Representational Cortex in Musicians

Plastic Alterations in Response to Musical Practice

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ABSTRACT: The lifelong ability to adapt to environmental needs is based on the capacity of the central nervous system for plastic alterations. In a series of neurophysiological experiments, we studied the impact of music and musical training in musicians on the specific functional organization in auditory and somatosensory representational cortex. In one such study, subjects listened to music from which one specific spectral frequency was removed. This led to rapid and reversible adaptation of neuronal responses in auditory cortex. Further experimental evidence demonstrated that long years of practice and training by professional musicians to enable them to reach their capacity is associated with enlarged cortical representations in the somatosensory and auditory domains. This tuning of neuronal representations was specifically observed for musical tones and was absent when pure sinusoidal tones were used as stimuli. In the somatosensory cortex, plastic changes proved to be specific for the fingers frequently used and stimulated. These changes were not detected in the fingers of the hand that were not involved in playing the particular instrument. Neuroplastic alterations also may be driven into a domain where they may become maladaptive. The clinical syndrome of focal hand dystonia that may occur in musicians who engage in forceful practice may be one such consequence. We will discuss the possibilities of reversing maladaptive responses leading to the successful treatment of focal hand dystonia, which relies on basic research about cortical reorganization. This example elucidates how neuroscientific progress can guide the development of practice guidelines and therapeutic measures for the benefit of professional musicians.

INTRODUCTION

The structural and functional organization of the human brain becomes increasingly differentiated during child development. In higher mammals, including humans, neurons are formed prenatally as are some of their interconnections into neural networks. For many years the prevailing opinion suggested that network connections between neurons are built primarily during cerebral maturation processes in childhood, with the exception of only those structures that were directly involved

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in memory. It was thought that this network pattern, almost like a connection diagram, would not change later. However, humans respond with considerable flexibility to new challenges throughout their entire life. Since the early 1980s, increasing experimental evidence demonstrated that the connectivity of the adult brain is in fact only partially determined by genetics and early development, and may be substantially modified through sensory experiences, even during adulthood.

Practicing and performing music entails intense auditory and somatosensory peripheral sensory excitations, which are transmitted via specific receptors and fiber systems to the corresponding specialized regions of the cerebral cortex. Because the functional organization of representational cortex has been intensely studied, the examination of sensory cortical areas in the somatosensory and auditory systems provides an excellent model for studying the plastic changes that are associated with being a musician. The sensory cortex of both systems has a known topographical order of neuronal representations: a homuncular mapping of the body surface on somatosensory cortex[1–3] and a tonotopic mapping of acoustic frequency in auditory cortex.[4–7] Thus, modifications of representations can be specifically assessed. For example, different fingers of a given hand may not be equally used (and thus not equally stimulated) when playing certain musical instruments.

Based on W. James's suggestion at the end of the nineteenth century that learning may alter synaptic connectivity, the prominent Canadian neuropsychologist Donald Hebb formulated an important and innovative theory to view the brain not as a static but as a dynamic system. Hebb's rule asserts that effective connections between neurons are formed depending on synchronous activation: "Cells that fire together, wire together."[8] The development of new scientific methods for recording neuronal activity has made it possible to prove the hypothesis of plasticity in functional neuronal networks. The electrical activity of single neurons can only be recorded invasively in animals, but derived potentials that reflect the activity of a group of neurons can be recorded noninvasively on the scalp surface by means of electroencephalography (EEG). The magnetic counterpart of the EEG is the magnetoencephalography (MEG), which has become an established method for noninvasive study of the activity of the human cortex.[9] The main sources of cortical evoked magnetic fields are the pyramidal cells, which produce currents flowing tangentially to the surface of the head. Though MEG measurements provide only a macroscopic view of the function of the brain, the spatial resolution achieved with this technique is sufficient to give indications of functional organization and reorganizational plasticity of the human cortex by localizing the sources of evoked magnetic fields, which are elicited by defined and standardized peripheral excitation.

