Music, the food for neuroscience? *Nature*, **434**, 312–315.
10. A. Pascual-Leone (2001) The brain that plays music and is changed by it. *Annals of the New York Academy of Sciences*, **930**, 315–322.
11. B. B. Johansson (2002). Music, age, performance and excellence: a neuroscientific approach. *Psychomusicology*, **18**, 46–58.
12. B. B. Johansson (2004) Brain plasticity in health and disease. *Keio Journal of Medicine*, **53**, 231–246.
13. G. Berlucchi (2004) The origin of the term plasticity in the neurosciences: Ernesto Lugaro and chemical synaptic transmission. *Journal of the History of Neurosciences*, **11**, 305–309.
14. D. O. Hebb (1949) *The Organization of Behavior* (New York: Wiley).
15. E. L. Bennett, M. C. Diamond, D. Krech and M. R. Rosenzweig (1964) Chemical and anatomical plasticity of brain. *Science*, **146**, 610–619.
16. B. Kolb (1995) *Brain Plasticity and Behaviour* (Hillsdale, NJ: Lawrence Erlbaum).
17. B. B. Johansson and P. V. Belichenko (2002) Neuronal plasticity and dendritic spines: effect of environmental enrichment on the intact and postischemic rat brain. *Journal of Cerebral Blood Flow & Metabolism*, **22**, 89–96.
18. B. B. Johansson (2004) Functional and cellular effects of environmental enrichment after experimental brain infarcts. *Restorative Neurology and Neuroscience*, **22**, 163–174.
19. J. H. Kaas (1991) Plasticity of sensory and motor maps in adult mammals. *Annuals Reviews of Neurosciences*, **114**, 137–167.
20. C. V. Buonomano and M. M. Merzenich (1998) Cortical plasticity: from synapses to maps. *Annual Review of Neuroscience*, **21**, 149–186.

21. P. V. Hickmott and M. M. Merzenich (2002) Local circuit properties underlying cortical reorganization. *Journal of Neurophysiology*, **88**, 1288–1301.
22. A. Pascual-Leone, J. Grafman and M. Hallett (1995) Modulation of cortical motor output maps during development of implicit and explicit knowledge. *Science*, **263**, 1287–1289.
23. S. E. Petersen, H. van Mier, J. A. Fiez and M. E. Raichle (1998) The effects of practice on the functional anatomy of task performance. *Proceedings of the Academy of Science*, **95**, 853–860.
24. J. Bertoncini, J. Morais, R. Bijeljac-Babic, S. McAdams, I. Peretz, and J. Mehler (1989) Dichotic perception and laterality in neonates. *Brain and Language*, **37**, 591–605.
25. J. F. Demonet, G. Thierry & D. Cardebat (2005) Renewal of the neurophysiology of language: functional neuroimaging. *Physiological Reviews*, **85**, 49–95.
26. P. M. Matthews and P. Jezzard (2004) Functional magnetic resonance imaging of the brain. *Journal of Neurology, Neurosurgery and Psychiatry*, **75**, 6–12.
27. R. Hari, S. Levanen and T. Raij (2000) Timing of human cognition: role of MEG. *Trends in Cognitive Sciences*, **4**, 455–462.
28. S. Koelsch, E. Kasper, D. Sammler, K. Schulze, T. Gunter and A. D. Friederici (2004) Music, language and meaning: brain signatures of semantic processing. *Nature Neuroscience*, **7**, 302–307.
29. M. Hallett (2000) Transcranial magnetic stimulation and the human brain. *Nature*, **406**, 147–150.
30. J. Ashburner and K. J. Friston (2000) Voxel-based morphometry – The methods. *NeuroImage*, **11**, 805–821.
31. E. Luders, C. Gaser, L. Jancke and G. Schlaug (2004) A voxel-based approach to gray matter asymmetries. *Neuroimage*, **22**, 656–664.
32. D. Le Bihan, J. F. Mangin, C. Poupon, C. A. Clark, S. Pappata, N. Molko and H. Chabriat (2001) Diffusion tensor imaging: concepts and applications. *Journal of Magnetic Resonance Imaging*, **13**, 534–546.
33. J. A. Sloboda (2000) Individual differences in music performance. *Trends in Cognitive Sciences*, **4**, 397–403.
34. A. R. Damasio and H. Damasio (1977) Musical faculty and cerebral dominance. In M. Critchley and R. A. Henson (eds) *Music and the Brain* (London: William Heinemann Medical Books).
35. R. J. Zatorre and P. Belin (2001) Spectral and temporal processing in human auditory cortex. *Cerebral Cortex*, **11**, 946–953.
36. D. Poeppel (2003) The analysis of speech in different temporal windows: Cerebral lateralization as asymmetric sampling in time. *Speech Communication*, **41**, 245–255.
37. R. M. Warren, D. A. Gardner, B. S. Brubaker and J. A. Bashford, Jr. (1991) Melodic and Nonmelodic sequences of tones: effects of duration on perception. *Music Perception*, **8**, 277–290.
38. I. Peretz, and M. Coltheart (2003) Modularity of music processing. *Nature Neuroscience*, **6**, 688–691.

