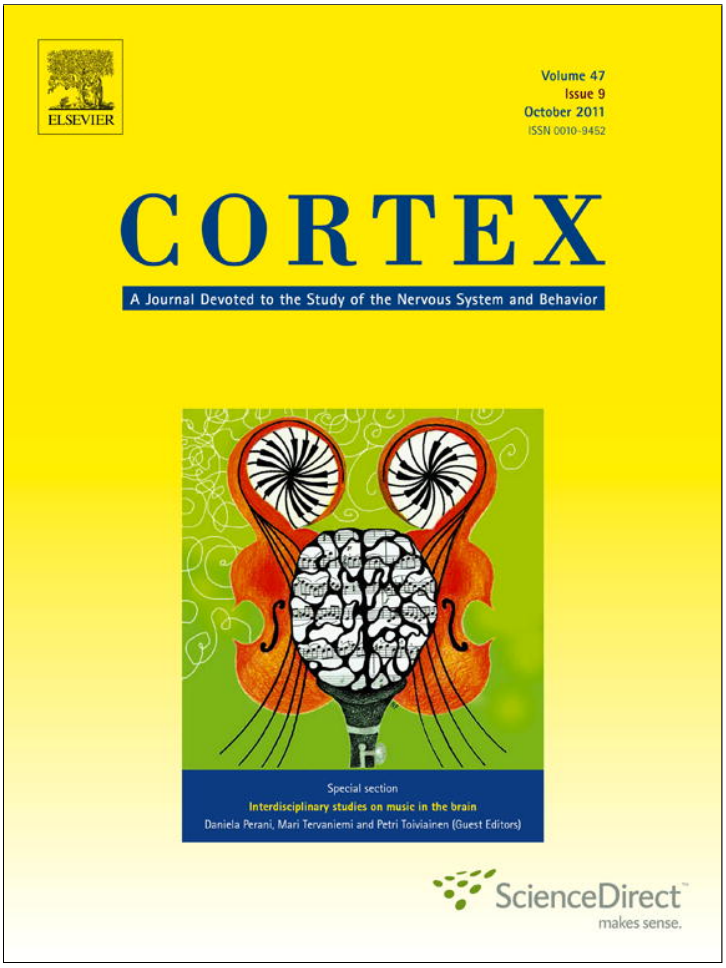
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Review

Sensitive periods in human development: Evidence from musical training

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ABSTRACT

One of the primary goals of cognitive neuroscience is to understand the interaction between genes, development and specific experience. A particularly fascinating example of this interaction is a sensitive period – a time during development when experience has a differential effect on behavior and the brain. Behavioral and brain imaging studies in musicians have provided suggestive evidence for a possible sensitive period for musical training; showing that musicians who began training early show better task performance and greater changes in auditory and motor regions of the brain. However, these studies have not controlled for likely differences between early- (ET) and late-trained (LT) musicians in the number of years of musical experience. This review presents behavioral work from our laboratory comparing the performance of ET (before age seven) and LT musicians who were matched for years of experience on the ability to tap in synchrony with auditory and visual rhythms. The results demonstrate the existence of a possible sensitive period for musical training that has its greatest impact on measures of sensorimotor integration. Work on motor learning in children and how this might relate to the observed sensitive period effect is also reviewed. These studies are described in the context of what is currently known about sensitive periods in animals and humans; drawing on evidence from anatomy and physiology, studies of deafness, as well as structural and functional neuroimaging studies in trained musicians. The possible mechanisms underlying sensitive periods for musical training are discussed based on current theories describing the influence of both low-level features of sensory experience and higher-level cognitive processing.

My husband is a trained musician who practices almost every day. I am a musical klutz, but have a facility for learning foreign languages. The striking individual differences in our skills and talents, along with the underlying structural and functional differences in our brains are the outcome of a long-term interaction between pre-existing genetic make-up and experience. A particularly intriguing example of this interaction occurs during a “sensitive” period; a limited time during development where specific experience can contribute to long-lasting changes in behavior and in the brain (Dahmen

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and King, 2007; Knudsen, 2004; Kral and Eggermont, 2007; Trainor, 2005; Kuhl et al., 2005; Bischof, 2007). Examples of sensitive periods in humans come from second-language learning, and language acquisition in deaf individuals after cochlear implantation. In both cases, studies show that earlier start of training or earlier implantation result in greater language proficiency later in life (Johnson and Newport, 1989; Weber-Fox and Neville, 2001; Geers, 2006; Nicholas and Geers, 2007). Recent behavioral and brain imaging studies in musicians have provided evidence of possible sensitive periods for musical training. These studies have found that musicians who began training early show enhancements in the auditory and motor systems of the brain, along with better pitch and rhythm abilities, compared with musicians who begin later (Bailey and Penhune, 2010; Elbert et al., 1995; Schlaug et al., 1995; Watanabe et al., 2007; Amunts et al., 1997; Kraus et al., 2009). Using musicians to investigate possible sensitive periods is advantageous because we can select groups that differ in the age they started training and equate them for total years of experience. This article will review behavioral studies from my laboratory that have used this design to show that early musical training has long-lasting effects on adult ability to synchronize with musical rhythms. These findings will be described in the context of what is currently known about sensitive periods in animals and humans; drawing on evidence from anatomy and physiology, studies of deafness, and structural and functional neuroimaging studies in trained musicians. I will discuss possible mechanisms underlying sensitive periods for musical training based on current theories describing the influence of both low-level features of sensory experience and higher-level cognitive processing. Finally, I will discuss the contributions of possible pre-existing factors such as individual differences in motor and musical abilities; as well as environmental factors such as family support for music training and exposure to music in the home.