The first studies to clearly demonstrate reorganizational plasticity of the adult cortex were performed in the 1980s in "deafferentation" experiments. Typically, in these studies the afferent information influx specific to certain cortical areas was eliminated.[10–15] One mechanism of change observed was that neurons that had lost their regular input were recruited by neighboring regions. For example, neurons that were specialized for processing information from the fifth digit (little finger) may process information coming in on the second digit after the fifth digit was amputated. Similarly, neurons that were specific to a certain acoustic frequency may respond to neighboring spared frequencies after the part of the cochlea transmitting their originally preferred input was destroyed.

Experimental studies in monkeys have demonstrated that intensive sensory stimulation may lead to an expansion of the corresponding cortical area.[16,17] Here we briefly review the experimental paradigm for one such study in the somatosensory modality concerning finger representation in adult monkeys. The animals were trained to touch a rotating disk with the tip of their index and middle fingers for 15 seconds. The surface of that disk was an irregular grid, so that it caused a sensation (and somatosensory excitation) specifically for those two fingertips. Anytime the monkeys touched the disk for 15 s, they received a reward (chips with banana taste). After about 600 stimulation periods, the representation of the hand in the somatosensory cortex was measured. The representation for the two stimulated fingers had become enlarged. Recanzone *et al*. trained owl monkeys for 60–80 daily sessions to make fine-pitch discriminations in selected regions of the auditory frequency spectrum (these regions differing among animals).[17] Tonotopic mapping carried out invasively afterward showed that the cortical area tuned to the trained frequencies was enlarged by a factor of 2 to 3 compared to untrained monkeys or to animals that experienced the same acoustic stimuli passively while being trained on a somatosensory discrimination task. Thus, the organization of the brain seems capable of significant change to adapt to the changing demands of the organism's environment. Synchronized sensory stimulation may be of particular importance for such changes. The common observation captured in the German proverb *Übung macht den Meister* [practice makes perfect] could therefore have its neurobiological correlate in an augmented simultaneous stimulation of neurons, which entrains a reorganization of the functional neuronal network.

Musicians practice and train for many years before they achieve their professional skills. Coordination and synchronization of somatosensory and motor control on the one hand, and audition on the other hand, are crucial when playing a musical instrument. We therefore hypothesized that musical aptitude and the training to fulfill it may be associated with plastic changes of neuronal representations in the cortical organization. We will describe below a series of experiments that support this hypothesis for the somastosensory and auditory domains.[18–20]

Neuronal representations in the given cortical field of interest were determined by measuring evoked magnetic fields contralateral to the stimulated side with a 37-channel BTi Magnes system. For the somatosensory modality, a brief pneumatic stimulation was applied to the fingertips; for the auditory modality, a variety of different auditory stimuli were delivered to the right ear. The following sections describe some experimental examples in more detail.

SHORT-TERM PLASTICITY EFFECT OF THE AUDITORY CORTEX INDUCED BY NOTCHED MUSIC

Most studies of deafferentation-induced cortical reorganization have investigated cortical reorganization on a timescale of days to weeks, or longer. However, other more recent studies have documented rapid changes in cortical dynamics following deafferentation. These studies have shown that neurons broaden and shift their receptive fields to sensory surfaces near or beyond the edge of the lesioned zone within minutes of deafferentation in the somatosensory[21] and visual systems,[22] and within hours in the auditory one.[23] Rapid retuning of sensory neurons has also been observed following reversible "functional" deafferentation in which sensory input from the environment is altered by procedures such as artificial scotomota[24] or digit ligation[25] rather than by permanent lesions of the receptor organs.

