

Do musicians have different brains?

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ABSTRACT – The search for anatomical correlates of special skills dates from the end of the 19th century, when post-mortem brains of gifted individuals, including musicians, were examined for clues as to origins of their prized abilities. Modern neuroimaging techniques provide the chance to interrogate the brains of living musicians. Structural and functional specialisations have been demonstrated across several sensory, motor and higher order association areas. These specialisations are often instrument- or effector-specific and correlate with aspects of the training history supporting the view that they are the result, rather than the cause, of skill acquisition. Musicians constitute a model, par excellence, for studying the role of experience in sculpting brain processes. A key challenge for the future will be to develop theoretical frameworks within which musicians and other occupationally specialised groups can be studied in order to investigate the nature, scope and limits of neuroplasticity.

KEY WORDS: adaptations, learning, musical, skill

In a museum in Salzburg hangs a sketch of two ears, dated from the 16th century. The one on the left belongs to one of the most eminent musicians in recorded history, the one on the right is that of an ‘ordinary’ individual. The exhibition notes do not reveal whether scholars of the time made anything of the larger lobe or more gradual curvature of the ear on the left but it is hard not to see the sketch as an attempt to shed light on the basis of Mozart’s prodigious abilities. The role of the brain in mental processes was established in the 19th century, after which time the origins of ‘gifts’, including music, were sought in the cortex. Auerbach examined the post mortem brains of several notable musicians and noted peculiarities in temporal and parietal areas that were hypothesised to account for the superior musical skills seen in these individuals.¹ In the absence of rigorous statistical methods, however, it was impossible to determine whether these variations were anything other than individual differences in brain configuration. The development of modern techniques such as magnetic resonance imaging (MRI) has made it possible to obtain three-dimensional,

high resolution images of the living brain. Statistical approaches now allow precise quantification of different aspects of brain structure, making it possible to determine whether groups of individuals with special skills exhibit anatomical specialisations.

These technical advances have been accompanied by a revolution in the understanding of the brain’s capacity to change in response to experience. Only a few decades ago, the mature brain was considered to be hard-wired and immutable but animal and human studies have now demonstrated considerable capacity for reorganisation following deafferentation or stroke; environmental enrichment or learning. The reconceptualisation of the brain as a malleable system forces us to consider the direction of causality in cases where anatomical features are linked to the possession of musical, artistic or intellectual gifts. While these features would once have been considered to be innately determined, evidence of the brain’s plasticity now invites an alternative view. The following review summarises the structural and functional specialisations exhibited by musicians, and presents evidence to suggest that they are the result, rather than the cause, of skill acquisition.

Altered motor and somatosensory maps in musicians

A professional keyboard player can produce up to 1,800 notes per minute, with a precision in space and time that is unsurpassed in any other sphere of human behaviour.² This expertise in fine finger control has a correlate in the brain. A morphometric study revealed that the intrasculal length of the precentral gyrus (ILPG), a marker for the cortical motor hand area, is longer in keyboard players relative to non-musician controls.³ Although it is possible to propose that individuals born with a longer ILPG will have greater aptitude for playing the keyboard compared with those with a shorter ILPG; the association between ILPG and the age at which training commenced suggests that anatomical differences in motor cortex are the result, not the cause of learning. By exploiting the differences in motor demands required for different instruments, it is possible to further explore the relationship between anatomy and expertise. In string players, for instance, there is an asymmetry in the requirements for fine finger

control between the two hands, with the left hand (right motor cortex) performing the fast finger movements and the right hand (left motor cortex) performing bowing. In pianists, there is a more equal division of labour, with fine finger control required of both hands. A recent study compared motor cortex anatomy between keyboard players, string players and non-musicians.⁴ The inverted omega sign or 'hand knob' of the precentral gyrus is a gross-anatomical feature that is associated with the representation of finger movements. Its prominence can range from being barely present, to clearly visible, sometimes to the extent that a double omega can be discerned. Since increased cortical volume results in enhanced gyral folding, the extent of prominence can be used as an indirect index of the volume of this motor hand area. Based on the results of raters who scrutinised structural MRI images from keyboard players, string players and non-musicians, musicians were found to have a more prominent omega sign (OS) configuration than non-musicians. While string players showed greater OS prominence in the right hemisphere, consistent with the fine finger control required of the left hand, keyboard players showed greater prominence in the left hemisphere. While a bilateral prominence may have been expected in the keyboard group, the

authors point out that the right hand is often more involved in fast finger movements than the left, which often has an accompanying role. Instrument-specific differences in anatomy would seem to provide further support for the view that anatomical specialisations in musicians are use-dependent. The alternative view, that innately specified differences in cortical anatomy determine instrument choice, seems unlikely given findings that emphasise the significant role of environmental factors in this decision.⁵