The concept of a sensitive period must be defined in relation to the concept of a "critical" period. The definition of a critical period in development is drawn from work showing that certain behaviours and their neural substrates do not develop normally if appropriate stimulation is not received during a restricted period of time (Knudsen, 2004). Critical periods have relatively abrupt onsets and offsets, and appear to be largely under endogenous or genetic control. In contrast, during a "sensitive" period, neural systems are particularly responsive to relevant stimuli, and are more susceptible to change when stimulated. Sensitive periods have more flexible onsets and offsets, and appear to be strongly influenced by experience. The classic example of a critical period comes from the work of Hubel and Wiesel (1965) who showed that if cats are deprived of vision to one eye during the first months after birth, they do not develop normal binocular vision, even when vision is restored to the deprived eye. At the neural level, the pattern of cellular connectivity is altered and cannot be changed after the critical period has elapsed. Evidence for a critical period in the auditory domain comes from studies in rats showing that rat pups over-exposed to tones of a specific frequency only develop an altered cortical representation for that frequency if exposure occurs during a specific 3-day window in the second week of life (de Villers-Sidani et al., 2007). In humans, studies of congenitally deaf children who later receive cochlear implants show that they never develop normal cortical responses to auditory stimuli if implantation occurs after a critical window around age 3–4 (see Kral and Eggermont, 2007; Sharma et al., 2009 for review). In line with this finding, studies of the cellular architecture of congenitally deaf cats show that without early auditory input, the normal organization is permanently altered (Kral et al., 2000).

In contrast to a critical period, where a function cannot be acquired outside the specific developmental window, a sensitive period denotes a time where sensory experience has a relatively greater influence on behavioral and cortical development. Sensitive periods may also be times when exposure to specific stimuli stimulates plasticity, enhancing changes at the neuronal and behavioral levels. There appears to be a sensitive period for learning auditory categories important for language, as demonstrated by studies in congenitally deaf individuals who receive cochlear implants. Those who receive implants before the ages of 3–5 develop better auditory language processing skills later in life compared with those who receive their implants later (Geers, 2006; Nicholas and Geers, 2007). Those who receive implants later in childhood still develop language skills, but not to the same level as those who receive them earlier.

Until recently, most evidence for sensitive periods in humans was drawn from the domain of language acquisition. Case studies of individuals chronically deprived of linguistic stimulation in early childhood showed that these individuals failed to develop normal language, even after intensive exposure (Curtiss, 1977). In parallel, studies of children with complete removal of the language-dominant left hemisphere revealed that as long as the removal occurred early, language could develop relatively normally. These findings, while not always easy to interpret, led Lenneberg (1967) to propose that there was a critical period for neural plasticity underlying language functions that extends from early infancy to puberty. We would now probably describe this as a sensitive period, because even under conditions of extreme deprivation, the rudiments of language develop very consistently. Lenneberg's hypothesis has been applied to the study of second-language acquisition to suggest that exposure to a second language during this sensitive period results in greater fluency than exposure after that time. This has been supported by the results of a number of studies showing that second-language proficiency is greater in individuals who were exposed to the second language before age 11–13 (Johnson and Newport, 1989; Weber-Fox and Neville, 2001).

While I am drawing a clear conceptual distinction between critical and sensitive periods in development, by now it is probably clear that this distinction is really more of a continuum; with genetics and experience contributing more or less strongly to the development of brain and behavior depending on the system, the function and the point in development.

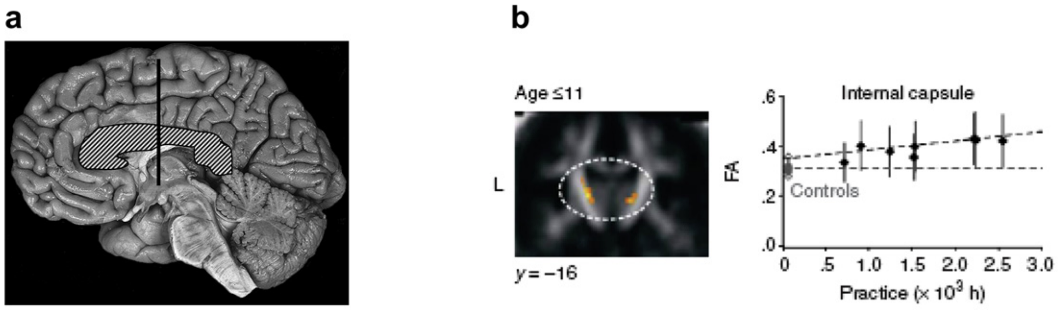
A number of recent behavioral studies have presented evidence for critical or sensitive periods for musical training. Evidence for the impact of early training on auditory perception comes from studies of musicians with absolute or "perfect" pitch. Absolute pitch is the ability to name an individual pitch without reference to an external standard. Baharloo et al. (1998) tested a large sample of 691 musicians.

