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Cortical functional activations in musical talents and
nontalents in visuomotor and auditory tasks: implications
of the effect of practice on neuroplasticity

Doctoral Dissertation
For the completion of the Dr. Phil.

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A Thesis submitted to the Department of Psychology at the Philosophy Faculty III as a requirement for the graduation as a Dr. Phil.

For my beloved grandparents,
Dr. Blagoje Stojanovic and Honorary Judge Radmila Stojanovic

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Chapter 1

Introduction: Neural plasticity

The term – Classifications – Experience and plasticity – Clinical implications

*"The idea that the brain can change its own structure and function
through thought and activity is, I believe, the most important alteration
in our view of the brain since we first sketched out its basic anatomy
and the workings of its basic component, the neuron. Like all revolutions,
this one will have profound effects."*

Norman Doidge
(The Brain that changes itself, 2007)

The concept of neural plasticity, the types, levels, and implications, will be discussed in this chapter. The present study aims at confirming the plastic changes due to the long-term training in the domain of music with the neural plasticity is at its core. As such, it is here described with the goal of revealing the importance of neuroplasticity both as the premise of the current investigation, and for its clinical and educational applications. More specifically, plasticity sets the stage for the non hard-wired brain, providing an opportunity for the scientists to see the brain as a changeable structure, albeit to a limited extent. Thus, brain structure and function can be modified with experience and through the process of rehabilitation after a brain damage.

1.1   Neural Plasticity: General Introduction

Neuroplasticity, also termed 'brain plasticity' and 'cortical plasticity' is a term indicating structural and functional changes in the brain through the lifespan. Several individuals are credited with the coining of the term and/or putting forth the idea of neuroplasticity. Two of the most notable ones are Jerzy Konorsky, a Polish neuroscientist and a student of Ivan Pavlov, and Donald Hebb, a Canadian neuropsychologist. Each of these two remarkable scientists contributed uniquely to the concept of neuroplasticity.

Jerzy Konorski is credited for introducing the term "plasticity" into the field of neuroscience. He expanded on Pavlov's theory of classical conditioning, and additionally contended that the forming of the new synaptic junctions between neurons is related to the plastic changes. According to Konorski, the extent of the plastic changes will depend on the frequency of the stimuli occurrence, i.e. practice (Zielinski, 2006).

Although much, and perhaps the strongest evidence of plasticity, comes from the studies of sensory deprivation, it is feasible to say that plastic changes occur also as a result of learning and new experiences. It appears that the plastic changes that occur due to learning depend on the specific neurotransmitter dynamics, so that the connections are strengthened or the new ones are created due to the potentiation and/or depression of the neuromodulation. This notion stems from the earliest suggestions of neural plasticity by a Canadian neuropsychologist, Donald O. Hebb. Hebb (1949) contends that repetition of the stimulation leads toward the forming of the cell "assembly". More specifically, it is the repeated and persistent stimulation from the presynaptic to the postsynaptic cell, which leads to the formation of the cell assembly. Consequently, this theory is deemed "cell assembly" theory or Hebbian theory, with the basic premise that "cells that fire together, wire together." In the words of Hebb "when an axon of cell A is near enough to excite a 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" (p. 62). Hebb further emphasizes the importance of contiguity for the formation of strong connections. In other words, there must be a continuous pre to post-synaptic stimulation for the connections to become sufficiently strengthened. This might further be reminiscent of any skill acquired through the continuous practice.

By a similar token, an even earlier account for the strengthening of cortical connections is given by William James, who contended that "when two elementary brain processes have been active together or in immediate succession, one of them on reoccurring, tends to propagate its excitement onto the other" (James, 1890, in Berlucchi

and Buchtel, 2009). These notions may further imply that practice, both in the form of skill perfection, and as the means of therapeutic recovery within the clinical realm, is crucial for the re-organization of the cortical networks to achieve better efficiency or restoration of the damaged or lost function.

A widely accepted view of the localized cortical function in the past has relied heavily on the notion that any specific brain area holds the responsibility for a specific function. For example, due to the findings by the French physician Paul Broca, we now deem the inferior frontal gyrus or Broca's area, as the structure crucial for the production of speech. Throughout the years, it has been shown that this structure has multiple functions in addition to speech (e.g. visuospatial cognition, Sluming, 2007), thus it is no longer acceptable to acknowledge any particular brain area as being rigidly dedicated to just one function. This sets the stage for the possible extension of any given function to the cortical areas not principally regarded as its 'enablers'. It is due to the brain plasticity that functions can be restored or perfected by utilizing different brain structures instead of only depending on a specific one.

Experiences leading to the plastic changes could be both clinical and non-clinical. Important for the concept of neuroplasticity is the view that in the case of the loss of any particular cortical structure due to a variety of clinical conditions, given sufficient time and persistent practice, other brain areas can "take over" or substitute the responsibilities of the damaged structure. Consequently, the function associated with the respective structure is accommodated or compensated for (Kolb, 1999; Kaas, 2004).

While it was once believed that the mammalian brain is rigid and resistant to change, lately, there is evidence that the brain structures are a subject to mutability (Kaas,

2004; Grafman 1999; Buonomano and Merzenich, 1998). According to Kaas (2004),

mammalian brain is highly plastic. The cortical maps are modified as a result of

experience and learning. The time frame within which these changes occur varies

depending on the neuromodulation and the regulation of neurotransmitters. For example,

improved sensorimotor skills due to practice may be the result of the rearranged

sensorimotor maps. In addition, the plastic changes may aid the recovery of the Central

Nervous System (CNS) damage. Furthermore, the plastic changes in the brain do not end

at the end of the early development (by 2 years of age). To that end, Kolb (1999), defines

plasticity as the cortical reorganization throughout life. The highest level of plasticity is

available in the first 2 years of life however it is possible for the plastic changes to take

place through the lifespan, with experience (Poldrack, 2000). In addition, structural

changes, as well as the neurogenesis, are and can be continuous. Recoveries after the

brain injuries as well as the learning and perfection of new skills show that there is a need

for an acknowledgment of the brain's ability to undergo changes and reorganization

through the lifespan. These changes occur not only in terms of the already existing

connections being strengthened, but also in terms of the creation of the new connections.

Plasticity in fact seems to be critical for normal development. More specifically,

the changes and adaptations of neurons are necessary to occur through development via

learning, in order to accommodate the learned material and/or to perfect a skill. At the

level of synapses, plasticity can be viewed in the form of long-term potentiation and

long-term depression (Abraham, 2008; Bunomano and Merzenich, 1998). Abraham

(2008) goes even further with the term and function of plasticity deeming it

"metaplasticity" or "the plasticity of synaptic plasticity" (p.387). This implies possible

physiological changes of neurons that may affect synaptic plasticity itself.

In addition to neurogenesis, plasticity is manifested by synaptic pruning, a process

by which unused synapses are eliminated via the cell death (Kolb, 1999). This contributes

to the more efficient processing of information where no additional time needs to be

utilized on the unused synapses. According to Brecht and Schmitz (2008), synaptic

plasticity is perhaps the most fundamental process for the lasting plastic changes leading

to an improvement in learning and skill perfection.

Developmentally, Kolb contends that plasticity gradually declines after the age of

2 to adulthood. However, there plastic changes seem to differ at different ages. For

example, the pattern of the cell growth differed in rats placed in enriched environments

depending on the age of the rats when placed into these environments (Kolb, 1999).

Research on the adult monkeys, trained on a cognitively demanding task, and

subsequently showing increased cortical representation of the sensory maps of digit

surfaces as a result of training (Bunomano and Merzenich, 1998), supports the notion of

the lifelong brain plasticity.

Neurocognitive development appears to be a result of the nature and nurture

interplay (Neville and Bavelier, 2004). Some evidence points toward genetic

conduciveness to plasticity, that is, the extent of the brain's ability to undergo plasticity

depending on the specific genetic polymorphisms (Kleim et al., 2006; Cheeran et al.,

2008). Thus, while the evidence for lifelong experience-induced plasticity is

overwhelming, as will be discussed in the upcoming section on plasticity and experience,

the effect of genetic mechanisms can not be completely disregarded. However, for the

sake of the present arguments, plasticity will be observed in terms of environmental influences.

According to Neville and Bavelier (2004): "The developing brain displays progressive and regressive events during which axons, dendrites, synapses, and neurons show exuberant growth and major loss leading to a remodeling of the neural circuitry. This period of remodeling is hypothesized to be a time during which environmental factors can have a major impact on cortical organization." (p. 83). Kolb (1999) claims that the aging brain is capable of plastic changes, however the speed at which these changes occur later in life is lower.

It is possible that certain regions with differing learning mechanisms have a different ability of plasticity, so that some are plastic and a subject to change throughout life, while others are plastic only during the sensitive period of development. This may explain the notion that the earlier onset of the practice in some domain is more likely to result in lasting structural and functional changes.

Kolb (1999) created 10 postulates of the ecological theory of the cortical organization. These postulates indicate the plastic changeability of the cortex, and elegantly summarize the notion of plasticity regarding the development and the process of plastic changes as they are affected by experience.

1.2 Classifications of Cortical Plasticity

Neuroplasticity is further supported by Buonomano and Merzenich (1998), who claim that "cortical representations in adult animals are not fixed entities, but rather are dynamic and are continuously modified by experience" (p.149). They propose three

levels of plasticity: 1. synaptic plasticity, which refers to the plastic changes in the synaptic parameters, or in other words, "the ability of neurons to modulate the strength and structure of their synaptic connections with experience" (Martin et al., 2004, p.121); 2. cellular conditioning, which refers to the selective responses of the single neurons after a short conditioning; and 3. representational plasticity referring to the changes that occur after a neuronal damage or after training.