A study of "functional deafferentation" was carried out to determine whether plastic changes of frequency representation occur on a short timescale of a few hours when the adult human auditory cortex is deprived of sensory input. Ten normal test subjects were asked to provide three favorite CDs from their CD collection. The music was manipulated in such a way that a notch between 0.7 and 1.3 kHz, centered around 1 kHz, was produced using a band rejection filter (Bessel, 96 dB/oct) in the broad-band spectrum of the music (cf. FIG. 1a). Although this manipulation initially produced a clearly noticeable change in perception, subjects reported that they quickly adapted to the modified sound and that their appreciation of the music during the listening time was unchanged. The subjects were asked to listen attentively to the music for a continuous period of three hours. Due to the notch filtering during this period, any afferent input to cortical neurons tuned to frequencies around 1 kHz was abolished. In order to measure the effect of notching of the music on the neuronal representation of 1 kHz, MEG recordings to the test stimulus (band-passed noise bursts centered at 1 kHz) were compared to MEG recordings to the control stimulus (band-passed noise bursts centered at 0.5 kHz; cf. FIG. 1a). The experiment was repeated three times in each subject on consecutive days in order to address the time course and the reversibility of cortical remodeling induced by this procedure. These repetitions served to investigate the dynamics of cortical reorganization over a period of 24 h. The auditory evoked fields (AEF, channels 12 and 35, depicting the maximum and minimum of the AEF, respectively) obtained for test and control stimuli before and after listening to notched music are shown for one representative subject in FIGURE 1b. Whereas the AEF amplitudes measured before and after listening to notched music are almost the same for the control stimulus, the AEF amplitude for the test stimulus is about 10% smaller after listening to notched music than before. FIGURE 1c demonstrates the differences of the strength of the cortical sources before and after listening to the notched music for the test and for the control stimulus, averaged over all subjects and days. Whereas the strength of the cortical source decreased significantly after the listening to the notched music for the test stimulus ($p < 0.01$), this value did not change appreciably for the control stimulus. In order to provide information on the reversibility of the notching effect within the time period of 24 h, the measurements taken before listening to notched music on each day were compared. Between days, no significant differences between the strength of the cortical sources were observed for these measures, a result that proves the reversibility of the short-term plasticity effect provided by the "functional deafferentation" with respect to listening to the notched music.

Taken together, our results suggest that reorganization of cortical representations can occur within time periods as short as a few hours following functional deafferentation of the adult human auditory cortex. The temporal properties of the notching effect are consistent with animal studies that have shown that cortical neurons deafferented by cochlear lesions display elevated response thresholds initially and then shift their tuning preferences away from the lesioned area to frequencies near the edge of the deafferented region over a period of 1–3 h or longer.[23] Several interre-