They found that of the 92 musicians who exhibited perfect pitch, 78% began training before the age of six; and 92% before age nine. Thus, the developmental window for absolute pitch may be more similar to a critical than a sensitive period. Similar results have been obtained by other groups (Miyazaki and Rakowski, 2002; Costa-Giomi et al., 2001), and it has been suggested that there may be a genetic component to the development of this skill (Baharloo et al., 1998).

Maturational changes in the human brain coincide with and underlie changes in a wide range of cognitive and motor abilities (Giedd et al., 1999; Paus et al., 1999; Casey et al., 2005; Shaw et al., 2008). A large number of neuroimaging studies have shown differences in brain structure and function between musicians and non-musicians (see Gaser and Schlaug, 2003b; Peretz and Zatorre, 2004 for review). Further, there is a strong body of evidence that changes in structure and function are related to the number of years of musical training (Bermudez et al., 2009; Foster and Zatorre, 2009; Pantev et al., 1998; Trainor et al., 1999). Of these studies, several provide suggestive evidence that musicians who begin training early in childhood show greater plasticity in auditory and motor regions of the brain than those who start later (Elbert et al., 1995; Gaser and Schlaug, 2003a; Koeneke et al., 2004; Bengtsson et al., 2005; Schneider et al., 2002). Elbert et al. (1995) showed that expert string players had a larger cortical representation of the digits of the left hand. Further, they found a strong correlation between the size of the digit representation and the age of start of musical training; with those who began earlier having larger representations. Schlaug et al. (1995) reported that musicians had a larger anterior corpus callosum than non-musicians, and that those who began training before age seven showed a greater difference than those who began after age seven (Fig. 1, panel a). More recently, professional pianists were shown to have greater density of white matter in motor pathways, and that density was related to the number of hours they had practiced before age eleven (Bengtsson et al., 2005; see Fig. 1, panel b). In the auditory domain, musical training affects the processing of musical chords and linguistic pitch perception, with those who begin earlier showing a greater enhancement of the brainstem response (Wong et al., 2007; Lee et al., 2009).

There are a number of longitudinal studies that support the idea that childhood musical training can directly impact brain structure and function. Hyde et al. (2009) found that six-year-old children who took piano lessons for one year showed structural changes in auditory and motor regions of the brain that were correlated with performance on musically relevant tasks. Similarly, studies of children before and after their first year of Suzuki music lessons showed changes in electrophysiology, particularly for the sounds of their trained instrument (Fujioka et al., 2006; Shahin et al., 2004, 2008). Finally, other studies of musical training have shown transfer effects, both to specific auditory language skills and to more general cognitive functions (Besson et al., 2007; Moreno et al., 2009; Schellenberg, 2004).

Taken together, these findings suggest that there may be a sensitive period for musical training, similar to that observed for language acquisition. However, none of these previous studies were designed to directly address the impact of early training, and thus did not control for differences between early- (ET) and late-trained (LT) musicians in the total number of years of musical training and experience. By definition, a musician who begins training early has more years of experience than one who begins later when both are the same age. Therefore, it is possible that the observed differences in the brain could be accounted for simply by the duration of



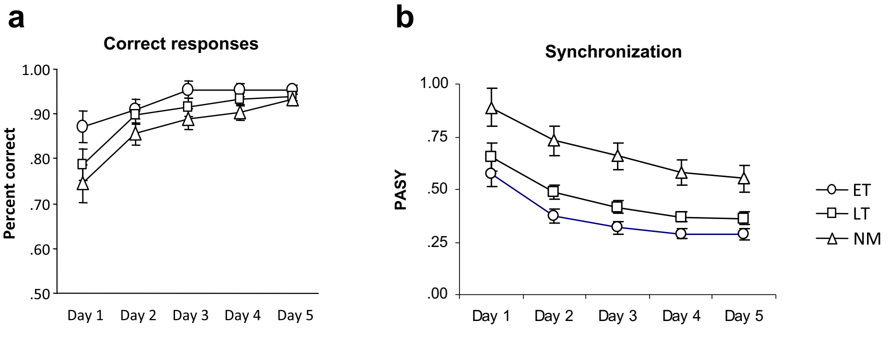
	Total CC area	Anterior half of CC area	Posterior half of CC area
ET (< 7) **(n= 21)**	709 ± 81	384 ± 42	321 ± 44
LT (≥ 7) **(n= 9)**	637 ± 77	340 ± 43	297 ± 38

Fig. 1 – Panel a illustrates the differences found in the volume of the anterior corpus callosum between musicians beginning practice before and after the age of seven (Schlaug et al., 1995). Panel b illustrates data showing the relationship between white-matter density measured using diffusion tensor imaging (DTI) and hours of practice in childhood for a group of highly trained musicians (Bengtsson et al., 2005). The left panel shows the regions of the internal capsule where fractional anisotropy (FA) – a measure of white-matter integrity derived from DTI data – was correlated with hours of practice before age eleven (L indicates the left hemisphere in the image). The right panel shows the correlation of individual subject's FA values with the cumulative number of hours practiced before age eleven.

musical training. The relationship between the number of years of musical training and brain structure and function has been consistently demonstrated (Amunts et al., 1997; Bengtsson et al., 2005; Foster and Zatorre, 2009). In addition, none of the studies addressing the impact of early training tested behavior to assess the relationship between brain changes and changes in performance. In order to accurately assess the impact of early training on performance and brain structure, we first have to show that any such differences are the result of the time of training, and not just a result of greater years of musical experience. Further, while studies in children are important in showing that significant training-induced plasticity can occur in childhood, only studies in adult musicians can identify long-term effects. Therefore, a series of experiments in our laboratory have examined possible behavioral differences in ET and LT musicians who were matched for years of musical training and experience.

