## Brain plasticity and music

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Neuroplasticity refers to experience-driven changes in the organization of the brain. On a structural level we distinguish synaptic changes/ synaptic plasticity (microscopic level) and cortical plasticity. On a functional level we distinguish short-term plasticity and long-term plasticity.

Early studies of experience-driven neuroplasticity at behavioural, cortical, neuronal and molecular level often used animal models, especially rats and monkeys. Studying such effects in humans is difficult, but recently published studies showed professional musicians to be an ideal model to investigate plastic changes in the human brain.

This brief description of "neuroplasticity and music" will as well begin with the "rats" explaining key definitions and highlighting general problems. The second part will turn to neuroplasticity and music in particular. It will conclude with a clinical example of maladaptive plasticity: Focal Dystonia also known as "musicians' cramp".

## Neuroplasticity of the Brain

Brain plasticity (variously referred to as neuroplasticity, cortical plasticity or cortical re-mapping) refers to the ability of the (developing) brain to respond to and be modified by experience, to compensate for injury and disease and to adjust its activities in response to new situations or to changes in their environment.

Several decades ago, the consensus was that lower brain and neocortical areas were immutable after development, whereas areas related to memory formation, such as the hippocampus and dentate gyrus, where new neurons continue to be produced into adulthood, were highly plastic. Decades of research have now shown that substantial changes occur in the lowest neocortical processing areas, and that these changes can profoundly alter the pattern of neuronal activation in response to experience. According to the theory of neuroplasticity, thinking, learning, and acting actually change both the brain's physical structure, or anatomy, and functional organization, or physiology.

## Hebbian Theory

The idea of learning as the establishment of neural networks was first proposed in 1949 by the Canadian psychologist Donald Hebb. He hypothesized that memories are stored in the brain in the form of networks of neurons that he called cell assemblies. His idea was that through experience (i.e., learning) these assemblies come to represent specific objects or concepts. To explain how these neurons come to be linked Hebb proposed a cellular mechanism (known today as Hebbian learning). His hypothesis was that when presynaptic and postsynaptic neurons fire action potentials together the strength of the synaptic connections between them are enhanced. As a result , synaptic associations would grow stronger and tend to persist (cells that fire together, wire together). "When an axon of cell $A$ is near enough to excite cell $B$ and repeatedly or persistently takes part in firing it, some growth process or metabolic change takes place in one or both cells such that A's efficiency, as one of the cells firing $B$, is increased." [1]

Eric Kandel (Nobel Prize in Physiology or Medicine, 2000) investigated biochemical changes in neurons associated with learning and memory storage. Some of the synaptic changes observed by Kandel's laboratory provide examples of Hebbian learning.

## Environmental Enrichment during Development

The phenomenon of early environments influence on brain development was first noted in the 1950s by Hebb. He observed that when he took rats from his laboratory home as pets, the animals showed superior performance to littermates raised in standard laboratory conditions. Since then more formal experiments have examined how systematic manipulation of environmental complexity and physical activity in rats and other animals affects the developing brain.

Environmental enrichment that enhances the prevalence of social interactions, non-social stimulation, and exercises in rats increases the survival of newborn neurons in the dentate gyrus of hippocampus and improves performance in a variety of memory tasks. The rats' improved behaviour is correlated with a higher density of synapses and increased dendritic complexity in the hippocampus and other regions.

## Critical Period

A further important point is that many effects of experience during development are most influential within a particular time window. These windows are referred to as sensitive periods or critical periods.
One example in the field of ophthalmology is a form of functional blindness called amblyopia. When infants fail to experience normal visual stimulation of one retina (because of lens defect or strabismus) the visual system suppresses input from one eye. David Hubel and Torsten Wiesel at Harvard Medical School showed that the underlying problem was a failure of the cortical neurons related to the deprived eye to compete normally in establishing connections with their thalamic and other inputs. If the eyes are aligned early in development the developmental failure and resulting deficit can be prevented.

## Kennard principle

Another observation that indicates the variability of neural plasticity over developmental time concerns the recovery of neurological function after injury (i.e. stroke). In general, recovery is better the earlier in development the injury has taken place. This generalisation is known as the Kennard principle. Margaret Kennard showed on monkeys in the 1930s and 1940s that insults to motor cortex in infancy result in less severe deficits than the same insults in adulthood.

## The Nature-Nurture Debate

Perhaps the most commonly asked question about the determination of brain organization and brain structure and its plasticity during development is the relative influence of learning and experience versus the role of individual's genotype. In general terms, this issue is referred to as the Nature-Nurture debate. In the 18th century the philosopher Jean Jacques Rousseau argued that humans come into the world as a tabula rasa. The preformationism proposed that the completely formed being exists within the germ cells and that maturation is nothing more the growth.
These historical debates about nature versus nurture have evolved in modern times in a more sophisticated investigation of the interaction between genes and environment.