39. I. Peretz and R. J. Zatorre (2004) Brain organization for music processing. *Annual Review of Psychology*, **56**, 89–114.
40. B. S. Maess, S. Koelsch, T. C. Gunder and A. D. Friederici (2001) Musical syntax is processed in Broca's area: an MEG study. *Nature Neuroscience*, **4**, 540–545.
41. A. D. Patel (2003) Language, music, syntax and the brain. *Nature Neuroscience*, **6**, 674–681.
42. S. Koelsch, E. Kasper, D. Sammler, K. Schulze, T. Gunder and A. D. Friederici (2004) Music, language and meaning: brain signatures of semantic processing. *Nature Neuroscience*, **7**, 302–307.
43. S. Koelsch (2005) Neural substrates of processing syntax and semantics in music. *Current Opinion in Neurobiology*, **15**, 207–212.
44. G. Buzsáki and A. Draguhn (2004) Neuronal oscillations in cortical networks. *Science*, **304**, 1926–1929.
45. J. Bhattacharya, H. Petsche and E. Pereda (2001) Long-range synchrony in the γ band: role of music perception. *The Journal of Neuroscience*, **21**, 6329–6337.
46. K. J. Gerhardt and R. M. Abrams (2000) Fetal exposures to sound and vibroacoustic stimulation. *Journal of Perinatology*, **20**, S20–S29.
47. C. T. Best, H. Hoffman and B. B. Glanville (1992) Development of infant ear asymmetries in speech and music. *Perception in Psychophysics*, **31**, 75–85.
48. S. E. Trehub (2001). Musical predispositions in infancy. *Annals of the New York Academy of Sciences*, **930**, 1–16.
49. E. G. Schellenberg and S. Trehub (1999) Culture-general and culture-specific factors in the discrimination of melodies. *Journal of Experimental Child Psychology*, **74**, 107–127.
50. N. Lessard, M. Pare, F. Lepore and M. Lassonde (1998) Early-blind human subjects localize sound sources better than sighted subjects. *Nature*, **395**, 278–280.
51. B. Roder, W. Teder-Salejarvi, A. Sterr, F. Rosler, S. A. Hillyard and H. J. Neville (1999) Improved auditory spatial tuning in blind humans. *Nature*, **400**, 162–166.
52. F. Gougoux, F. Lepore, M. Lassonde, P. Voss, R. J. Zatorre and P. Belin (2004) Pitch discrimination in the early blind. *Nature*, **420**, 309.
53. V. J. Schmithorst and M. Wilke (2002) Differences in white matter architecture between musicians and non-musicians: a diffusion tensor imaging study. *Neuroscience Letters*, **321**, 57–60.
54. S. L. Bengtsson, Z. Nagy, S. Skare, L. Forsman, H. Forssberg and F. Ullén (2005) Extensive piano practicing has regionally specific effects on white matter development. *Nature Neuroscience*, **8**, 1148–1150.
55. G. Schlaug, Y. Jancke, Z. Huang, J. F. Staiger and H. Steinmetz (1995) Increased corpus callosum size in musicians. *Neuropsychologia*, **33**, 1047–1055.
56. D. J. Lee, Y. Chen and G. Schlaug (2003) Corpus callosum: musician and gender effects. *Neuroreport*, **14**, 205–209.
57. S. Hutchinson, L. H-L Lee, N. Grab & G. Schlaug (2003) Cerebellar volume of musicians. *Cerebral Cortex*, **13**, 943–949.