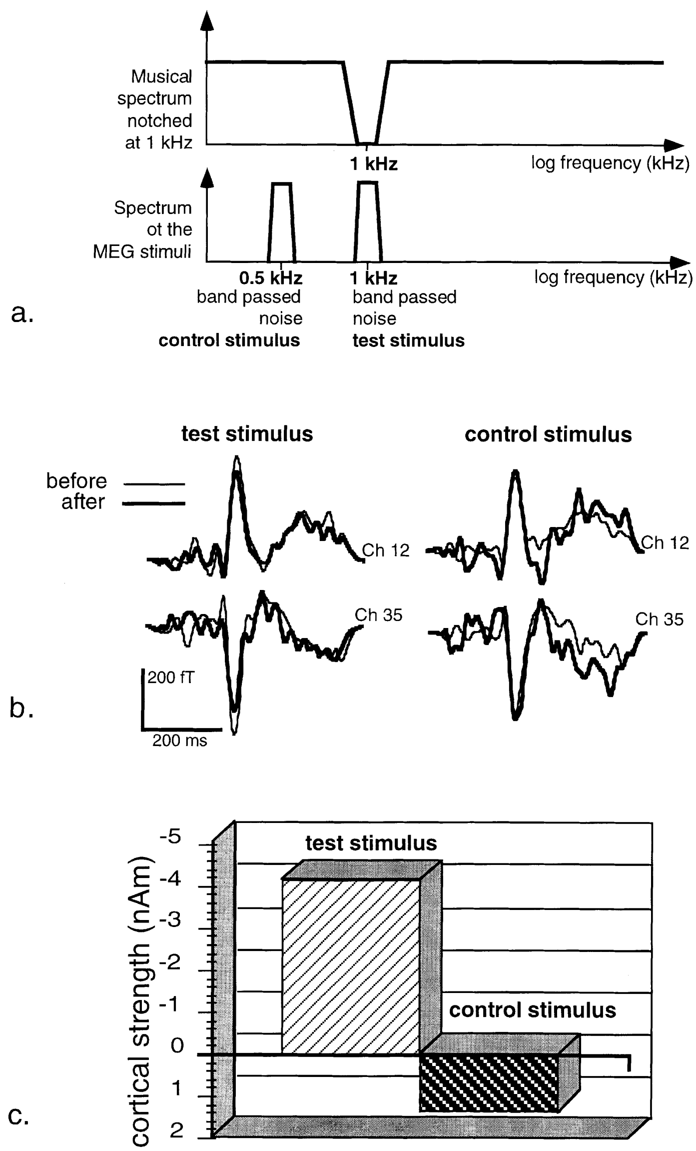

FIGURE 1. Short-term plasticity effect of the auditory cortex induced by notched music. (a) Music spectrum notched at 1 kHz (*top*) and spectral characteristics of the test and control stimuli for MEG recording (*bottom*). (b) Auditory evoked fields (AEF) of a single subject recorded for test stimulus (1 kHz, *left panel*) and control stimulus (0.5 kHz, *right panel*) before and after listening to notched music. (c) Change in cortical representation or respectively in the strength of the cortical source produced by listening to the notched music and calculated as the moment (Q, nAm) of the equivalent current dipole fitted to the N1m component of the AEF for test and control stimuli averaged over subjects and days (Modified from Pantev *et al.*[20])

lated mechanisms appear to contribute to cortical remodeling induced by deafferentation, including (1) changes in the efficacy of existing excitatory synapses unmasked by lesioning,[26] (2) modification of synaptic efficacy by transcription of immediate early genes,[27] and (3) the sprouting of new connections.[28] Of these mechanisms the first and second appear to be probable candidates to account for our findings. Synaptogenesis may occur within hours,[29] but axonal sprouting and dendritic growth may require more time and hence would be less likely to be involved.

CORTICAL PLASTICITY AND MUSICAL TRAINING

Somatosensory Representations

Two groups of subjects were examined. The first group consisted of nine musicians who played string instruments: six violinists, two violoncellists, and one guitarist. The subjects' average age was 24 ± 3 years. They had started to play their instruments 12 years earlier on average, ranging between 7 and 17 years. They practiced on their instruments for an average of nine to ten hours per week. The second group consisted of six control subjects who had never played a musical instrument and did not frequently carry out tasks that involved a systematic and rhythmic finger stimulation such as typing (on a typewriter or computer). All subjects were right-handed. The fingers D1 (the thumb) and D5 (the little finger) of both hands were consecutively excited with a brief, nonpainful standardized pneumatic pressure.

After excitation of the left-hand fingers D1 and D5, the strength of the cortical sources as determined with MEG were stronger in musicians than the corresponding sources in control subjects (FIG. 2). Thus, the cerebral representation was increased representing the excitation of those fingers that are intensively used in string instrument musicians. This effect was particularly pronounced for the fifth digit (D5). The cortical representation of the left thumb was also enhanced, but not as strongly as the one for left D5. Cortical representations obtained for right-hand stimulation did not differ between control subjects and musicians.

The amount of increase in somatosensory cortical representations of left-hand fingers in musicians depended on the age at which the musicians had started to play their instrument (FIG. 3). The cortical response for stimulation of D5 was greater in those musicians who had begun to play their instrument earlier. Among the musicians who started to play violin or violoncello later (after the age of 13 years), the cortical representations for D5 were somewhat smaller, but still larger than those observed in the control subjects who had never played an instrument.

Auditory Representation

Three groups of subjects were examined. The first group consisted of musicians with absolute pitch ($n = 9$), the second group of musicians with relative pitch ($n = 11$), and the third group of subjects were controls who had never played a musical instrument ($n = 13$). In the first group, the mean number of years the musicians had played their instruments was 21 ± 6, in the second group 15 ± 3 years. The musicians were recruited from the conservatory in Münster. The musicians with absolute pitch reported practicing their instruments for 27 ± 14 h per week, and the musicians with