Another classification of plasticity was proposed by Grafman (1999) as following: *1. homologous area adaptation*, by which it is suggested that if a brain area suffers damage early in life, a homologous area in the other hemisphere takes over its functions (for example, the left parietal lobe taking over the functions of the damaged right parietal lobe). This process comes with some cost to the regular, full capacity of the functions of the area that has taken over the functions of the damaged one. It is also possible that the area deprived of its input can begin to respond to the input provided to the neighboring areas. Experiments in monkeys (Buonomano and Merzenich, 1998) showed that after transecting a nerve, the unresponsive cortical area began to respond to the inputs from the neighboring areas after a period of a few weeks. To make up for the loss of the dead neurons, the remaining ones can enlarge their fields (Kolb and Whishaw, 1998). These findings are similarly seen in humans following an amputation (Buonomano and Merzenich, 1998; Kaas, 2004); *2. compensatory masquerade*, where if a function can not be carried out due to impairment an alternative strategy for carrying out that function will be developed (by for example relying remembering landmarks rather than intuition in determining the direction of movement); *3. cross-modal reassignment*, which is also referred to as a *cross-modal plasticity* (Rauschecker, 1995, Bavelier and Neville, 2002)

and by which it is suggested that if a brain area has been deprived of its normal inputs (e.g. visual), it will begin to respond to a different input (e.g. touch instead of visual). The best example is that of blind individuals, whose primary visual cortex responds to the tactile stimuli. A similar example comes from the visually deprived cats whose auditory localization of the sound becomes much more precise than that of normal cats (Rasuchecker, 1995). These findings emerged in studies with the human subjects as well (Collignon et al., 2009); *4. map expansion*: frequent practice and/or exercise leads to the cortical enlargement of the area mostly dedicated to that domain of practice. The connections in this area strengthen due to practice. The most obvious example is that of musicians, details of which will be revisited in the later sections. Once learning is explicit, the cortical map size goes back to the baseline however the enlargement persists with the persistent practice.

1.3 Plasticity: brain injuries and clinical implications

Lesions, most frequently created by the cerebral insult (or stroke) and/or a brain trauma, provided the possibility to investigate the "behavior" of the structure and function, as they strive to compensate for the cortical damage. While it was once believed that no recovery, regeneration, or repair of the adult brain is possible after damage, now there is evidence that the functional recovery is possible after the brain injury (Stein and Hoffman, 2003). In the words of Stein and Hoffman: "it is no longer possible to deny the thousands of laboratory animal and human studies in which some extent of repair and regeneration can be stimulated under appropriate circumstances" (p. 317).

A plethora of evidence comes from the animal studies as well (Buonomano and Merzenich, 1998). For example, the lesioning of the receptive fields of the primary visual cortex (V1) in cats revealed the reorganization of the visual cortex several weeks after the lesioning (Kaas et al, 1990). V1 began to respond to the input from the new areas around the lesion. Similar findings emerged for the auditory cortex as well (Buonomano and Merzenich, 1998).

One of the most important implications of cortical plasticity perhaps lies in it's applicability to the clinical situations whereby training can lead to the recovery of the lost function. One example comes from the observed training-induced reorganization of the cortical areas adjacent to the lesion area in monkeys, after a stroke (Elbert and Rockstroh, 2004). In humans, Sturm et al. (2004) found that patients with the vascular damage in the right hemisphere showed a reactivation of the right hemisphere after training. Similarly, Saur et al. (2006) found that after a left-hemisphere stroke, causing aphasia, patients exhibited reactivation of the language areas as their language abilities recovered through the period of 12 months. During the regenerative process leading toward the functional recovery after stroke, an enriched environment providing the conditions for re-learning of the lost functions, can further enhance the post-stroke recovery, as it was shown in animals (Wieloch and Nikolich, 2006). In addition, congenital blindness, acquired blindness, and the phantom limb studies, provide further evidence of the cortical reorganization due to damage (Grafman, 1999; Kaas, 2004). Understanding the timelines for the plastic changes following brain injuries would provide a valuable insight into the treatment and rehabilitation of the individuals suffering from the same.

Thus, the clinical instances also reveal that the organization of the cortex is anything but static and can be changed or in the clinical sense, restored with the goal of repairing the lost or damaged function.

1.4 Plasticity from learning and experience

The localization of function, by the token of the coupling of the lost function due to the brain injury with the location of the injury, is an invaluable source of information about the brain. However, the continuous information on the brain plasticity, without relying on the sole findings from the brain injuries, can be obtained with the research of healthy individuals undergoing practice. Practice can lead to many cortical plastic changes (Elbert and Rockstroh, 2004) that can in turn provide us with the information of the possible multiple functions of any respective brain area.

Learning-induced plasticity has been shown to occur at the levels as small as those of synapses (Brecht and Schmitz, 2008; Clem, Celikel, and Barth, 2008). Brecht and Schmitz (2008) provide an example of the synaptic plasticity at the micro-level of synaptic transmission in their investigation of the synaptic modification in the cortex of mice as a result of learning (Figure 2). If we are to apply these concepts to the human learning, we can further reinforce the idea of synaptic strengthening via the process of practice. Application of this process on the musicians' brains will be discussed subsequently in the sections on music practice and talent. Examples of the learning-driven plasticity exist for different cortical areas, such as visual (Spolidoro et al., 2009), auditory (Spierer et al., 2007; Rauschecker, 1999), and even in terms of the whole cortical weights investigated in animal studies (Rosenzwieg and Bennett, 1995).
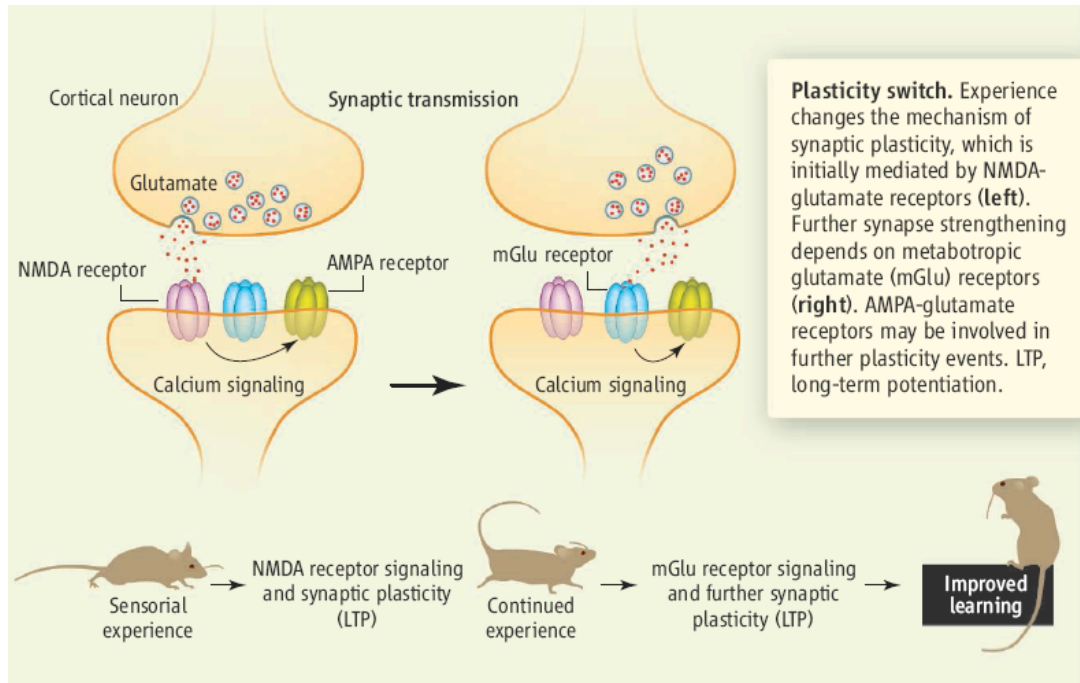
Figure 1.1 (from Brecht and Schmitz, 2008. Rules of Plasticity. *Science*, 319, 39-40. Reprinted with permission from AAAS)

 Kolb and Wishaw (1998) contend that "experience is a major stimulant of brain plasticity in animal species as diverse as insects and humans" (p. 43). They claim that experience can indeed influence the modification of the brain structure after the brain development has finished. They identify cortical changes at multiple levels as a result of experience such as the brain size, the cortical thickness, dendritic branching, synapses per neuron, the size of the neuron, and so on. This notion that the plastic changes occur as a result of experience from the level of synapse to the level of cortex through the lifespan, has been termed the 'nascent revolution' once again replacing the belief that brain is hard-wired and resistant to change (Kelly et al., 2006). Abraham (2008) also contends that enriched environments and conversely, stressful events, can facilitate synaptic plasticity. Further, Cramer (2008) defines plasticity as a process of the changed cortical

response to experience and learning. Experience also seems to increase dendritic growth (Kolb and Whishaw, 1998).

One of the more striking findings were reported by Jacobs, Schall, and Scheibel (1993), who found the positive relationship between the dendritic springing in the Wernicke's area and the level of education, by examining the brains of the deceased individuals. There was some linearity in these findings, whereby dendritic growth and branching increased with the increasing level of education. This further indicates that the brain plasticity is indeed influenced by experience.