58. C. Gaser and G. Schlaug (2003) Brain structures differ between musicians and nonmusicians, *The Journal of Neuroscience*, **23**, 9240–9245.
59. T. Elbert, C. Pantev, C. Wienbruch, B. Rockstroh and E. Taub (1995) Increased cortical representation of the fingers of the left hand in string players. *Science*, **270**, 305–307.
60. C. Pantev, R. Oostenveld, A. Engelien, B. Ross, L. E. Roberts and M. Hoke (1998) Increased auditory cortical representation in musicians. *Nature*, **392**, 811–814.
61. C. Pantev, L. E. Roberts, M. Schulz, A. Engelien and B. Ross (2001) Timbre-specific enhancement of auditory cortical representations in musicians. *Neuroreport*, **12**, 169–174.
62. A. Norton, E. Winner, K. Cronin, K. Overy, D. J. Lee and G. Schlaug (2005) Are there preexisting neural, cognitive, or motoric markers for musical ability? *Brain and Cognition*, in press. (Epub ahead of print)
63. T. F. Münte, C. Kohlmetz, W. Nager and E. Altenmüller (2001) Neuroperception. Superior auditory spatial tuning in conductors. *Nature*, **409**, 580.
64. D. E. Kim, M. J. Shin, K. M. Lee, K. Chu, S. H. Woo, Y. R. Kim, E. C. Song, J.W. Lee, S.H. Park and J.K. Roh (2004) Musical training-induced functional reorganization of the adult brain: functional magnetic resonance imaging and transcranial magnetic stimulation study on amateur string players. *Human Brain Mapping*, **23**, 188–189.
65. N. Gaab, J. P. Keenan and G. Schlaug (2003) The effects of gender on the neural substrates of pitch memory. *Journal of Cognitive Science*, **15**, 810–820.
66. S. Koelsch, B. Maess, T. Grossmann and A. D. Friederici (2003) Electric brain responses reveal gender differences in music processing. *Neuroreport*, **14**, 709–713.
67. T. Ohnishi, H. Matsuda, T. Asada, M. Aruga, M. Hirakata, M. Nishikawa, A. Katoh and E. Imabayashi (2001) Functional anatomy of musical perception in musicians. *Cerebral Cortex*, **11**, 754–760.
68. M. Lotze, G. Scheler, H. R. Tan, C. Braun and N. Birbaumer (2003) The musician's brain: functional imaging of amateurs and professionals during performance and imagery. *NeuroImage*, **20**, 1817–1829.
69. M. Schürmann, T. Raij, N. Fujiki and R. Hari (2002) Mind's ear in a musician: where and when in the brain. *Neuroimage*, **16**, 434–440.
70. M. Popescu, A. Otsuka and A. A. Ioannides (2004) Dynamics of brain activity in motor and frontal cortical areas during music listening: a magnetoencephalographic study. *NeuroImage*, **21**, 1622–1638.
71. W. F. Thompson, E. G. Schellenberg and G. Husain (2001) Arousal, mood and the Mozart effect. *Psychological Science*, **12**, 248–251.
72. A. Lints and S. Gadbois (2003) Is listening to Mozart the only way to enhance spatial reasoning? *Perception and Motor Skills*, **97**, 1163–1174.
73. R. Fudin and E. Lembessis (2004) The Mozart effect: questions about the seminal findings of Rauscher, Shaw and colleagues. *Perception and Motor Skills*, **98**, 389–405.