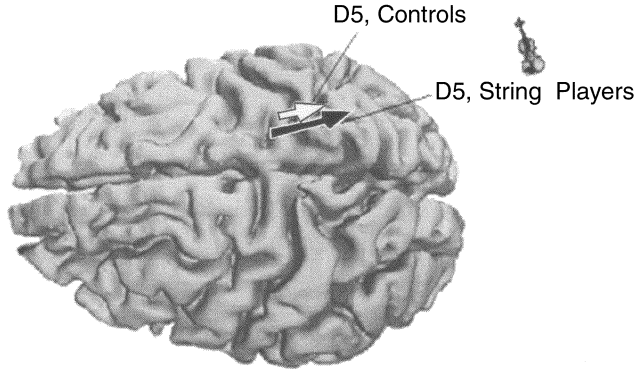

FIGURE 2. Equivalent current dipoles (ECD) elicited by stimulation of the digit 5 (D5) of the left hand of control subjects and string players, superimposed onto an MRI-reconstruction of the cerebral cortex of a control subject, selected to provide anatomical landmarks for the interpretation of the MEG-based localization. The arrows represent the location and orientation of the ECD vector for D5 averaged across musicians (*black arrow*) and control subjects (*white arrow*). The length of the arrows represents the mean magnitude of the dipole moment for D5 in each group. The dipole moment is larger for the musicians' D5 as indicated by the greater magnitude of the black arrow. (Modified from Elbert *et al.*[39])

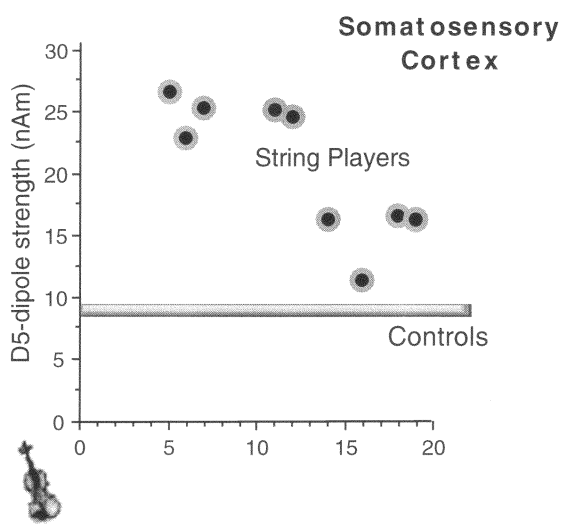

FIGURE 3. The magnitude of the D5 cortical strength as a function of the age of inception of musical practice: string players (*circles*), mean value for control subjects (*line*). Note the larger dipole moment for individuals beginning musical practice before the age of 12. (Modified from Elbert *et al.*[39])

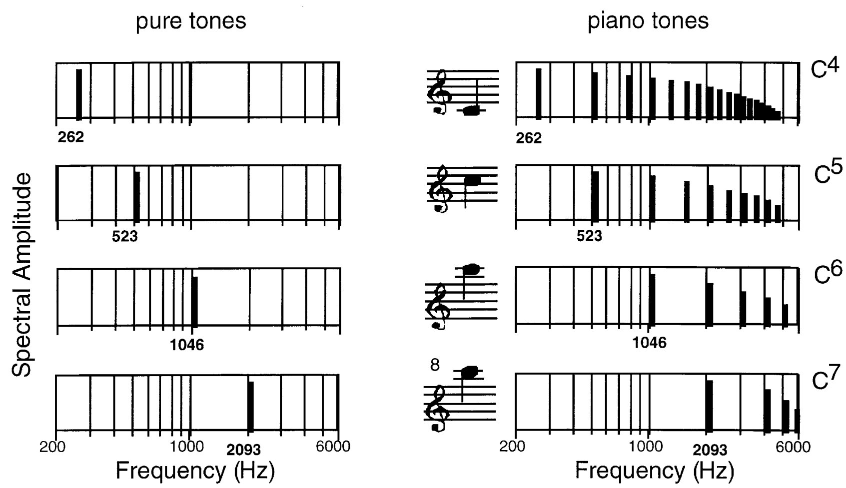

FIGURE 4. Spectra of piano tones C4, C5, C6, and C7 (American notation, having fundamental frequency at 262, 523, 1046, and 2093 Hz, respectively) and four pure tones of the same fundamental frequencies. (Modified from Pantev *et al.*[19])

relative pitch 23 ± 12 h per week, during the five years preceding participation in the study. The musicians who claimed to have absolute pitch were subjected to a testing procedure that was developed according to criteria established in the musical psychological literature.[30–34] A random sequence of 35 piano tones from H2 to C7 was presented to the musicians. For our study, in order to be considered a musician with absolute pitch, correct recognition of at least 90% of the tones was required. Musicians with relative pitch were either self-identified ($n = 9$) or were subjects who failed the test for absolute pitch ($n = 2$). The mean age in the three groups was 29 ± 6 years for musicians with absolute pitch, 26 ± 5 years for musicians with relative pitch, and 26 ± 4 years for control subjects. All participants were right-handed, as established by the Edinburgh handedness questionnaire[35] and did not have recent or past audiology, otology, or neurology medical history. Audiological status was normal at the time the study was performed for each subject.