In the first experiment, we tested musicians on learning of a visual rhythm imitation task (Watanabe et al., 2007; Fig. 2). The participants were predominantly piano and string players, with an average of 14.3 years of experience. Musicians were separated into two groups, ET musicians who began training before age seven, and LT musicians who began after age seven. The age-of-start cutoff was based on previously described findings that musicians who began training before age seven show greater enlargement of the anterior corpus callosum than those who began later (Schlaug et al., 1995). The task used in this experiment requires participants to imitate a complex rhythm by tapping in synchrony with a series of visual stimuli (Fig. 2, panel c). The stimuli were ten-element visual sequences consisting of a series of white squares presented sequentially in the centre of a computer screen. The sequence was composed of five long (750 msec) and five short (250 msec) elements, with a constant inter-stimulus interval (500 msec). The sequences were constructed to have no more than two repeating elements as well as seven transitions from short to long. This results in sequences that are temporally regular, but do not conform to a standard musical rhythm.

Participants were required to tap in synchrony with the sequences using a single button of the computer mouse. They were instructed to reproduce the sequence by depressing and holding the mouse key for the duration of each of the elements. The task is practiced over five days, and two measures of performance were assessed: accuracy and response synchronization. Accuracy measured participants' ability to reproduce the correct order of short and long elements in the sequence. Response synchronization measured participants' ability to synchronize with the onset and offset of each element in the sequence. These measures examined learning of two different aspects of the task. Accuracy reflects learning of the more explicit component of the task – encoding of the correct order of short and long durations in the sequence. Response asynchrony reflects the ability to precisely time key-press and key-release responses relative to the visual stimuli. This task is advantageous for two reasons. First, the tapped sequences are presented visually and are non-metrical, making them relatively difficult even for musicians, and requiring them to generalize from the more common auditory, metrical rhythms encountered in musical training. Second, because the task is learned over five



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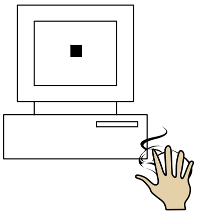


Group	Age	Age of Onset	Years of Musical Experience	Years of Formal Training	Hours of Current Weekly Practice
ET (<7)	22.1	5.9	14.8	7.7	11.8
LT (>7)	27.5	11.4	13.7	6.3	13.4
***t*-Test**	** p <.01*	** p <.001*	*n.s*	*n.s.*	*n.s.*

Fig. 2 – Panels a and b show the results of an experiment comparing performance of ET and LT musicians on a visual rhythm imitation task (Watanabe et al., 2007). For global accuracy (panel a), ET musicians performed better than LT musicians on the first day of practice, but LT musicians caught up on subsequent days. For the measure of response synchronization (Percent asynchrony – PASY; panel b), ET and LT musicians performed similarly on the first day, but ET musicians subsequently improved, and maintained their advantage over LT musicians for the remaining days of practice. Panel c illustrates the experimental set-up. The table shows how the two groups were matched for variables related to musical training and practice.

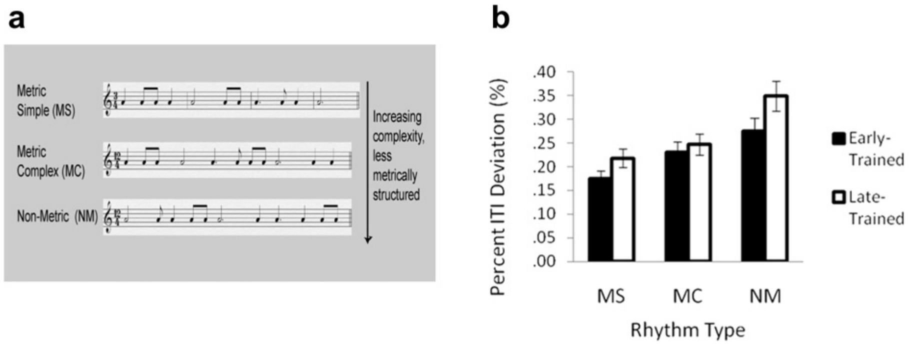
days, we could assess whether any differences between ET and LT musicians were persistent, or if their performance would equalize with practice.

The ET and LT groups were matched for years of musical experience, years of formal training and hours of current practice using a detailed musical experience questionnaire (Fig. 2, table). Results showed that on the first day of training ET musicians performed better than LT musicians on the accuracy measure, but that on subsequent days, performance was equal. For the measure of response synchronization, on the first day of training, performance of the two groups was equal, but on day two, ET musicians performed better than LT musicians, and this performance advantage persisted for the remaining days of practice (Fig. 2, panel b). These findings support the idea that there may be a sensitive period in childhood where enriched motor training through musical practice results in long-lasting benefits for performance later in life. Because performance differences were greater for the measure of response synchronization compared to accuracy, this suggests that early training has its greatest effect on neural systems involved in sensorimotor integration and timing.

Although these results were intriguing, at least two questions could be raised regarding the findings from this experiment. Firstly, would performance differences between ET and LT musicians still be observed using a more familiar, musically relevant task such as synchronization with auditory rhythms? Secondly, could group differences in cognitive abilities contribute to the observed differences in task performance? It could be the case that ET musicians possess enhanced cognitive abilities that would account for the observed differences in rhythm synchronization performance.