With the improvement in performance and the increase in the challenge of the task at hand, activity in the respective cortices also increases (Rauschecker, 1999). However, maintaining the same level of performance does not result in an increase in activation, but rather results in a decrease and the settling onto automatic responses. According to Frakowiack (1999), with the novel task, attentional resources are focused on executing that task thus other areas, not associated with the task, tend to be deactivated. Through practice, the activation is sometimes increased and sometimes decreased in specific regions (Poldrack, 2000). On the global level of the brain, these changing levels of activation may imply utilization of additional resources for the learning of the novel information. With the skill acquisition, the attentional demand lowers, thus there is a decrease in activation. When the task becomes automatized, the activation in the "non-related" cortical areas resumes by going back to the baseline. According to Grafman (1999): "when the exact unit of representation to be used to process the bottom-up or top-down information is still undecided, the entire network needs to be active. When the exact unit of representation is selected, the network can

relax and less energy is expended" (p.135). Thus, it appears feasible to assume that

continuously "raising the bar", thereby increasing the challenge, results in the

continuation of the cortical plastic changes.

Even a short-term practice in many different domains can lead to the plastic

reorganization of the cortex. For example, shape learning shows a pattern of increased

and decreased functional magnetic resonance imaging (fMRI) recorded activation in the

visual areas after training (Kourtzi, 2005). Similarly, a visual working memory task

shows differing activation patterns recorded by fMRI after training (Hempel et al., 2004),

as does the practice of the Tower of London task, additionally characterized by a

decreased activation associated with the planning and execution of responses after

practice (Beauchamp et al., 2003). Plastic changes due to training can also lead to an

improvement in cognitive functions. For example, Mahncke et al. (2006) demonstrated

that there was an improvement in the memory in aging adults after the training program.

The cognitive functions remained improved even at the follow up testing after several

months.

Kelly, Foxe, and Garavan (2006) classify practice-related plastic changes into

three categories to reflect a variety of findings that emerged from the studies on cortical

plasticity due to practice. These changes are classified as following: activation increase,

activation decrease, and reorganization of activation (encompassing both reorganization

of functional activations and the redistribution of the functional activations). The

functional and structural changes as a result of practice will be revisited in the following

chapters. Figure 1 shows the illustration of the summary by Kelly, Foxe, and Garavan,

which also includes the potential locations of the most likely practice-induced plastic

changes.
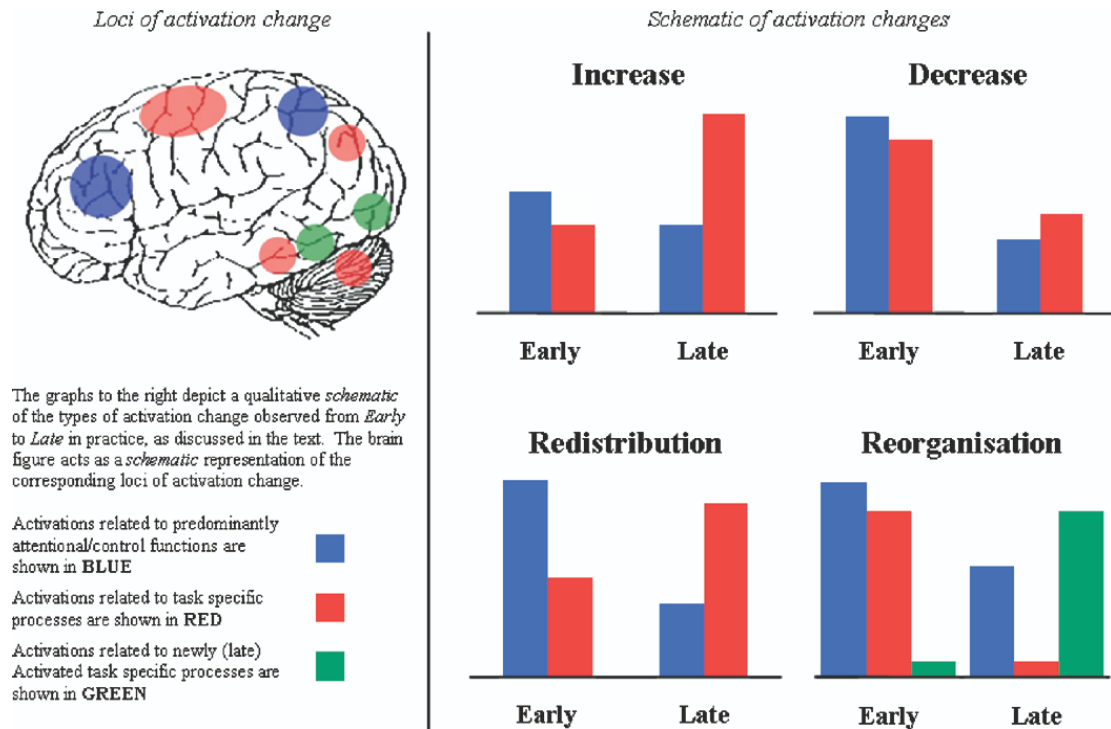
Fig. 1.2 Summary of the plastic changes induced by practice. (Reprinted from Kelly, C., Foxe, J.J., & Garavan, H. (2006). Patterns of normal human brain plasticity after practice and their implications for neurorehabilitation. *Archives of physical medicine and rehabilitation*, 87, s20-s29, Copyright (2010) with permission from Elsevier).

A similar equivalent is provided by the studies of animals raised in enriched

environments (Abraham, 2008; Nakashima and Dyck, 2008). For example, Anderson et

al. (2002) found that the cortical thickness increased in rats placed in enriched

environments. Furthermore, they found that just so much as a simple exercise resulted in

the cortical thickening, though not to the same extent as in enriched environments. In

addition, olfactory training in mice via fear conditioning also showed plastic changes

leading to the increase or a decrease in olfactory sensitivity (Jones et al., 2008).

On an even smaller scale, there is evidence that experience may increase the

neurotrophin production (Kolb, 1999). This further supports the role and the ability of the

cortex to undergo reorganization in response to experience (Rauschecker, 1999).

1.5 Conclusion: why do we care?

Why do we care about plasticity? As seen in the previous sections, research on

plasticity has provided us with the information that can successfully be applied to such

processes as child development, education and skill perfection, aging, and recovery from

the brain injuries. The presented evidence clearly shows that cortical plasticity is a true

dynamic process that can occur through the lifespan. By keeping this in mind, the

following sections will focus on the plastic consequences of training in various domains,

with the focus on musical training. Further, evidence of structural and functional changes

due to practice will be presented, with the focus on musical talents.

Chapter 2

Introduction: Music and neuroplasticity

Functional implications – Structural differences

"Studies of experience-driven neuroplasticity at the behavioural, ensemble, cellular, and molecular levels have shown that the structure and significance of the eliciting stimulus can determine the neural changes that result. Studying such effects in humans is difficult, but professional musicians represent an ideal model in which to investigate plastic changes in the human brain"

Thomas F. Muente, Eckart Altenmüller, and Lutz Jäncke
(The musician's brain as a model of neuroplasticity, 2002, Nature Reviews Neuroscience, 3)

2.1 Introduction

Clinical studies are clearly a great source of beneficial information about the brain structure, function, and plasticity. However, in terms of the intact brains, perhaps the best source of information may come from the studies on 'advanced' brains, especially in terms of the high abilities in a specific domain. The commonly accepted term for individuals possessing such skill is 'talent'. Talents differ from the general population by the fact that they possess a skill manifested as the above average ability. The most clear and obvious talent expression may be contained in the domain of music. In fact, Bhattacharya and Petsche (2005) find that "the investigation of functional and anatomical reorganizations in the musicians' brain due to their unique aspects of skill learning and acquisitions over many years of time is potentially considered as a role model for studying neuroplasticity" (p. 2162). Further, Muente, Altenmüller, and Jäncke (2002) suggest that musicians represent an ideal population for investigating neural plasticity. In addition, due to the complexity involved in music processing, many cognitive processes can be studied by investigating the functional and structural characteristics of the musicians' brains (Koelsch and Siebel, 2005). Professional musicians have been of interest to the studies of brain plasticity and high ability information processing for years. They were studied for both structure (Bangert and Schlaug, 2006; Peretz and Zatorre, 2005; Muente, Altenmüller, and Jäncke, 2002; Gaser and Schlaug, 2003; Koelsch and Siebel, 2005; Elbert et al., 2007; Schlaug et al., 1995; Schlaug et al., 1995a; Limb, 2006; Schneider et al., 2002) and function (Peretz and Zatorre, 2005; Muente, Altenmüller, and Jäncke, 2002; Bhattacharya and Petsche, 2005; Ridding, Brouwer, and Nordstrom, 2000; Zatorre, Chen, and Penhune, 2007; Koelsch and Friederici, 2003; Koelsch, Schmidt, and

Kansok, 2002; Ohnishi, 2001), not only within the realm of music, but also in terms of the extension of their abilities to other tasks (Sluming, 2007). When we consider the years of training that musicians endure we can easily grasp the notion of why musicians represent a good population for investigating brain plasticity.