The acoustic stimulation consisted of a pseudorandom sequence of four piano tones (C4, C5, C6, and C7; with the fundamental frequencies of 262, 523, 1046, and 2093 Hz), and four pure (sinusoidal) tones matching the fundamental frequencies (FIG. 4). Each stimulus was presented 128 times to determine the location and strength of the electrical source in the auditory cortex.

In all musicians larger neuronal excitation was noted for piano tones as compared to pure tones. Our measure for the cortical neuronal representation, the strength of the electrical dipole moment in both musician groups, was significantly 25% stronger for the piano tones as compared to the one for the pure tones ($p < 0.001$). By contrast, in the control subjects, who never played an instrument, no such difference was noted (FIG. 5).

This finding demonstrates an increase in neuronal representation specific for the processing of the tones of the musical scale in musicians. Similar to the described

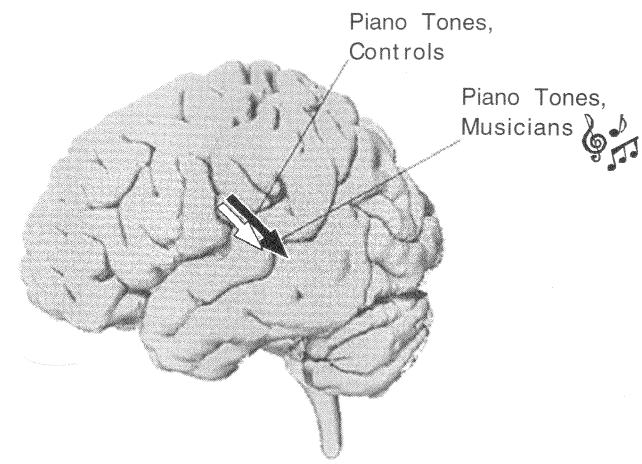

FIGURE 5. Mean values of the strength of cortical activation during the auditory N1 evoked field for piano tones as compared to pure tones in control subjects and musicians with absolute or relative pitch. (Modified from Pantev *et al.*[19])

enhancement of somatosensory representation, the degree of this increase was also dependent on the age at which the musicians had started to play their instruments. The earlier the initiation of musical practice, the stronger the neuronal response to the piano tones. In this study a marked difference was found between those who had begun practicing music before and after nine years of age.

The cortical representations for processing information from the fingers and the ears of musicians give an impressive demonstration that not only deafferentation, but also intensive training, can trigger a functional adaptation of the cortical organization. In general, this suggests that training can induce plastic changes of the adult human brain. In the musicians proficient in playing stringed instruments, the representation of the frequently used left-hand fingers is enlarged relative to control subjects. The more a given finger is stimulated, the larger the expansion of the cortical response. The representation for the thumb, which is not as frequently used as the other fingers, is not increased as much. However, the amount of practice is not the only factor that influences the organization of the somatosensory cortex. The plastic change of cortical representation is not directly correlated to the number of hours played per week, but rather to the age at which the training was started in childhood.

For the auditory system, the representation of pure tones, which are not part of our natural acoustic environment and also not encountered in musical training and practice, does not differ between musicians and control subjects. By contrast, the representation of piano tones, which in control subjects is of the same strength as the one for pure tones, is specifically enhanced in musicians. The analysis of reports of these musicians revealed that neither the passive exposure to music as a child nor the amount of time spent listening to music passively as an adult significantly influences functional cortical organization. It seems that active practice is necessary to induce plastic alterations. This reorganization of the auditory system also exhibits a trend