To address these questions, a second sample of ET and LT musicians, again matched for years of formal training, hours of current practice and years of experience, were tested on an auditory rhythm synchronization task (Bailey and Penhune, 2010; Fig. 3, table). The musicians in this sample were again predominantly piano and string players, with an average of 17.5 years of experience across the two groups (see Fig. 3, table). The task required participants to tap along with six auditory rhythms; two rhythms at each of three levels of metrical complexity (Chen et al., 2008a, 2008b; Fig. 3, panel a). All rhythms used the same 11 notes, and differed only in their temporal organization. The 11 notes were reorganized to create three levels of increasing metrical complexity based on Povel and Essen's rules (Povel and Essens, 1985; Essens and Povel, 1985). Simple rhythms were highly predictable, complex rhythms were more unpredictable and frequently syncopated, and non-metrical rhythms were unpredictable and did not fall into a countable beat. Because we were looking for subtle differences between ET and LT musicians, we felt that it was advantageous to use a task that included rhythms that would be difficult for all musicians to imitate.

Based on previous studies (Schellenberg, 2004, 2006) that showed a relationship between music training and performance on a range of cognitive variables, musicians were also tested standardized measures of vocabulary, non-verbal reasoning and auditory working memory [Vocabulary, Matrix Reasoning, Digit-Span and Letter-Number Sequencing (Wechsler, 1997, 1999)]. Because both the ET and LT groups were highly trained musicians, we hypothesized that they would not differ on measures of global cognitive function, such as Vocabulary and Matrix Reasoning, but might differ on measures of working memory, and that performance on



Group	Age	Age of Onset	Years of Musical Experience	Years of Formal Training	Hours of Current Weekly Practice
ET (<7)	25.0 (±3.8)	5.92 (±1.0)	18.67 (±4.5)	10.00 (±4.2)	19.50 (±10.9)
LT (>7)	27.8 (±4.7)	10.67 (±3.0)	16.42 (±4.3)	7.33 (±4.2)	23.75 (±16.3)
***t*-Test**	*n.s.*	$p < 0.001$	*n.s.*	*n.s.*	*n.s.*

Fig. 3 – Panel a illustrates the rhythm stimuli used in the experiment comparing ET and LT musicians on an auditory rhythm synchronization task (Bailey and Penhune, 2010). Panel b shows rhythm synchronization for the two groups as measured by the percent deviation of responses from the correct inter-stimulus intervals in the rhythms. The results show that ET musicians are more accurate than LT musicians across rhythm types. The table shows how the two groups were matched for variables related to musical training and practice.

working memory measures might be related to task performance.

The results of the experiment showed that ET musicians performed better than LT musicians in reproducing the temporal structure of the rhythms (Fig. 3, panel b). There were no differences between the groups for any of the cognitive measures. However, across both groups, individual task performance correlated with auditory working memory abilities and years of formal training. Hierarchical regression analysis showed that although working memory was correlated with task performance, group, or time of start of training, accounted for a significant proportion of the variance, even when working memory was controlled for. In addition, partial correlation analyses showed that working memory abilities and years of formal training accounted for independent portions of the variance in task performance. These results indicate that for all musicians, formal training and working memory are important for task performance, but are not affected by the age of start.

Taken together with the previous experiment, these results support the existence of a sensitive period during development when musical training can have long-lasting impacts on adult performance, particularly for sensorimotor integration and timing. In the second sample, ET and LT musicians did not differ on any cognitive measure, indicating that adult cognitive ability does not contribute to the observed group differences in task performance. While ET and LT musicians were matched for years of musical experience, individual musicians were not randomly assigned to begin earlier or later. Therefore, although these results go a long way toward demonstrating the existence of a sensitive period, there are a number of factors other than the age of start of training that might contribute to ET musicians' better performance, such as early ability, motivation and family background. Some factors, such as individual differences in auditory, motor or general musical abilities may be largely under genetic control; while others, such as family support for training and exposure to music in the home are predominantly environmental. These factors will be discussed in detail below, after a review of possible developmental mechanisms that might underlie the sensitive period effect.

1. Developmental mechanisms underlying sensitive periods

Maturational changes in the human brain are greatest in childhood, but continue into early adulthood. Following birth, the number of synapses, and therefore the volume of grey matter, continues to increase for between 3 and 15 months, depending on the region of the brain (Huttenlocher and Dabholkar, 1997). Once this peak is reached, the number of synapses decreases through the process of pruning, which is thought to underlie experience-dependant specialization. In contrast, the amount of white matter increases throughout development. Therefore, although the total size of the brain does not change substantially after the age of five, the amount of white matter increases until sometime around age 20 (Casey et al., 2000). Over the last ten years, a number of studies using structural magnetic resonance imaging (MRI) techniques have examined developmental changes in the volume and proportion of grey and white matter in the brain. The results of these studies have shown that increases in white-matter volume are age- and region-specific, with sensory and motor regions showing increases earlier, and frontal and temporal–parietal association areas later (Casey et al., 2000; Gogtay et al., 2004; Sowell et al., 2004). Increasing white-matter volume measured by MRI is thought to correspond to increasing number of axons, greater diameter of axons, or greater thickness of the myelin sheath that surrounds them. Very interestingly, changes in white-matter volume with development have been shown to be related to changes in language ability and executive control processes (Durston and Casey, 2006; Durston et al., 2006).