If we are to consider the complexity of music performance, by for example, a pianist, we should take the following into account: the visual stimuli coming from the sheet music in front of the pianist as well as the piano keys; the auditory stimuli coming both from the outside as the music is produced by playing, as well as from within as the tones can be "heard" internally by reading the sheet music, termed "sight-reading"; the tactile stimuli as the piano keys are stroked; the motor response observed through the complex bimanual movement, which also implies the spatial orientation and coordination; and emotion that may be connected to the particular musical piece. Considering such a picture of a performing pianist, we become aware of the complexity involved in his/her performance. This complex ability of performing music necessitates the recognition of clear cortical plastic distinctions between musicians and non-musicians. Such differences indeed exist, as will be further described in this chapter.

As the most crucial brain development takes place by the age of 2 (Grafman, 1999), it appears that the early commencement of music practice may lead to a plethora of functional reorganizations in musicians somehow differing from those in individuals without the music practice or with the later commencement of practice (Neville and Bavelier, 2004). However, as mentioned in the previous chapter, plasticity continues to occur through the lifespan, thus musical practice may result in enduring plastic changes also apparent later in life. There is evidence for the short-term plastic changes as well.

For example, Lappe et al. (2008) conducted musical training on the nonmusicians by teaching them to play a musical sequence on a piano and compared them to the subjects simply listening to music. The magnetoencephalography (MEG) measurement showed that the subjects trained to play the musical sequence exhibited enlarged mismatch negativity (MMNm) as compared to the non-trained group, which according to the authors implied the enhancement of musical representation in the auditory cortices. Thus the plastic changes took place even after only a short-term, 8 day long musical training. The more enduring plastic changes, on the functional as well as on the structural level in musicians, will be discussed subsequently.

2.2 Sensory transference

Given the complexity of information processing while performing music, it is feasible to assume that the manner in which musicians come to process auditory and motor information is characterized by a degree of sensory transference. In other words, the sensory stimulation in one modality is accompanied by the activation of the sensory perception and/or response of another modality. According to Bangert and Altenmüller (2003), auditory stimulation in musicians is accompanied by the activation in the motor areas and vice versa. Bangert and Altenmüller state that years of musical practice likely lead toward "quick feedforward or feedback" mechanisms linking the "audible targets to the respective motor programs" (p.1) further leading toward better connections subserving these processes. For example, musicians report that listening to a musical piece that they were trained on can evoke involuntary finger movements. Vice versa was shown when professional musicians' auditory areas became activated when they were

asked to produce a motor performance of a well-trained musical piece. Bangert and

Altenmüller conducted an electroencephalograph (EEG) study with the non-musicians

describing the process of the auditory-sensorimotor co-activation. They found that the co-

activation of the auditory and motor areas occurred after as little as 20 minutes of piano

learning, concluding that musical training initiates plasticity instantly. They further

pointed out the anterior regions of the right hemisphere as a possible site of this

"auditory-motor interface" that may provide musicians with the ability of the sensory

transference from auditory to the motor activation and vice versa. In fact, musicians may

have better developed structures involved in the sensorimotor integration (Hyde et al.,

2009). Zatorre, Chen, and Penhune (2007) suggest that this sensorimotor, or more

specifically, auditory-motor interaction occurs due to the demands that the specific music

components place on the information processing, such as the musical rhythm, meter,

pitch, tone, and so on. Fig 2.1, adopted from Zatorre, Chen, and Penhune offers an

elegant visualization of this sensory-motor feedback and interaction.

      In the present investigation, the sight-reading accompanied by the motor

performance has been taken into consideration as a premise for the task (the task will be

described in more detail in the Chapter containing the Methods section), thus involving

the visuo-motor transference, hereby hypothesized to be more prominent in the musical

subjects, as reflected in the functional magnetic resonance imaging (fMRI) recorded
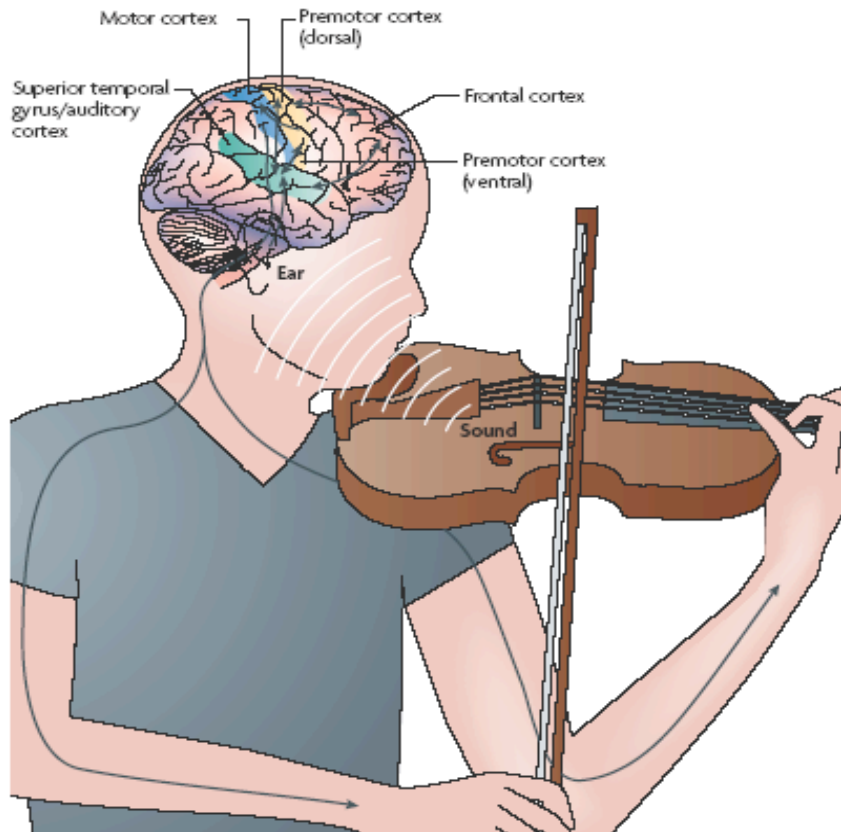
functional activations.

Figure 1 | **Auditory–motor interactions during musical performance.** This figure illustrates the feedback and feedforward interactions that occur during music performance. As a musician plays an instrument, motor systems control the fine movements needed to produce sound. The sound is processed by auditory circuitry, which in turn is used to adjust motor output to achieve the desired effect. Output signals from premotor cortices are also thought to influence responses within the auditory cortex, even in the absence of sound, or prior to sound; conversely, motor representations are thought to be active even in the absence of movement on hearing sound. There is therefore a tight linkage between sensory and production mechanisms.

Fig. 2.1 (Reprinted by permission from.Macmillan Publishers, Ltd., *Nature Reviews Neuroscience*, 8, Zatorre, R.J., Chen, J.L., Penhune, V.B. (2007). When the brain plays music: auditory--motor interactions in music perception and production, 547-558. Copyright 2010)

2.3 Functional differences between musicians and non-musicians

Merely by the token of the long-term training and skill acquisition, the cortical

plastic changes would inevitably lead toward the functional differences in the information

processing between musicians and non-musicians. For example, according to Muente,

Altenmüller, and Jäncke (2002), subtle changes in the auditory stimuli may be

automatically detected by musicians due to the years-long training, and accordingly neuronal shaping of the musician's cortical structures.

Furthermore, in terms of finding the differences between the auditory information processing in musicians versus non-musicians, in an EEG study by Bhattacharya and Petsche (2005) and in an fMRI study by Ohnishi et al. (2001), the authors found that musicians processed musical information favoring the left hemisphere, while the non-musicians' processing was more contained within the right hemisphere. In both studies, the authors discuss the possible analytical approach to music listening in musicians as one of the reasons for the increased left hemisphere activation. In a study by Bhattacharya and Petsche, there were no differences between musicians and non-musicians when listening to the text being read. Although the findings of this study pointed toward the differing hemispheric dominance in music perception between musicians and non-musicians, the authors emphasize that it is most likely the harmony and interaction between the two brain hemispheres that is crucial for the optimal music perception. To this effect, it has been suggested that interhemispheric inhibition is reduced in musicians (Muente, Altenmüller, and Jäncke, 2002; Ridding, Brouwer, and Nordstrom, 2000). This indicates a better communication between the two hemispheres in musicians (Limb, 2006), as the components of both are involved in some aspects of music perception and performance. In fact, different impairments, either of the left or the right hemisphere results in different musical deficiencies (Brust, 2003).