The expanded representations seen in the motor system in musicians are paralleled by changes in the somatosensory system. Stimulation of the digits of the left (fingering) hand of string players has been shown to produce an enhanced somatosensory evoked response that correlates with the age at which training commenced.⁶ The evoked response from the right (non-fingering) hand was no different between string players and non-musicians, suggesting that the expanded cortical representation results from the increased afferent input received by the fingering hand. Evidence pertaining to the likely functional significance of the enhanced somatosensory responses comes from a study in which pianists were found to have improved tactile sensitivity of both hands compared with non-musician controls, correlating with duration of daily practice.⁷ The effector specificity and the relationship between the size of the effect and aspects of the training history in these two studies supports a use-dependent view of these specialisations.^{6,7} Both these paradigms would lend themselves to longitudinal designs, whereby evoked responses and tactile sensitivity could be measured during the course of learning. Emergent behavioural and neurophysiological differences learning would be irrefutable evidence for the causal role of learning and such an approach would also shed light on the time course of these changes.

Increased interhemispheric processing in musicians

Fine finger control is of critical importance for skilled musical performance, but of equal significance is the ability to coordinate sensorimotor processing across the effectors – not only hands, but sometimes feet, lips and respiratory muscles. Coordination between the hands is the simplest case of sensorimotor coordination, requiring extensive neural transmission between the hemispheres. Evidence from morphometric studies suggests that interhemispheric connections are enhanced in musicians. Professional musicians who commenced their training before age seven were found to have a larger anterior portion of the corpus callosum compared to non-musician controls (see Lee *et al* for an interaction with gender that remains to be explored).^{8,9} While suggestive of enhanced interhemispheric communication, structural differences alone say nothing about the functional role of these anatomical differences. A transcranial magnetic stimulation (TMS) study investigated the interhemispheric communication in musicians and non-musicians.¹⁰ Transcranial magnetic stimulation involves the delivery of a magnetic pulse to the brain via a coil placed against the

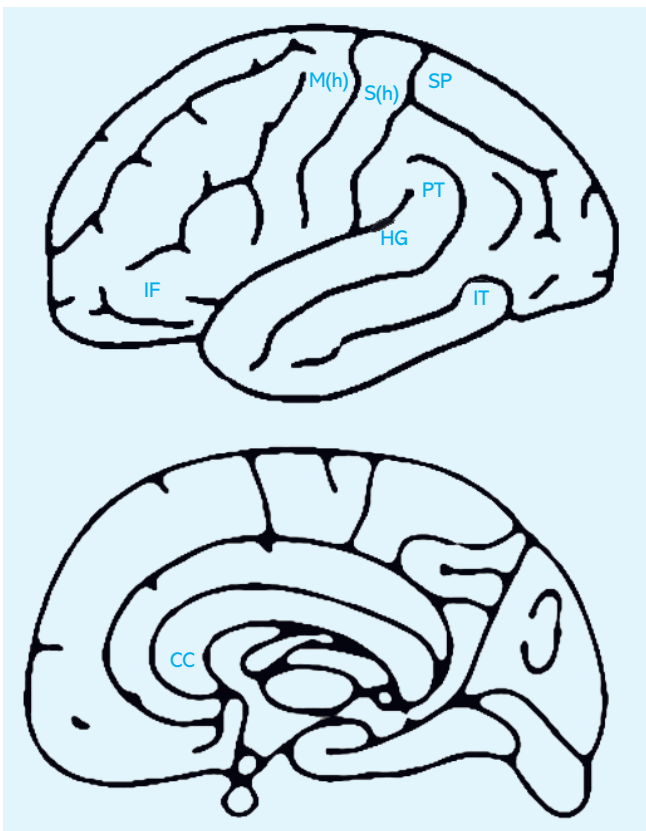


Fig 1. A schematic representation showing regions of specialisation in the brains of musicians. CC = corpus callosum; HG = Heschl's gyrus (site of primary auditory cortex); IF = inferior frontal cortex; IT = inferior temporal cortex; M(h) = hand area of motor cortex; PT = planum temporale; S(h) = hand area of somatosensory cortex; SP = superior parietal cortex.