The auditory cortex appears to have an unusually long period of developmental plasticity compared with other sensory systems; changes in its cellular organization and connectivity continue into late childhood (Kral and Eggermont, 2007 for review; see Moore, 2002). Some features of auditory cortex organization may be largely genetically determined. For example, some form of rudimentary tonotopic organization and binaural sensitivity appears to develop in the absence of any auditory input (Hartmann et al., 1997; Tillein et al., 2006). Further, gross anatomical asymmetries in auditory cortex that are thought to be related to language processing are present at birth (Smith et al., 2009), and are relatively resistant to deprivation due to deafness (Emmorey et al., 2003; Penhune et al., 2003). Direct thalamic input to the auditory cortex only develops during the first year of life, and the density of this input does not reach adult levels until the age of 4–5 (Moore, 2002; Moore and Linthicum, 2007). This is likely to account for the relatively slow and low-amplitude cortical responses measured with electrophysiology in infants (Thomas and Crow, 1994; Cheour et al., 2001; Trainor, 2008).

Between the ages of 1–5, there is a massive growth in the number of synapses, or connections within the auditory cortex (Moore and Guan, 2001; Moore and Linthicum, 2007). These connections are stimulated both by direct sensory input and by feedback from other brain areas. Simultaneously, connections that are not stimulated are eliminated, through synaptic pruning. Connectivity is also enhanced by increasing myelination of auditory fibres which remain unmyelinated until one year and only reach adult levels at age 4–5 (Moore and Linthicum, 2007). This is quite different from the visual system, where the adult level of myelination is reached in the first few months of life (Kinney et al., 1988). These changes in connectivity result in changes in electrophysiology, where cortical auditory evoked potentials (ERP), such as the P1 and MMN show significant changes across the first year of life (Kraus et al., 1993; Ponton et al., 2000; Cheour et al., 2001; He et al., 2007; Trainor, 2008). At the same time, children develop preferential processing of speech sounds from their native language (Kuhl et al., 1992) and for tonal information from the music of their culture (Trainor and Trehub, 1992). This period of maximum change in connectivity also coincides with optimum period for cochlear implantation, when deaf children develop more normal auditory cortical physiology, and have better language abilities as adults (see Sharma et al., 2009 for review). However, maturation of the auditory cortex does not end here. Between the ages of 5–12, there is continuing maturation of the intracortical connections which increase connectivity with higher-order auditory processing areas and other regions of the brain (Moore and Linthicum, 2007; Pujol et al., 2006). This extended development is reflected in the development of cortical potentials such as the N1, P1 and P2 (Ponton et al., 2000; Trainor, 2008); and in continuing improvements in children's ability to process degraded speech (Eisenberg et al., 2004; Elliott, 1979) and the development of sensitivity to more complex aspects of music in their culture (Costa-Giomi, 2003; Trainor and Trehub, 1994; Hannon and Trainor, 2007). Very importantly, it has also been shown that these electrophysiological responses can be modified by musical training in childhood (Shahin et al., 2004, 2008; Fujioka et al., 2006).

It is hypothesized that this extended period of plasticity in auditory cortex facilitates the acquisition of language – and music – by allowing lower-level sensory processing to be sculpted by feedback from higher-level cognitive processing areas (Kral and Eggermont, 2007; Kraus et al., 2009). Kral and Eggermont (2007) have theorized that experience shapes the cortex directly through "bottom-up" processes driven by the type and frequency of specific auditory features in the environment. "Top-down" processes also shape cortex through feedback from higher-order processing areas, such as those involved in language and attention, as well as other sensory regions, such as motor and visual areas. Higher-level processing assigns behavioral significance to the incoming auditory information, and integrates it with other sensory modalities. The impact of top-down feedback on auditory processing has been shown in both animals and humans at the level of the cortex (Davis and Johnsrude, 2003; Polley et al., 2006), and more recently the effects of musical training have been shown to impact auditory processing in the brainstem as well (Kraus et al., 2009). The impact of both top-down and bottom-up processes may be greatest from ages 1 to 5, when plasticity in the auditory cortex is greatest. However, we also know that there is a further period of development from ages 5 to 12. Based on this, we can speculate that there may be multiple sensitive periods for musical training. Development of absolute pitch may require training during the earlier period in order to develop very precise pitch categories and labels. Other abilities, such as the rhythm synchronization described in our experiments, may continue to develop during the later period, when on-going myelination enhances connectivity between auditory and motor regions. Finally, while training during a sensitive period may be particularly effective in driving behavioral changes and brain plasticity, our work and that of others indicate that learning and plasticity continues through adulthood (Ragert et al., 2004; Watanabe et al., 2007).