The functional and anatomical studies about the phenomenon of Absolute Pitch are another example for investigations in the tradition of nature-nurture debate.

## Neuropsychological Phenomenon: Absolute Pitch

Perfect or absolute pitch is defined as the ability to identify the pitch of a single tone heard in isolation. Estimates of the prevalence of absolute pitch vary from $0.1 \%$ to up to $15 \%$ in students at music schools. Absolute pitch was initially considered to be an innate ability. Today researchers agree that AP relies on both: genetic predisposition and (early) musical training. An MRI morphometric study of musicians has shown increased left-sided asymmetry of the planum temporale in individuals with absolute pitch.

The ability to identify the pitch of every single tone may be genetic (some scientists argue for an autosomal dominant genetic trait). Absolute pitch sense may as well appear to be influenced by cultural exposure to music, especially in the familiarization of the equal-tempered C-major scale. Many neuropsychologists propose the acquisition of absolute pitch requires early training during a critical period of development, regardless of whether or not a genetic predisposition toward development exists. Absolute pitch is more common among speakers of tonal languages such as most dialects of Chinese or Vietnamese, which depend heavily on pitch variation across single words for lexical meaning (Mandarin with 4 possible pitch variations, Cantonese with 9). The prevalence of absolute pitch is higher among those who are blind from birth, due to optic nerve hypoplasia, and has been claimed to be higher among individuals with Williams Syndrome and those with an autism spectrum disorder. The talent of absolute pitch can change over lifetime. Frequency levels can move or misalign.

## Neuroplasticity and Music

As in every learning process there have to be adaptations and changes in the brain during learning an instrument. These changes are growth and improvement of new dendrites, synapses and neurons or the disinhibition or inhibition of preexisting lateral connections between neurons by sensory input.

## Professional Musicians

Perfomring music at a professional level is without doubt among the most compex of human accomplishments. There are two advantages to studying plasticity in musicians: the complexity of the produced stimuli, and the extent of their exposure to these stimuli. Professional musicians need special skills which are necessary to interpret and play music, a highly complex and multidimensional task, including besides others the following skills:

- Bimanual coordination of many notes (up to 1800 per minute for pianists)
- Integration of sensory and motor information, such as the translation of visually presented musical symbols into complex sequences of finger movements
- Structuring of tones in time (rhythm)
- Improvisation, Memorization of long musical phrases
- Identification of tones without reference tone
- Memorization of the immediate past, prediction of the immediate future and categorization of the input according to its features


## Structure: Anatomical Differences

Since the age of phrenology neuroscientists have tried to relate skills and attributes to changes in skull or brain anatomy. At the beginning of the twentieth century Auerbach reported that the middle and posterior thirds of the superior temporal gyrus were larger than normal in several post-mortem studies of the brains of famous musicians.

Modern brain-imaging techniques such as high resolution MRI allow us to study anatomical details in the brains of living humans.

Music stimuli mostly influence auditory and motor areas. In line with this, a musician's brain differs anatomically in these regions. The structural differences are more pronounced when starting a professional career at an early age (q.v. Kennard principle, 1.4).

Studies using MRI techniques have shown that several brain areas, including the planum temporale, the anterior corpus callosum, the primary hand motor area and the cerebellum differ in their structure and size between musicians and control subjects.

The cortical representation of the left hand digits is larger in string-players than in controls because of the independent finger movements required when playing a string instrument. When musical training started before the age of seven, the interaction between the hemispheres is improved due to a higher number of axons that cross the midline. Furthermore, the gray matter has more volume in musician's brains, especially in primary sensorimotor regions, left basal ganglia,
the bilateral cerebellum and the left posterior perisylvian region. A higher gray matter volume means that there are more synapses per neuron, more glia cells and glial volume per Purkinje cell. The higher amount of gray matter in the left Heschl's gyrus (HGL) is associated with differences in source activity while listening to tones.
The superior parietal region (SPCR) is of great importance for the integration of multimodal sensory information and for guiding motor operations. Professional musicians show higher gray matter volume in this area. While playing an instrument the continuous projection of the inferotemporal cortex into the ventral prefrontal cortex is necessary to choose actions from visual cues. An increased gray matter volume was found in musicians in the inferior temporal gyrus.

Together the findings indicate that the musicians have anatomical differences in several brain areas that are involved in motor and auditory processing.

## Timeline of Brain Plasticity

In every learning process synapses are altered by temporal input patterns in a competitive network. The structure of the stimulus and its significance determine the resulting neural changes. Motor learning occurs in several phases and leads to gradual performance increases:

1. Fast initial phase of performance gains
2. Period of consolidation for several hours
3. Slow learning phase during continued practice

In musician there is a rapid increase in blood flow in the primary motor cortex during exposition to a novel tapping task. This is due to pre-practice experience. The higher efficiency of professionals in learning new musical skills is represented by a more efficient movement control and recruitment of smaller neural networks in the supplementary motor area (SMA).