scalp. The induced electric field depolarises neurons underlying the coil, in the surface of the cortex. When given over the hand area of the primary motor cortex, this elicits muscle contraction in the contralateral hand that can be measured via surface electrodes applied to the first dorsal interosseus muscle. When a 'conditioning' pulse is given over the ipsilateral motor hand area before the 'test' pulse is given, the muscle contraction is of lower amplitude, owing to the activation of inhibitory circuits between the motor hand areas of each hemisphere. This inter-hemispheric inhibition is known to have an important role in motor control, for instance, by preventing mirroring movements and allowing the effectors to operate independently of one another. Musicians, however, were shown to have reduced interhemispheric inhibition, since the conditioning pulse was less effective in reducing the amplitude of muscle contraction in response to the test pulse compared with non-musician controls.¹⁰ At first sight this may seem counterintuitive since the ability to independently control the two hands, is a defining feature of pianistic skill. However, the role of interhemispheric inhibition may depend on the level of expertise. The beginning pianist might experience involuntary mirroring when the two hands play together, but once independence of movement has been achieved, there is an obvious need for coordination in the execution of these separate motor programs. Expert performers may be able to accommodate and benefit from the effects of reduced interhemispheric inhibition between their motor hand areas because they have already achieved automatic and independent control of the two hands.

Auditory processing differences in musicians

Sensorimotor processing in musicians subserves one overarching goal: to produce sound. Musicians are intensely attuned to the sounds that they produce, employing feed-forward control in order to refine and modulate the sounds produced until what they hear corresponds to an internal model of the desired sound.¹¹ Musicians have been shown to have more gray matter than non-musicians in anterior medial Heschl's gyrus (HG), corresponding to primary auditory cortex.¹⁶ A subgroup of musicians who possess absolute pitch (AP), the ability to identify tones by name, in the absence of a reference pitch have further differences in planum temporale, an auditory association area.¹² Two studies suggest that AP possessors show an exaggeration of the normal leftward asymmetry of this region, brought about by a reduction in cortical volume in the right hemisphere, as opposed to an increased volume in the left.^{13,14,15}

At a functional level, musician-specific differences have been found in the early and late components of the auditory evoked response, following presentation of pure and complex tones respectively.^{16,17} The latter component is influenced by the behavioural relevance of the spectral properties of the tones. When violinists hear violin tones, they show an enhanced response relative to when they hear trumpet tones, while the reverse is true for trumpeters.¹⁷ On the one hand, this effect may have arisen from having had greater experience with the spectral features of one's own instrument. It is also possible, however,

that the enhancement emerges from a striving to produce or modulate the timbral qualities of one's instrument.

The obligatory coupling between sound and action in musical performance is well known to musicians. Singers who need to rest their voices before a performance are instructed not to listen to music, in order to avoid straining the voice through automatic subvocalisation (Collyer, personal communication, 2007). Two recent functional (f)MRI studies compared activation when musicians listened to a piece of music without playing it versus when they played a piece of music without auditory feedback.^{18,19} Both studies showed areas of overlap between the two conditions, including premotor cortex, supplementary motor area and planum temporale. A magnetoencephalography (MEG) study showed that purely listening to music which was within the listeners repertoire resulted in a response from primary motor cortex.²⁰ Moreover, a dissociation in evoked response was seen between those notes which would have been played by the thumb and the little finger. Similarly, when pianists listened to a piano piece at which they were practised, they demonstrated higher motor cortex excitability than when they listened to a flute piece on which they had not been trained.²¹ The demonstration that perception and action can be closely coupled through musical performance opens possibilities for using music to affect action, for instance, in promoting motor function recovery following stroke.²²