In the motor system less is known about the detailed cytoarchitectonic changes that occur across childhood. We do know that mature cortical architecture develops by about one year, but that white matter, and thus connectivity, continues to develop well into early adulthood (Marin-Padilla, 1970). A number of structural MRI studies have shown increases in the white-matter concentration of the corticospinal tract and corpus callosum between childhood and late adolescence (Barnea-Goraly et al., 2005; Paus et al., 1999; Wilke et al., 2007). In addition to changes in cortical motor pathways, structural imaging studies have also shown changes in the white-matter pathways of the striatum and in the total volume of the cerebellum that continue into late adolescence (Barnea-Goraly et al., 2005; Mackie et al., 2007; Sowell et al., 1999). It has been hypothesized that increases in myelination in motor pathways may underlie decreases in nerve conduction time that are observed with development, and that increased myelination might be related to behavioral phenomena such as decreasing reaction times and increasing motor speed associated with the improvement of fine motor skills across early childhood. Children show increasing speed in simple reaction time and repetitive finger tapping (Garvey et al., 2003), and motor evoked potentials show decreasing conduction times and increasing inhibition between the hemispheres (ages 10–13). At the same time, mirror movements, which are relatively common in children up to the age of 6–7, decrease. It appears likely that motor development depends on the maturation of multiple cortical and subcortical control mechanisms. Additionally, as described above, increasing connectivity between auditory and motor regions through white-matter development may underlie on-going development of functions related to sensorimotor integration and timing.

If there is a sensitive period for musical training before age seven, we would predict that children's ability to learn motor skills relevant for music might change during this period. In order to test this, a recent study from our laboratory examined motor learning in 6-, 8-, and 10-year-old children (Savion-Lemieux et al., 2009; Fig. 4). We used a finger sequencing task that is similar to learning a simple tune on the piano. Children have to "catch the animal," appearing in one of four locations on a computer screen, by pressing the corresponding key on an electronic keyboard using four fingers of the right hand (Fig. 4, panel a). Children were tested across two days, and performance was assessed using two measures: accuracy and response synchronization. Overall, our results showed a developmental progression in motor sequence learning within and across days of practice. Interestingly, the two components of performance, accuracy and response synchronization, showed different developmental trajectories (Fig. 4, panels b and c). For accuracy, which measures explicit stimulus–response associations, 6- and 8-year olds performed more poorly early in learning, and also showed the greatest rate of improvement with practice. By the end of Day 2, only the 6-year olds still lagged behind all other groups. For response synchronization, which measures more procedural, sensorimotor integration and timing, all child groups differed from adults early in learning, but both child and adult groups showed similar rates of improvement across blocks of practice. By the end of Day 2, 10-year olds reached adult levels of performance, whereas 6- and 8-year olds did not. We postulate that this differential pattern of results is consistent with the idea that brain systems required for stimulus–response association develop earlier than those involved in fine-grained sensorimotor integration and timing.

Having reviewed current information about brain development, we can now ask the question: How might musical training during a sensitive period influence auditory and motor development? Based on our results in ET and LT musicians and motor learning in childhood, we would suggest

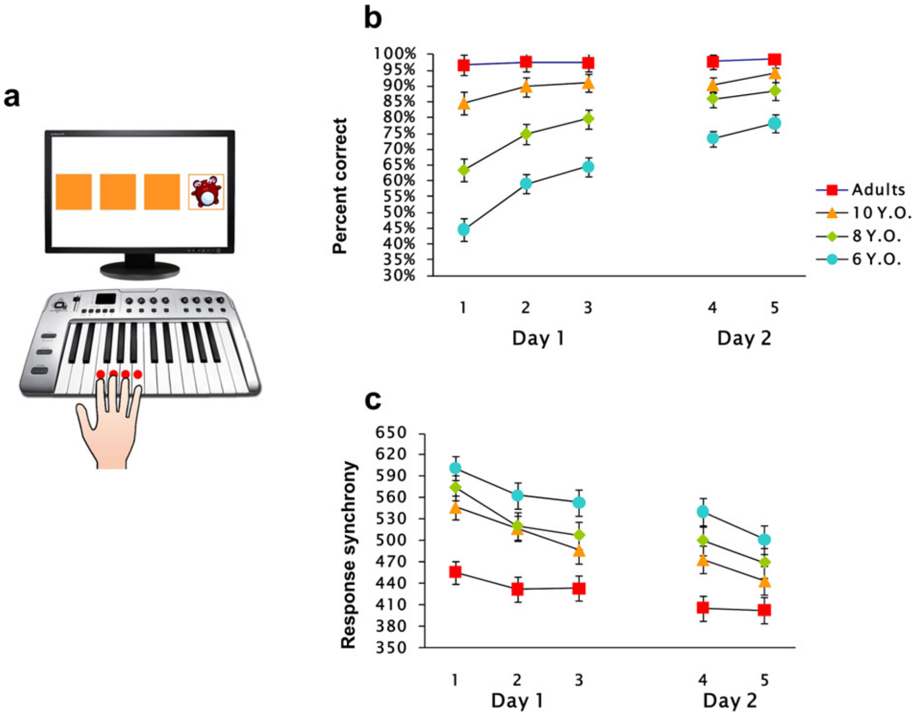


Fig. 4 – Panel a illustrates the experiment set-up for an experiment comparing 6-, 8- and 10-year-old children on a motor sequence learning task (Savion-Lemieux et al., 2009). Panels b and c illustrate the data for key-press accuracy and response synchronization. The results revealed that the two components showed different developmental trajectories. For accuracy, which measures explicit stimulus–response associations, 6- and 8-year olds performed more poorly early in learning, and also showed the greatest rate of improvement with practice. By the end of Day 2, only the 6-year olds still lagged behind all other groups. For response synchronization, which measures more procedural, sensorimotor integration and timing, all child groups differed from adults early in learning, but both child and adult groups showed similar rates of improvement across blocks of practice. By the end of Day 2, 10-year olds reached adult levels of performance, whereas 6- and 8-year olds did not.