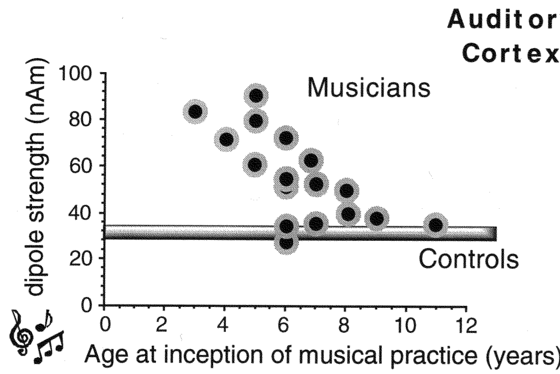

FIGURE 6. Mean strength of cortical activation for the different piano tones as a function of the age at which musical training began in musicians with absolute or relative pitch. The line denotes mean dipole moment in control subjects who never played a musical instrument. (Modified from Pantev *et al.*[19])

toward more pronounced brain plasticity with a younger age of starting to play the musical instrument (FIG. 6). The musicians who started playing before they were nine years old demonstrated the largest cortical representations.

The fact that the degree of expansion of the neuronal representations depends on the age training is started suggests that the enormous capacity of plasticity in the adult brain is, however, more limited than the plasticity of the infant brain. This corresponds to the prescientific observation that it is more difficult for adults to learn to play a musical instrument. To achieve an equivalent musical aptitude, adults can still adapt their cortical organization but they have to work harder to do so.

THE DARK SIDE OF NEUROPLASTICITY IN MUSICIANS

As mentioned above, neuronal networks are thought to be particularly plastic during "sensitive periods" in the development of cortical structures. However, they maintain the ability to alter their architecture and function to afferent input throughout life. Perceptual and behavioral correlates of this reorganization indicate that neuroplasticity can be adaptive, as illustrated previously. Another type of reorganization includes the smearing of representational zones. An example has been described in blind multifinger Braille readers where overlap of digit representation may aid the ability to process different types of digital input simultaneously, thus enabling more rapid reading.[36] However, cortical reorganization can also be maladaptive, as is indicated by its association with phantom limb pain,[37] tinnitus,[38] and focal hand dystonia.[39,40] Intense training, as found in professional musicians, employs mechanisms of cortical plasticity with the inherent danger that maladaptive processes may also occur. Evidence from several laboratories suggests that one such danger is focal hand dystonia. Focal dystonia of the hand falls into a class often termed oc-

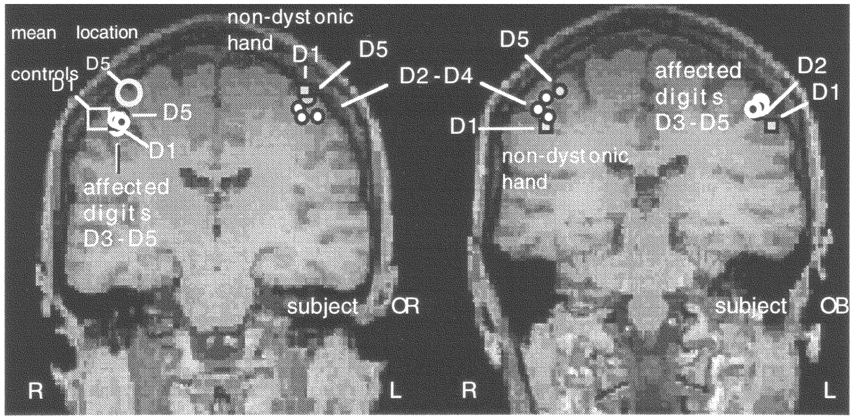

FIGURE 7. A coronal MRI section is shown through the somatosensory cortices of an organ player (*left*) and an oboist (*right*), both suffering from focal hand dystonia. The symbols indicate cortical representations (dipole locations) of digits 1–5 (D1 to D5) resulting from contralateral stimulation of the finger tips. The large *open symbols* in the right hemisphere of subject O.R. indicate the mean location of dipoles for D1 and D5 in normal control subjects. (Modified from Elbert *et al.*[39])

cupational hand cramp.[41,42] It involves manual discoordination occurring in individuals engaging in extensive or forceful use of the fingers. The disorder involves a disorganization of control of the digits such that the movements of some fingers on a hand become involuntarily linked to those of others, something particularly incapacitating to professional instrumental musicians.