In addition to the possible hemispheric asymmetry in music perception, other structures have been implicated in terms of the differences between the musicians' and non-musicians' music perception. Ohnishi et al. (2001) found that there was a negative

correlation between the age of the commencement of musical training and the degree of

activation in the left planum temporale (Figure 2.2), a structure suggested to analyze the

incoming complex sounds (Zatorre, Chen, and Penhune, 2007).
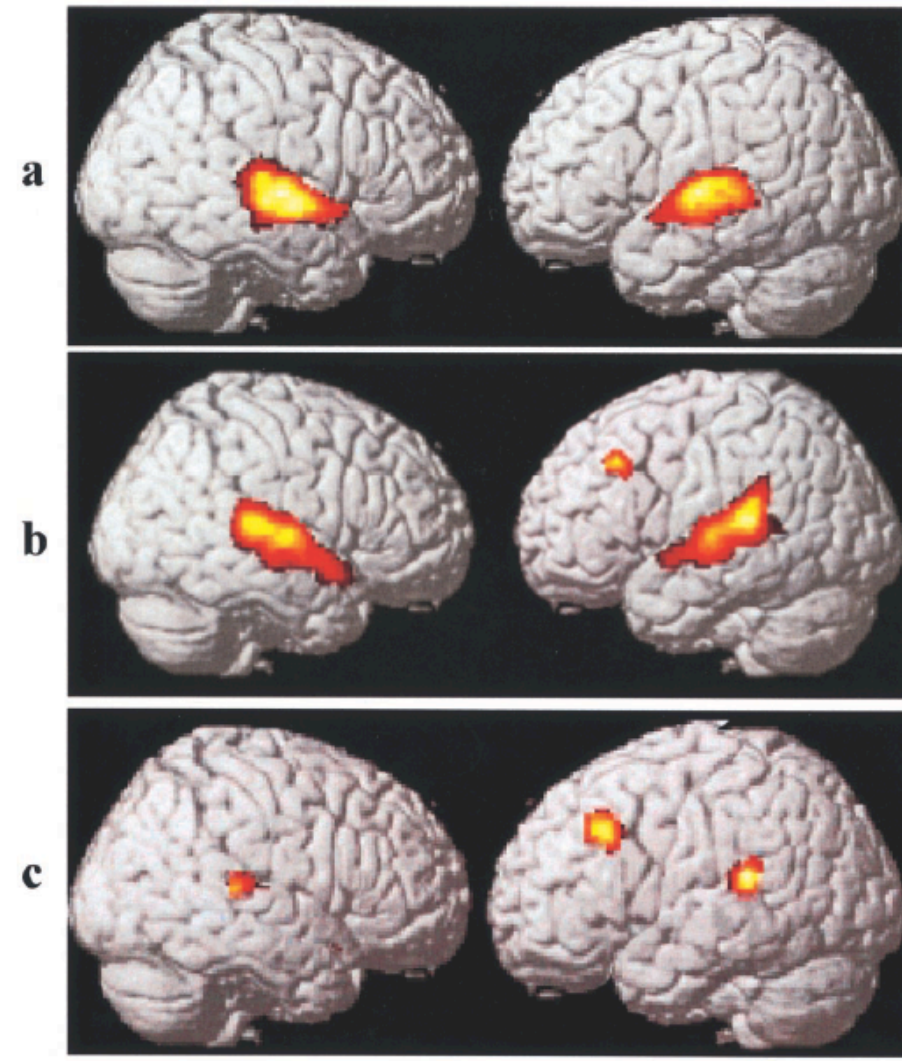
Brain surface projection of activated areas during passive music listening in control subjects and musicians. (a) The activation map of control group view from the right (right); the view from the left (left) shows right dominant activation in the temporal areas. (b) The activation map in the musicians group shows left dominant activation in the temporal areas. Activation in musicians are leftward and extend more posteriorly than those in the control group. An additional activation in the left posterior dorsolateral prefrontal cortex is noted. (c) A group difference map of the activation between musicians and control subjects shows stronger activations in musicians than in controls in the bilateral PT, especially in the left one and the left posterior dorsolateral prefrontal cortex.

Figure 2.2 (reprinted from Ohnishi, T., Matsuda, H., Asada, T., Aruga, M., Hirakata, M., Nishikawa, M., Katoh, A., & Imabayashi, E. (2001). Functional anatomy of musical perception in musicians. *Cerebral Cortex*, 11, 754-760, by permission of Oxford University Press).

A difference in the EEG patterns between musicians and non-musicians has also been shown to occur, for example in response to the violation of the musical structure (Koelsch and Friederici, 2003), and between musicians and musical novices in response to the harmonically inappropriate chords (Koelsch, Schmidt, and Kansok, 2002). In both cases, it was the early right anterior negativity (ERAN), an event-related potential reflecting fast and automatic processing of complex musical irregularities, which differed between the groups of musicians and non-musicians. More specifically, musicians exhibited a larger ERAN than novices in response to the aforementioned musical violations (Fig. 2.3 from Koelsch, Schmidt, and Kansok). The authors also indicated that interestingly, ERAN is also characteristic for detecting syntactic incongruities in language. Koelsch, Schmidt, and Kansok further speculate that the differing activation pattern between musicians and non-musicians may be due to the modulation of responses to musical irregularities by the token of expertise.

Sight-reading in music (the reading of the musical notation) is somewhat similar to the word reading, due to some meaning is derived from the reading in both cases. The possible similarities between the processing of language and music have been considered (Peretz and Zatorre, 2005; Sergent et al., 2007; Koelsch, 2005; Koelsch et al., 2004).

Functional activation patterns reveal a feasible underlying difference between the word reading and the musical notation reading. While the language areas are normally activated during the visual word processing, sight-reading in music results in the activation of the occipitoparietal areas, consistent with the spatial processing (Sergent et al., 2007). Sergent et al. emphasize that the information processed while sight-reading is in fact the information of the spatial position and/or orientation of the musical notes, on

which is the sound pitch depends. Further in reference to language, it appears that the

most traditional language processing cortical region, Broca's area, acquires other

specializations in musicians after years of musical practice. In a study by Sluming et al.

Experts
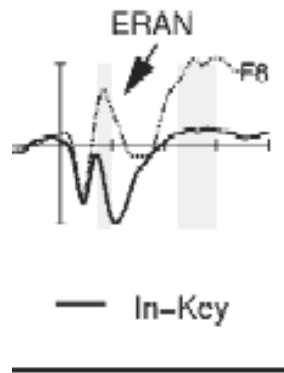
Novices
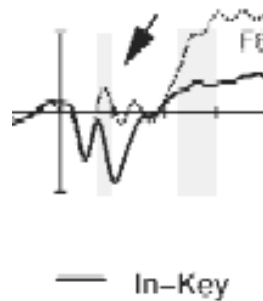
Figure 2.3 (Reprinted from Koelsch, S., Schmidt, B-H., Kasok, J. (2002). Effects of musical expertise on the early right anterior negativity: an event-related brain potential study. *Psychophysiology*, 39, 657-663)

(2007), the fMRI recordings showed that Broca's area subserved the musicians'

performance on a 3-D figure mental rotation task, designed to tackle the visuospatial

skills. Visuospatial skills are clearly important for musical processing as is evidenced by

deficiencies in spatial processing in individuals with amusia, also known as the tone-

deafness (Douglas and Bilkey, 2007). In the present study, the task focusing on

performance utilizes this notion by engaging the visuomotor skills, where the finger

positioning and the correct button presses are crucial for the accuracy of responses.

With many functional activation pattern differences between musicians and non-musicians, it follows to assume that there are observable structural differences as well.

2.4 Structural differences between musicians and non-musicians

Plastic changes leading to the reorganization of the neuronal population, likely lead toward the increase/decrease in the gray matter volume depending on the experience endured. The structural changes in musicians have been revealed (Bangert and Schlaug, 2006; Schlaug, G., 2003), reflecting still debatable interplay between the genetic factors and the years of practice. Some of the most prominent brain areas indicated to differ in size and structure between musicians and non-musicians are the planum temporale, corpus collosum, primary motor areas (M1) and the cerebellum (Muente, Altenmüller, and Jäncke, 2002) (Fig 2.4).
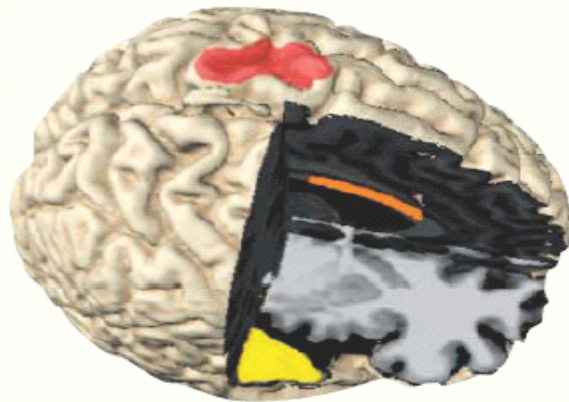
Figure 2 | **Structural changes in the brains of musicians.** Some of the brain areas that have been found to be enlarged in musicians in morphometric studies based on structural magnetic resonance imaging. Red, primary motor cortex; yellow, planum temporale; orange, anterior part of the corpus callosum.

Figure 2.4 (Reprinted by permission from Macmillan Publishers, Ltd. *Nature Reviews Neuroscienc*e, Münte, T.F., Altenmüller, E., & Jäncke, L. (2002). The musician's brain as a model of neuroplasticity. 473-478).

According to Peretz and Zatorre (2005), the primary structures to focus on when investigating the structural differences between musicians and non-musicians are the motor areas. Due to the complexity of the motor output, as well as the motor planning in musical performance, it can be concluded that the motor structures will undergo certain reorganization. One of the best contributions to this assumption is the finding that there is an increased cortical representation of the left-hand (or the fingering hand) fingers in string players (Elbert et al., 2007). Further contributing to the notion of the plastic changes through musical practice, Elbert et al. found that the extent of the increase in cortical representation of the left hand fingers was negatively correlated with the age of commencement of musical training. The authors suggest that this finding indicates the modification due to the need for adaptability on the part of the string players, whereby they have an extensive use of the fingers of the left hand when playing their instrument.