## Function: Neurons and Networks

Before long-term neural changes can occur, short-term changes and excitatory as well as inhibitory modulations in response to an auditory stimulus are required. These effects can also be caused by selective attention and crossmodal effects of visual stimulation which are discussed below. Short-term plasticity is defined as any feed-forward (bottom-up) or feedback (top-down) input, excitatory or inhibitory, that transiently modulates the responsiveness of the target neurons to a subsequent stimulus. It can also change the oscillatory properties of local neuronal populations that influence the processing in other cortical structures. As mentioned above it can be driven through by distinct types of input:
1.) bottom-up input (auditory stimuli)

The tuning via this route works by suppression of neurons of the auditory cortex for several seconds after their initial excitatory response to an auditory stimulus. This phenomenon is called stimulus-specific adaptation (SSA). SSA is supposed to delay and weaken responses to stimuli that slightly differ in frequency and is vital for speech comprehension and working memory tasks for which auditory information has to be accessed over a few seconds. SSA in the anterior and posterior cortex gives rise to mismatch negativity (MMN). MMN is a frontal negative wave in the event related potential (ERP) and a marker of pre-attentive detection of changes in regular sequences of auditory stimuli. MMN occurs in absence of attention to the stimuli and can rise in professional musicians for tones that are mismatched by as little as 20 ms in a series of regularly spaced tones. A MMN for slightly impure chords among perfect major chords is also present in professional musicians. The MMN arises mainly from neurons on the supratemporal plain of the temporal lobe with contributions from the frontal cortex.
2.) top-down input (from other cortical areas)

Focusing attention on a given acoustic feature seems to enhance neural selectivity by selectively elevating the activity in that part of the auditory cortex that specializes on processing this feature. For example, human anterior auditory cortex (putative "what" pathway) shows enhanced activity to phonemes when attention is drawn to phonetic features. Similarly, the posterior auditory cortex (so-called "where" pathway) is enhanced while attention is directed to stimulus locations. The neurophysiological correlate of this selective attention mechanism are spectrotemporal receptive fields (STRF) of A1 neurons. Changes in the STRF correlate with improved behavioral task performance and persist only during the performance. The fields are transiently modulated to encompass the frequency of the targeted tone. It is caused by top-down center excitation spanning one octave around the target frequency and inhibiting the surrounding. The STRF of a neuron can change during different task conditions. [insert Figure 3b, Jaeaeseklinen] As shown above top-down input is as important as bottom-up input for the tuning of
neurons. The auditory cortex serves as an interaction surface between bottom-up information from the environment and top-down information representing the goals of the organism.
3.) cross-modal input (visual stimuli)

Multisensory processing is anatomically supported by connections between auditory and visual cortex, heteromodal cortex and the prefrontal "mirror-neuron" system. It has been suggested that visual input influences auditory processing mainly through top-down feedback at an early processing stage. The visual stimuli can either be related to speech and help speech processing as in the case of lip-reading or they can be as complex as a natural scene, activating audiovisual associations. It has further been suggested that crossmodal input initially causes excitation followed by post-stimulus inhibition. The pattern of the responses are not random and might help the auditory cortex to detect relevant features more easily. The reaction strongly depends on the stimulus timing, its type and the specific task.
There is much evidence that short-term plasticity of the hierarchically organized parallel auditory system supports perceptual long-term training. To conclude, the neuronal adaptations achieved during professional musical training are evident in enhanced connections between specific brain regions but the exact mechanisms are still far from being fully understood.

## Clinical Example: Focal Hand Dystonia (FHD)

Focal hand dystonia (FHD) is a primary dystonia produced by excessive cocontraction of antagonist pairs of hand and forearm muscles. In many cases the abnormal movement is unilateral and task specific occurring during a skilled motor task such as writing or playing a musical instrument. It is a common clinical observation that FHD patients have a long history of repetitive stereotyped hand movements before the onset of the disease.

Neuronal representations are believed to be shaped by prior experience through physiological processes commonly referred to as neuroplasticity. Numerous studies have revealed that neuronal representations may be altered in focal hand dystonia. One such alteration is a severe degradation of finger representations in the somatosensory cortex which are normally highly somatotopically organized.

An MEG study of musicians with FHD showed fusion of the digital
representations in the somatosensory cortex, reflected in a decreased distance between the representations of the index finger and little fingers relative to healthy control musicians. Voxel-based morphometry studies reported cerebral anatomical abnormalities in primary FHD patients. FMRI studies argued an abnormal recruitment of cortical areas that are supposed to be involved in the control of complex movements.
FHD and its causes still remain far from being completely explicable but recent findings point to dysfunctional or maladaptive neuroplasticity as a crucial factor.

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