Repetitive and behaviorally relevant stimulation to several digits performed with healthy subjects results in a fusion and in a disordered arrangement of the representation of individual digits.[36,43] At the same time subjects in these experiments consistently mislocalize light pressure stimuli applied to the fingertips. Consistent with earlier work in animals, source imaging in humans demonstrates that synchronous stimulation of the digits may create a fusion of cortical representational zones, whereas asynchronous stimulation leads to separation. Could such a process of cortical reorganization become maladaptive and thus contribute to focal dystonia? By means of magnetic and neuroelectric source imaging, an overlap or smearing of the homuncular organization of the representation of the digits in the primary somatosensory and the motor cortex was indeed observed (FIG. 7).[39,44,45]

Work by N. Byl, M. Merzenich, and colleagues in New World monkeys has indicated that lack of digital motor coordination resulting from digital overuse is associated with an induced disorder in the representation of the digits in the somatosensory cortex.[42,46] These findings suggest that overuse-dependent central nervous system (CNS) plasticity is the basis of the focal hand dystonia. Therefore, because evidence suggests that behavioral usage and a CNS plastic response to this usage could be the cause of both the cortical disorder and the involuntary lack of movement coordination, it was thought that a behavioral intervention focusing on movement could be of value in reducing or eliminating these conditions. Any such treatment approach should include practice in a behaviorally relevant setting. A number of studies have shown that the behavioral relevance of the stimulation is the critical factor for reorganization to occur, whereas simple passive stimulation seems to be ineffective in altering cortical connectivity.[17] For example, Kilgard *et al*. suggested that the cholinergic nucleus basalis might play an important role in labeling stimuli as behaviorally relevant because nucleus basalis activation facilitated cortical plasticity induced by correlated stimulation in the periphery.[47] Further evidence points to the additional involvement of dopaminergic pathways. It seems possible that blockade of dopamine, released by a potentially rewarding condition, for example, through neuroleptics, will not allow cortical reorganization to occur.

On the basis of these considerations, Candia *et al*. have developed a successful therapy for focal hand dystonia.[40] Professional musicians (pianists, guitarists, and wind players), with long-standing symptoms, who had previously received a variety of treatments, practiced their instrument according to rules derived from insights into the mechanisms of cortical reorganization. The therapy involved immobilization by splints of one or more of the digits other than the focal dystonic finger. The focal dystonic finger was required to carry out repetitive exercises in coordination with one or more of the other digits for 1.5 to 2.5 h a day over an intended period of eight consecutive days under supervision of a therapist. The patients were instructed to continue the exercises using the splint at home for one hour every day for one year posttreatment. The wind players, who, in effect, constituted placebo controls, did not improve substantially. However, each of the pianists and guitarists showed marked and significant improvement in spontaneous repertoire performance without the splint at the end of treatment, up into the normal range. Neuroimaging results obtained in successfully treated subjects indicated normalization of the cortical representational maps, highlighting again the continued role of plasticity in the adult human brain for successful adaptation. The outcome demonstrates that learning-induced alterations in the functional architecture of the brain can be maladaptive, and that the resulting pathology can be treated using behavioral techniques that are based on learning principles that take into account recent research on neuroplasticity.

CONCLUSIONS

By use of MEG, it was shown that it is possible to noninvasively study mechanisms of cerebral organization and reorganization in humans. Listening to music attentively for as little as three hours can have a temporary influence on auditory cortical representation, as was shown in our study with music notched at a specific frequency. It was further shown that musical education and training is reflected in the organization of auditory and somatosensory representational cortex in musicians. From the results obtained, the following questions arise: Can we draw conclusions on the behavioral plasticity after knowing about the neuronal one? How do alterations in functional cortical organization affect musical accomplishment? Do the best virtuosos have the most atypical cortical organization?

The results of the studies presented here do not allow final conclusions. However, as shown in the case of focal dystonia, current research can lead to recommendations about musical practice and help design methods of treatment. The observed correlation between the age of initiation of musical practice and the amount of cortical change should not be overinterpreted from a music-pedagogical perspective. The complex relationships between genetic and familial, as well as educational pedagogical factors, would have to be studied by an interdisciplinary team of scientists. Such a team should comprise neuroscientists, as well as musicians and experts in music psychology, because it would be necessary to evaluate subtle differences in musical achievement to address these questions and establish causal links.

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