74. S. H. Anvari, L. J. Trainor, J. Woodside and B. A. Levy (2002) Relations among musical skills, phonological processing, and early reading ability in preschool children. *Journal of Experimental Child Psychology*, **83**, 111–130.
75. D. Schön, C. Magne and M. Besson (2004) The music of speech: music training facilitates pitch processing in both music and language. *Psychophysiology*, **41**, 341–349.
76. W. F. Thompson, E. G. Schellenberg and G. Husain (2003) Perceiving prosody in speech. Effects of music lessons. *Annals of the New York Academy of Sciences*, **999**, 530–532.
77. W. F. Thompson, E. G. Schellenberg and G. Husain (2004) Decoding speech prosody: do music lessons help? *Emotion*, **4**, 46–64.
78. A. R. Kilgour, L. S. Jakobson and L. L. Cuddy (2000) Music training and rate of presentation as mediators of text and song recall. *Memory & Cognition*, **28**, 700–710.
79. L. S. Jakobson, L. L. Cuddy and A. R. Kilgour (2003) Time tagging: a key to musicians' superior memory. *Music Perception*, **20**, 307–313.
80. Y. C. Ho, M. C. Cheung and A. S. Chan (2003) Music training improves verbal but not visual memory: cross-sectional and longitudinal explorations in children. *Neuropsychology*, **17**, 439–450.
81. P. Ragert, A. Schmidt, E. Altenmüller and H. R. Dinse (2004) Superior tactile performance and learning in professional pianists: evidence of meta-plasticity in musicians. *European Journals of Neuroscience*, **19**, 473–478.
82. M. Schultz, B. Ross and C. Pantev (2003) Evidence for training-induced crossmodal reorganization of cortical functions in trumpet players. *Neuroreport*, **14**, 157–161.
83. K. Vaughn (2000) Music and mathematics: modest support for the oft-claimed relationship. *Journal of Aesthetic Education*, **34**, 149–166.
84. V. J. Schmithorst and S. K. Holland (2004) The effect of musical training on the neural correlates of math processing: a functional magnetic resonance imaging study in humans. *Neuroscience Letters*, **354**, 193–196.
85. E. G. Schellenberg (2004) Music lessons enhances IQ. *Psychological Science*, **15**, 511–514.
86. S. Schuele and R. J. Lederman (2004) Long-term outcome of focal dystonia in string instrumentalists. *Movement Disorders*, **19**, 43–48.
87. N. N. Byl, M. M. Merzenich and W. M. Jenkins (1996) A primate genesis model of focal dystonia and repetitive strain injury: I. Learning-induced dedifferentiation of the representation of the hand in the primary somatosensory cortex in adult monkeys. *Neurology*, **47**, 508–520
88. D. T. Blake, N. N. Byl, S. Cheung, P. Bedenbaugh, S. Nagarajan, M. Lamb and M. Merzenich (2002) Sensory representation abnormalities that parallel focal hand dystonia in a primate model. *Somatosensory Motor Research*, **19**, 347–357
89. C. M. Stinear and W. D. Byblow (2004) Impaired modulation of intracortical inhibition in focal hand dystonia. *Cerebral Cortex*, **14**, 555–561.

90. A. L. McKenzie, S. S. Nagarajan, T. P. Roberts, M. M. Merzenich and N. N. Byl (2003) Somatosensory representation of the digits and clinical performance in patients with focal hand dystonia. *American Journal of Physiological Medicine and Rehabilitation*, **82**, 737–749.
91. S. Butterworth, S. Francis, E. Kelly, F. McGlone, R. Bowtell and G. V. Sawle (2003) Abnormal cortical sensory activation in dystonia: an fMRI study. *Movement Disorders*, **18**, 673–682.
92. L. M. Levy and M. Hallett (2002) Impaired GABA in focal dystonia. *Annals of Neurology*, **51**, 93–101.
93. K. E. Zeuner, W. Bara-Jiminez, P. S. Noguchi, S. R. Goldstein, J. N. Dambrosia and M. Hallett (2002) Sensory training for patients with focal hand dystonia. *Annals of Neurology*, **51**, 593–598.
94. K. E. Zeuner and M. Hallett (2003) Sensory training as treatment for focal hand dystonia: a 1-year follow-up. *Movement Disorder*, **18**, 1044–1047.
95. N. N. Byl, S. Nagajaran and A. L. McKenzie (2003) Effect of sensory discrimination training on structure and function in patients with focal hand dystonia: a case series. *Archives of Physical Medicine and Rehabilitation*, **84**, 1505–1514.
96. V. Candia, C. Wienbruch, T. Elbert, B. Rockstroh and W. Ray (2003) Effective behavioral treatment of focal hand dystonia in musicians alters somatosensory cortical organization. *Proceedings of the National Academy of Science USA*, **100**, 7942–7946.
97. G. Garraux, A. Bauer, T. Hanakawa, T. Wu, K. Kansaku and M. Hallett (2004) Changes in brain anatomy in focal hand dystonia. *Annals of Neurology*, **55**, 736–739.
98. S. J. Frucht, S. Fahn, P. E. Greene, O. Brian, C. Kolla, M. Gelb, D. D. Truong, J. Welch, S. Factor and B. Ford (2001) The natural history of embouchure dystonia. *Movement Disorders*, **16**, 899–906.
99. M. Hirata, E. Schulz, T. Altenmuller, C. Elbert and C. Pantev (2004) Sensory mapping of lip representation in brass musicians with embouchure dystonia. *Neuroreport*, **15**, 815–818.

About the Author

Barbro B Johansson is Emeritus Professor of Neurology at Lund University, Sweden. Her main research interests are cerebrovascular lesions, brain plasticity, and how current knowledge on plasticity can be applied in neuro-rehabilitation. Her interest in music goes back to early childhood.