Visiospatial processing in musicians

Musicians rely heavily on a sound to action link, but the majority of them are also required to translate rapidly and continually between visuospatial symbols and their associated actions, with a precision and fluidity that allows them to keep in time with their own predetermined beat, or the conductor's baton. The sequencing aspect of music reading appears to have a correlate in left inferior frontal cortex. Two groups reported increased grey matter in this area^{23,24} and one of these groups additionally showed that musicians, but not non-musicians, activated this area while performing a non-musical sequencing task.²⁵ Musician-specific differences have also been found in superior parietal cortex and inferior temporal gyrus, which are thought to reflect adaptations to different aspects of the music reading process.²⁴ Musical notation consists of spatial and featural information, respectively conveying the 'what' and 'when' of the musical response. A longitudinal fMRI study, in which musically-naïve adults were taught to read music and play piano over a period of three months, revealed different functional changes, associated with the learning of each of these aspects of musical notation.^{26,27} When participants were required to read music for pitch alone, learning-related changes were seen in superior parietal cortex. When the task was to read music for rhythm alone, learning-related changes were seen in temporal cortex. Although the experience of reading music is an integrated one, these findings reveal that different aspects of musical notation are, at least initially, dealt with by different brain regions, before these outputs are combined to produce a response that is unified in space and time.

Musicians as a model

Trained musicians provide the opportunity to study structural and functional plasticity associated with the acquisition of a number of sensory, motor and cognitive musical subskills but they also provide the opportunity to ask more generic questions concerning learning and plasticity. One such question concerns the role of sensitive periods in learning. Does early learning have a more profound impact on the development of ability compared with later learning? Several studies have shown correlations between brain differences and age at which training commenced, but in most cases, individuals who start training earlier have also been playing for a longer period of time, making it impossible to disambiguate the role of training duration from the stage at which the training commenced. A recent study, however, compared early-trained (pre-seven years) and late-trained (post-seven years) musicians on their performance of a novel complex rhythmic sequence.²⁸ Early-trained musicians showed enhanced performance, compared with late-trained musicians, even though the two groups were matched for the overall duration of training. One interpretation of this is that the early training may coincide more closely with relevant structural changes occurring in the brain, compared with the training that occurred later. This view finds support in a study using diffusion tensor imaging (DTI), a form of structural MRI that is optimised for assessing the integrity of white matter pathways.²⁹ This study used biographical data from a group of pianists concerning estimated practice time during childhood, adolescence and adulthood. When these data were correlated against white matter organisation, different areas of the brain were associated with practice during different periods of training. Practice in childhood was associated with structural integrity in the internal capsule and corpus callosum, while practice during adolescence was associated with structural organisation of corpus callosum and splenium. The fact that training interacts with the maturational time course of individual fibre tracts, gives support to the notion of sensitive periods, whereby the acquisition of certain skills is facilitated during certain periods of development. One view is that learning during sensitive periods not only affects the development of that particular skill at that particular time, but can also determine how the brain responds to future learning experiences. This so called 'metaplasticity' ('learning to learn') has been noted in two recent studies with early-trained musicians. Musicians showed greater improvement in tactile acuity, following fingertip stimulation and exaggerated changes in motor cortex excitability, following transcranial magnetic stimulation.^{7,30} Intensive experience during a period of exuberant neural development not only tunes brain circuits for the immediate processing requirements but appears to imbue brain circuits with the capacity to adapt when presented with future novel experiences, long after the sensitive period has terminated.³¹

Conclusions

In the 400 years since the sketch was made of Mozart's ear, there has been a seismic shift in how we think about the origins of

special abilities. The emerging view places training and practise centre stage, to the extent that musicians are now championed as models par excellence for understanding use-dependent reorganisation in the human brain. It is clear that we have now moved beyond the question, 'are musicians' brains different?' to asking how these differences can shed new light on the relationship between experience and brain function. A goal for the future should be to develop theoretical frameworks within which musicians can be considered alongside other groups of occupationally specialised or sensory-deprived individuals. By comparing and contrasting the effects of different parameters of experience on brain function, it will be possible to transcend the situational constraints of any one group and elucidate general principles of learning and plasticity that may find application in questions of educational and clinical significance.

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