that enriched auditory and motor experience when neural and behavioral systems are immature can induce lasting enhancement in performance and the brain. As described above, during a sensitive period neural systems are particularly sensitive to relevant stimuli, and are more susceptible to change when stimulated. It has also been suggested that training during a sensitive period has a unique advantage, because it can shape the way those circuits respond to additional experience later in the sensitive period and beyond (Knudsen, 2004; Kral and Eggermont, 2007; Kuhl et al., 2005; Trainor, 2005). Early training in motor implementation and sensorimotor integration may promote development of highly tuned circuits. This does not mean that there is no further plasticity in brain or behavior after this point. Later in development, these circuits can be further optimized by learning mechanisms that remain plastic throughout life. This is consistent with the results of our first study, which showed that ET musicians continued to improve on the measure of response synchronization, and to out-perform the LT musicians across five days of practice. Further evidence that musical training can enhance adult plasticity comes from a recent study of tactile discrimination in professional pianists (Ragert et al., 2004). This study showed that not only did pianists have lower sensory discrimination thresholds compared to non-pianists, but that with additional training pianists were able to improve those thresholds to a greater degree than non-pianists.

Because music requires a high degree of sensorimotor integration, it may be particularly efficient in driving plasticity during a given sensitive period because it can stimulate both bottom-up changes through specific sensory experience and top-down changes through feedback from other systems. In particular, because musical training acts on the auditory system, with its extended period of development, it can in turn exert an extended period of influence on the plasticity of earlier developing regions, such as the motor system. Finally, we know that motivationally relevant stimuli induce greater plasticity than those with no specific significance (Blake et al., 2006; Beitel et al., 2003). Music is highly rewarding (Blood and Zatorre, 2001; Blood et al., 1999; Salimpoor et al., 2011), and thus musical training may produce greater change than other types of auditory or motor experience.

2. Other factors contributing to sensitive period effects

The results of our studies in ET and LT musicians, along with work on absolute pitch, provide evidence for possible sensitive periods for musical training. This conclusion is strengthened by the fact that in our studies the groups were matched for years of experience, formal training and current practice. However, there were also clear individual differences in performance, and not all ET musicians performed better than LT musicians. Further, while we were able to control for differences in years of musical experience, individuals were not randomly assigned to begin earlier or later. Therefore, we cannot draw definitive conclusions about causality, and it is likely that there are other factors we did not assess that contribute to differences between the groups. The most important of these are pre-existing individual differences in early motor skill or ability. Early ability may be potentially related to two factors: 1) genetically determined differences in central and peripheral motor control, or auditory perception; and 2) individual differences in motivation or environment. Studies of musicians with absolute pitch show that there may be a genetic contribution to this ability (Baharloo et al., 1998; Zatorre, 2003), and recent work links some types of musical aptitude to genetic markers (Ukkola, 2009 #1015), but none of these can be developed without training. Similarly, a genetic predisposition for earlier development of motor skills or auditory tonal processing could underlie ET musicians' ability to start playing earlier and to obtain greater benefit from practice. Importantly, motivation can strongly affect learning and plasticity, as demonstrated by experiments in which auditory learning is enhanced by reward or survival saliency (Beitel et al., 2003; Knudsen, 2004; Blake et al., 2006). Therefore, children with greater intrinsic motivation or with greater family support may begin earlier and learn better. Finally, environmental factors such as access to musical training; family support and exposure to music in the home could also play important roles. In the future, studies examining matched groups of early- and late-starting children will shed light on the contributions of these factors.

Given the state of our current knowledge about sensitive periods for musical training, what are the next steps that we need to take? A clear direction for future research would be longitudinal studies in children that would seek evidence for incremental changes in behavioral and brain structure in and around a putative sensitive period. Some longitudinal studies testing children before and after musical training have already been done, showing improvements in performance on musical and speech tasks, along with changes in specific auditory ERP components (Shahin et al., 2004, 2008; Besson et al., 2007; Moreno et al., 2009; Fujioka et al., 2006) and changes in brain structure (Hyde et al., 2009; Schlaug et al., 2009). These studies show convincingly that children's brain structure and function can be changed by musical experience, but they do not tell us whether these changes are related to training during a specific period in childhood. Further, they do not address the long-term changes in ability or the brain that would be predicted to result from experience during a sensitive period in development. To do this, longitudinal studies in children who begin their training before and after the putative sensitive period would need to be conducted. Very importantly, in order to assess changes in performance in a longitudinal sample, behavioral tasks with norms for different ages will need to be developed to assess whether potential performance changes in children who begin training early differ from expected maturational changes. In addition to longitudinal studies, brain imaging studies investigating the relationship between brain structure and musical performance in ET and LT musicians would be useful in addressing these questions. A final category of future studies would investigate the relationship of other potential contributing factors, such as genetics or motivation. Heritability studies might address the question of whether more ET musicians come from families with musical training. Studies of motivation might ask whether ET musicians describe more family support/pressure to play or whether ET musicians describe greater intrinsic versus extrinsic motivation to play. As has been emphasized throughout this article, it is likely that a large number of factors contribute to the differences in brain and behavior seen between ET and LT musicians, and only through on-going research using converging methodologies will we be able to assess the relative weight and timing of these factors.

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