In terms of the cerebellum, Zatorre, Chen, and Penhune (2007), cite the importance of this structure for the movement timing. Since movement timing is an important concept in music performance, the role of the cerebellum in music performance is crucial. Cerebellum has been shown to regulate the movement timing, as well as the online error correction in movement and rhythm. Thus, the finding of the structural differences in the cerebellum of musicians vs. non-musicians is lent feasibility. Gaser and Schlaug (2003), reveal the positive correlation between the gray matter volume in the cerebellum of musicians with the musician status, comparing non-musicians, amateur musicians, and professional musicians. Figure 2.5 shows the location of these aforementioned cerebellar gray matter differences.
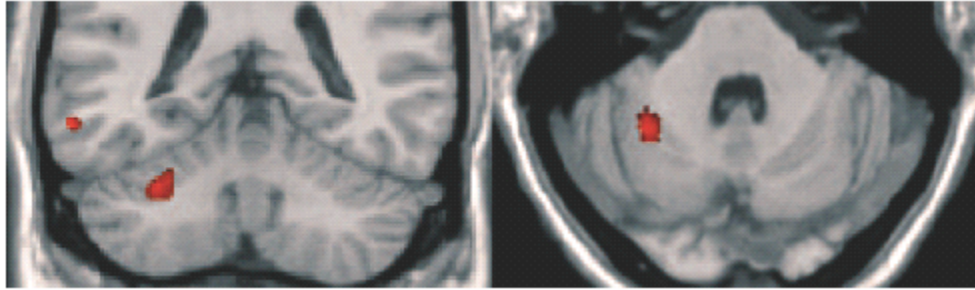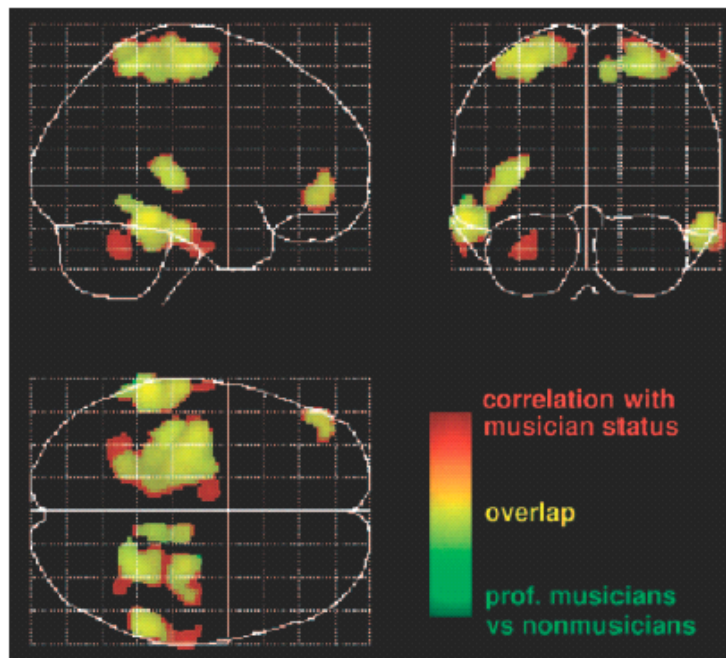
Figure 2.5 (Reprinted from Gaser, C. & Schlaug, G. (2003). Brain structures differ between musicians and non--musicians. *The Journal of Neuroscience*, 23, 9240-9245)

In addition to the cerebellum, Gaser and Schlaug list several other structures, the gray matter volume of which has been shown to correlate positively with the musician status. Some of these are: temporal gyri, precentral gyri, and the left Heschl's gyrus. Figure 2.6 shows a cumulative overview of the structures overlapping with the musician status.

Planum temporale, an auditory association cortex structure, also suggested to subserve the pitch intervals and sound sequences (Koelsch and Siebel, 2005), has been shown to contribute to the left-right asymmetry between musicians and non-musicians (Schlaug et al., 1995; Limb, 2006). This asymmetry is more prominent in musicians with the perfect (also called "absolute") pitch than either in non-musicians or musicians without the perfect pitch. Perfect pitch is a concept indicating the recognition of any tone without the reference from the adjacent tones. It has been suggested that the perfect pitch may in fact be a genetic, rather than an environmentally acquired ability (Peretz and Zatorre, 2005). The striking difference in the gray matter volume of the planum temporale between musicians with the perfect pitch and musicians without it as well as the non-musicians (Fig 2.7 from Schlaug et al., 1995), may in fact provide some evidentiary support for this claim. In addition, an extensive musical training is not

necessary for possessing the perfect pitch processing skills (Limb, 2006), deeming it

further to be a rather genetic than environmentally induced component of music

processing. Further studies, involving the young subjects, and/or longitudinal

investigations would be necessary to substantiate the premise of the genetic nature of the

perfect pitch ability.

Figure 4.   Overlap between different types of statistical analyses. This figure shows the results of the direct comparison between professional musicians and non-musicians (green) and the correlation with musician status (red) using the same statistical thresholds as in Figure 1. The overlap between both results is shown in yellow (as a result of mixing red and green). Results are displayed as maximum intensity projections ("glass brain"), which show highest values within each orientation.

Fig 2.6 Reprinted from Gaser, C. & Schlaug, G. (2003). Brain structures differ between musicians and non--musicians. *The Journal of Neuroscience*, 23, 9240-9245

 Subserving the aforementioned reduced interhemispheric inhibition in musicians,

corpus callosum, a bundle of fibers connecting the two cerebral hemispheres, is another

structure found to differ between musicians and non-musicians (Schlaug et al., 1995a).

This finding is further warranted by the fact that the musical performance requires a complex bimanual movement, thus a necessity for the better communication between the left and right motor cortices. Furthermore, the suggested increased gray matter volume in the anterior corpus callosum of musicians has been shown to correlate with the early commencement of the musical training (Schlaug et al., 1995a).

Fig. 1. Brain surface projections of the right and left planum temporale (PT) in a musician with perfect pitch (upper) and a nonmusician (lower). (Left) Views from the right; (middle) views from above with the left brain hemispheres to the reader's right; (right) views from the left. The images were reconstructed from stacks of 128 contiguous sagittal magnetic resonance image slices where the PT had been highlighted on each slice. The δPT values are −0.77 for the musician and −0.39 for the nonmusician (*16*).
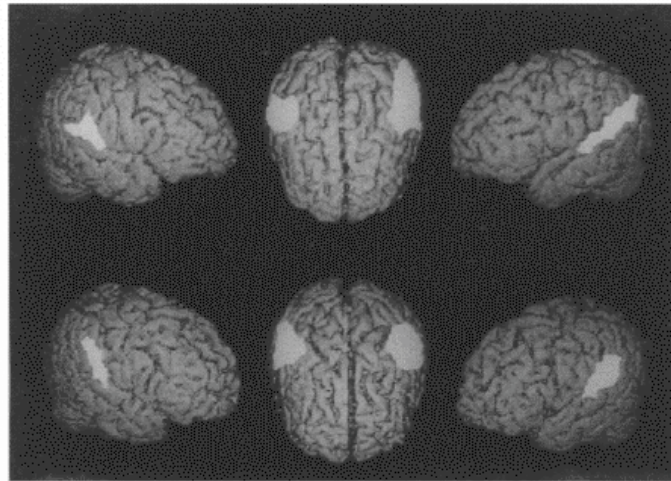
Figure 2.7 from Schlaug, G., Jäncke, L., Huang, Y., Steinmetz, H. (1995). In vivo evidence of structural brain assymetry in musicians. *Science*, 267, 699-701. Reprinted with permission from AAAS

Heschl's gyrus is another structure associated with the musical aptitude (Schneider et al., 2002) and a complex pitch processing, has been shown to be larger in the absolute size in professional and amateur musicians than in non-musicians (Fig. 2.8 from Schneider et al., 2002).
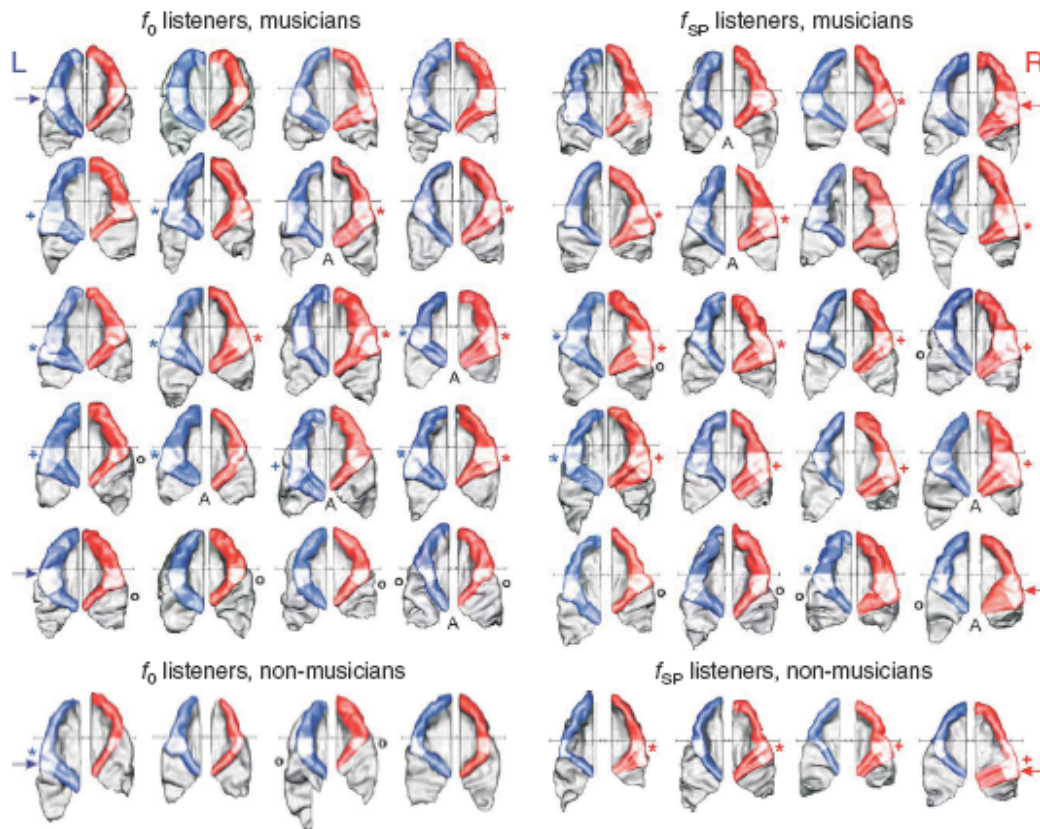
Figure 4 Individual HG morphology. f_0 listeners demonstrate a larger left IHG and f_{SP} listeners a larger right IHG in most cases (IHG highlighted, red and blue arrows). The occurrence of sulci and duplications (SI, asterisks; mHS, '+' symbols; PD, black open circles) depends on hemisphere and pitch perception preference. Professional musicians and amateurs (A) showed greater gray matter volume of the entire anterior convolution including HG and aSTG (colored structure) than non-musicians (bottom).

Figure 2.8 Reprinted by permission from Macmillan Publishers, Ltd *Nature Neuroscience* Schneider, et al. (2002). Structural and functional asymmetry of lateral Heschl's gyrus reflects pitch perception reference. *Nature Neuroscience*, 8, 1241-1247

2.5. Conclusion

It is clear, as the studies have shown that there are functional and structural differences in the brains of musicians from those of non-musicians. As indicated, these changes are likely the result of the many years of practice. The practice entails many different modalities: auditory, visual, motor, and so on. The following chapter will explore different findings on practice (or training), with the special focus on the motor component of practice as the motor practice is one of the most crucial facets of musicianship.

Chapter 3

Introduction: Training

Motor training – Non-motor training – Musical training

"If practice did not make perfect, nor habit economize the expense of nervous and muscular energy, (man) would therefore be in a sorry plight."

William James
(The principles of psychology, Vol. 1, 1890)

3.1 Introduction

As discussed in the previous chapters, neuroplasticity is frequently a consequence of learning and/or training. It is feasible to suggest that without the neural modifications based on the encountered experiences, learning would not occur or at least it would not be stable through time. Learning a skill, however, may involve more durable modifications, as shown in the previous chapter on the brains of musicians.

According to Jonides (2004), learning can be viewed either as an increase in the automaticity of one strategy or the development of a new one. From this argument, it follows that should the new strategy be developed, the activated brain regions might differ from the early to the later stages of training, or if the activation remains in the same regions, it will differ in intensity from the early to the later stages to a certain extent. However, if the same strategy is at work, but the learning is improved, the resulting activations will reflect the automatization of this strategy. This automatization can either result in a decrease of the activation in the same areas, reflecting neural efficiency, or it may lead to an expanded activation, reflecting the use of more neural resources. It is also possible that depending on the demands of the skill, all or some of these processes take place in stages as the skill becomes consolidated (Petersen et al., 1998). Finally, the processes of increase and decrease in cortical activations while learning a skill can take place at the same time, however in different brain areas (Büchel, C., Coull, J.T., and Friston, K.J., 1999), depending on the type of the skill.

A similar picture has been painted by Kelly and Garavan (2005), who suggest three different possible outcomes of practice: increase in activation, decrease in activation, and functional reorganization. According to these authors, a decrease in

activation suggests an improvement in responses as the skill is acquired through practice, reflecting a more efficient utilization of the neuronal circuits for the task in question. By the same token, an increase in activation reflects the recruitment of additional cortical circuits with practice. Finally, the reorganization may occur in two different forms: redistribution and true reorganization. Redistribution, also termed as pseudo-reorganization by the authors, refers to the fact that through practice, the activation map remains the same however, the extent of the activation would change. In other words, different cortical areas contribute with different intensities to the task as a result of practice. True reorganization occurs when the location of the activation changes with practice. The authors find that true reorganization is achieved if in fact the nature of the task after extensive practice is no longer the same as in the beginning of practice.

This chapter explores more specific examples of the training induced neural changes with the focus on the motor training, the non-motor training and musical training.

3.2 The effects of motor practice

Münte, Altenmüller, and Jäncke (2002) suggest that motor learning occurs in several distinct phases, where it becomes evident that with continued practice, there is an increase in performance. While the performance becomes better with practice, even without the significant differences in the behavioral outcome of the performed task, there may be underlying differences in the patterns of functional activations between the trained and the non-trained subjects.

Supported by a functional magnetic resonance imaging (fMRI) study on the

acquisition of a motor skill, Karni et al. (1998) point out three phases of motor learning: initial fast phase, followed by a period of the skill consolidation, and a slow learning phase, with the gradual further improvement of the skill. In addition, these authors emphasize the findings of the practice effects in the motor areas even after cessation of the practice for the period of 1 year. Thus, it can be assumed that the motor practice directs the functional cortical rearrangement to a certain extent.

Yin et al. (2008) provide an animal model example of the different stages of learning, during the acquisition of the motor skill. By recording the neuronal activity via the implanted electrodes, as the mice underwent motor training by running on an accelerated rotarod, these authors found that the location of the activations differed depending on the stage of training. Similar to Karni et al., they point out two distinct stages of training, one characterized by the more rapid improvement in performance, and the other one characterized with the slower or more gradual improvement. The authors further suggest that after the skill is consolidated, the plastic changes that occur as a result, are enduring. In their study, they showed that the initial stages of motor skill acquisition occurred in the dorsomedial or associative striatum, while the later stages resulted in activity in the dorsolateral or the sensorimotor striatum (Fig. 3.1 shows the human striatum, which consists of the caudate nucleus and the putamen).

Years earlier, Anderson, Alcantara, and Greenough (1996) showed that there was an increase in the number of synapses in rat cerebella as a result of motor practice, supporting the plastic reorganization as a consequence of practice.

Fig 3.1. Striatum (in green) (from Wikipedia.org)

Changes brought on by the motor practice specifically focusing on the cerebellum have been explored by Doyon et al. (2002). The activations during learning of the finger tapping sequence were recorded via the fMRI method over 3 separate scanning sessions. In addition to improvement on the task, the activations showed a specific pattern as the task was learned. There was an increase in activation from session 1 to session 2, followed by a decrease in session 3. Furthermore, the authors found that there was a transfer of activation through the sessions from the cerebella to the dentate nuclei (Fig. 3.2), suggesting the plastic cortical reorganization of the task-related circuits, as the task becomes better learned.
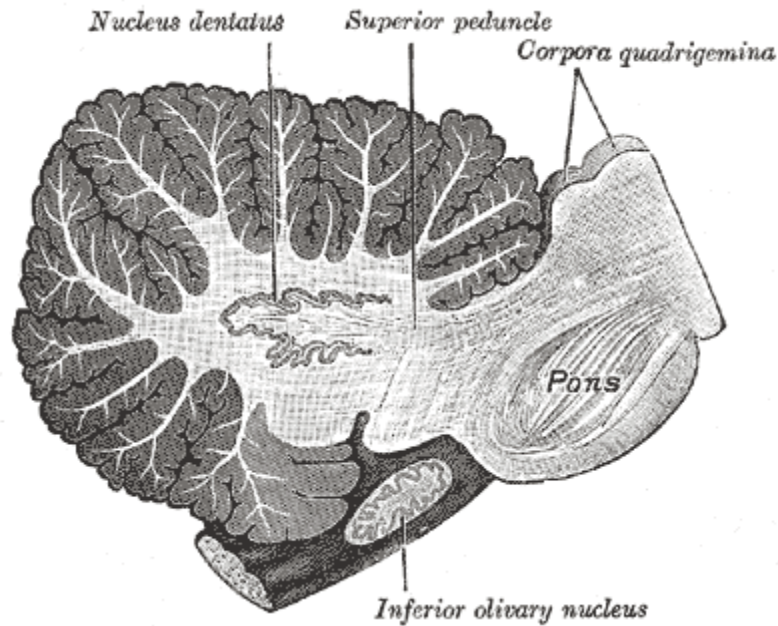
Figure 3.2 Nucleus dentatus or the dentate nuclei (from Wikipedia.org)

3.3 Motor practice and musicians

Hund-Georgiadis and von Cramon (1999) found via the fMRI method that there were different activation patterns in professional pianists and non-musicians as a result of learning a tapping (motor) task. They found that the supplementary motor area (SMA) was much less activated in professional pianists than it was in the non-musicians. In addition, there was an increase in activation of the pre-motor cortex in non-musicians in the initial stages of learning in comparison to musicians. One of the most prominent patterns of functional differences between musicians and non-musicians occurred in the primary motor areas (M1) and the cerebellar areas. Professional pianists recruited larger M1 areas, where they also exhibited an increase in activation throughout learning. Due to this pattern, the authors contend that the long-term motor practice leads toward expansion of the M1 areas. Furthermore, the cerebellar activation in musicians was much lesser and

sometimes did not even occur in some of the cerebellar areas, than it was in non-musicians. The authors call this effect the "pre-practice experience." In the present investigation, the musical talents are deemed as representing the population with the long-term musical practice, and thus might have the pre-practice experience.

Investigating the effects of the long-term motor training by utilizing the complex and simple motor tasks, Meister et al. (2005) found that while non-musicians showed distinct patterns of increased activation from the simple to the complex motor task, the musicians showed no differential activations between the simple and the complex task. The musicians in this study are reminiscent of the subjects with the long-term motor practice, as is claimed in the present investigation. The authors conclude that due to the long-term motor practice, musicians utilize less and different areas for the execution of the motor tasks with varying complexities.

In a study utilizing a motor task involving both bimanual and unimanual movements, Koeneke et al. (2004), recorded the fMRI responses in the cerebella of musicians and non-musicians. The results of the study showed that the musicians exhibited much less activation in the cerebellum than did the non-musicians in response to both the bimanual motor task and the unimanual-right-handed task, but not the unimanual-left-handed task (all subjects were right-handed). Thus, the authors concluded that due to the long-term motor practice that musicians endured, they need to exert less effort for the manual motor tasks, therefore recruiting a fewer number of neurons to complete the task. According to Kelly and Garavan (2005), throughout the practice of a motor task, the cortical motor structures including the cerebellum, begin to gain more involvement in the task completion and may become "the site of motor memory" (p. 3).

Figure 3.3 shows the cerebellar activations recorded in this study.

Further supporting the findings of the decreased activation in musicians as an effect of practice are the findings of the study by Haslinger et al. (2004). Finding the increased efficiency in the processing of bimanual movements, the authors showed via fMRI recordings that the cortical motor areas and motor association areas, including the supplementary motor area (SMA), bilateral cerebella, premotor cortex, as well as the right inferior temporal gyrus and the right striatum, were more activated in control subjects than in musicians. The authors credit a "highly developed motor control system" (p. 212) for the decreased functional involvement of the motor cortical systems in the bimanual movement of musicians. A decreased activation in the motor cortical areas in response to the bimanual movement task in musicians as compared to non-musicians was also supported by Jäncke, Shah, and Peters (2000).
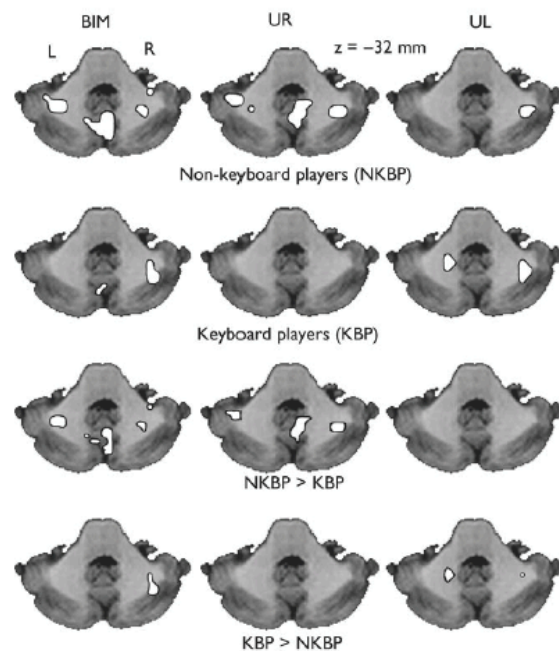
Fig. I. Significant hemodynamic responses in the cerebellum during the different tasks (BIM, UR, UL) broken down for non-keyboard players (NKBP) and keyboard players (KBP). The lower two rows represent activation differences between the two groups.

Figure 3.3 (reprinted from Koeneke et al., (2004). Long-term training affects cerebellar processing in skilled keyboard players. *Neuroreport*, 15, 1279-1282).

3.4 Evidence from the non-motor learning

The process of learning or acquiring a skill does not only apply to the motor learning. In their positron emission tomography (PET) study on the learning related changes during the recall of abstract designs, Petersson, Ingvar and Elfgren (1999) used the less and the well practiced state for the investigation of the cortical activations related to automaticity in skill acquisition. These authors claim that automaticity is related to the decreases in activation in the respective brain regions, a hypothesis that was confirmed in their investigation, yielding the findings of a decreased activation in the well practiced state. They further indicate that automaticity implies decreased reliance on the attentional resources and the working memory. Consequently, the need for attentional resources gradually diminishes as the skill becomes automatized.

Similar findings were provided in a PET study by Raichle et al. (1994). In this study, the subjects' cortical activation to naïve and practiced verbal response showed that the activation was lower for the practiced words. The authors conclude that the circuits utilized for performing the task can change after as little as 15 minutes of practice, which however depends on the extent to which the task is learned.

Learning of an abstract material as well, has been shown to lead to the neural changes even on the structural level. In a voxel-based morphometric (VBM) study, Draganski et al. (2006), showed that the brain areas of the medical students scanned at three different time intervals during their preparation for the exams, underwent a significant gray matter increase during the learning period. Some gray matter increases, such as the one in the hippocampus showed to be continuous and durable even after the learning period. The gray matter increase was also detected in a study on juggling

(Draganski et al., 2004), described as the task of "spatial anticipation of moving objects" (p. 311). The gray matter increase occurred after 3 months of juggling practice in the brain areas for retention of the visual motion information, rather than the motor areas, indicating that the functional and/or structural changes depend on the specificity of the practiced task.

There is a possibility that even without the behavioral improvement on the task there may be underlying functional changes with practice. In an fMRI study, Landau et al. (2004) found that even without an increase in performance, there were decreases of functional activations in different brain areas in the face recognition working memory task. Others have also shown the dynamics of functional changes brought on by the training on a working memory task (Kelly et al., 2006; Olesen, Westerberg, and Klingberg, 2003), reading based on an artificial grammar (Fletcher et al., 1999), as well as the mirror reading (Kassubek et al., 2001).

3.5 Musical training

In an EEG study, Johnson et al. (1996) found different patterns of the spontaneous EEG signal (at rest) between the subjects with the musical training and the subjects without the musical training. In addition to the overall differences in signal between the musically trained and non-trained subjects, the authors found a higher interhemispheric coherence values in the musically trained. The authors suggest that it is not far-fetched to assume that the musical training would result in cortical changes given the complexity of musical abilities. Further, the authors even suggest that musical training likely "influences the cortical basal electric mass" (p. 575).

In another EEG study, Shahin et al. (2008) presented adult professional violinists, amateur pianists, and 4-5 year-old children studying piano via Suzuki method, as well as the matched non-musician subjects, with the sounds that were either those of a violin, a piano or the pure tones. The authors claim that the brain responses to sound are enhanced in musicians, both young and adult, when compared to non-musicians. They proceed to suggest that "the presence of distinct EEG attributes in musicians invites the hypothesis that musical training modifies a neural system for auditory information processing" (p. 114). They, therefore, predicted that the gamma-band-activity (GBA) suggested to reflect a highly learned perceptual template matching, will be enhanced in musicians when listening specifically to the instrument that they play and practice on. Indeed, GBA was enhanced in musicians as compared to non-musicians. This GBA enhancement occurred in children even after only 1 year of musical training. The present investigation also utilizes the passive listening paradigm, however aiming to explore a more encompassing musical experience beyond the instrument of practice (the specifics of the passive listening task will be explored in the methods section of the following chapter).

In further support of the difference between musicians and non-musicians in processing of sounds, Schön, Magne, and Besson (2004) compared professional musicians to non-musicians to assess the effect of musical training on pitch processing in music and language. They showed via EEG recordings of the event-related potentials (ERPs), that musicians exhibit earlier ERPs than non-musicians in response to the pitch contour violations in both music and language. Musicians were also more accurate in detecting pitch violations. The authors conclude that these findings indicate that musical training has an effect on pitch processing in both music and language.

The training effect was shown also via the method of magnetoencephalography (MEG) in a study by Fujioka, et al. (2006). A group of 4-6 year old children, half of whom had the music lessons and the other half of whom did not, were presented with the violin tones and the noise bursts. The study aimed to investigate how the responses to music tones are affected by the musical training. The results showed that the children who had 1 year of musical training showed different MEG responses to the violin tones than those without the musical training, but not to the noise bursts. The authors additionally tested the subjects on the digit-span task and found an improved performance in children who underwent the musical training from the time that they began the training until after 1 year of training. Due to this finding, they further suggest that musical training can increase abilities in other domains, likely due to increasing working memory capacity to a certain extent, increased perseverance skills, and the more focused attention. The transfer of improved performance from the music domain to the verbal domain was reported by Ho, Cheung, and Chan (2003), who found that in children who were in musical training, the verbal memory improved with training as compared to the children who did not undergo musical training.

In an fMRI study, Schmithorst and Holland (2003), showed the differences in the location of the processing of musical stimuli during the passive listening paradigm between the musically trained and non-trained subjects. Their findings showed that musical training seems to lead toward recruiting additional cortical areas when processing music. The processing of musical information will be influenced by the formal musical training as the musically trained individual recognizes specific features of

the musical stimuli such as the "intervals, harmonic types and standard harmonic progressions" (p. 67).

In another study, Hyde et al. (2009) investigated the structural changes in children due to the musical practice. One group of children was provided with the 15 months of musical training and compared to the children with no musical training. The investigation was conducted via the MRI method of the deformation based morphometry (DBM) used for searching the local brain size and shape differences between groups. The findings indicated that there was a neural reorganization due to the 15-month long training. The trained children exhibited an increase in the gray matter volume in the areas important for music processing, such as the primary motor area or the precentral gyrus (Fig 3.3) and the corpus collosum. Given the absence of structural differences between the subjects prior to training, subsequently assigned to the trained and the non-trained group, the authors concluded that the emerging differences (or deformations) were due to training, rather than the underlying biological features.
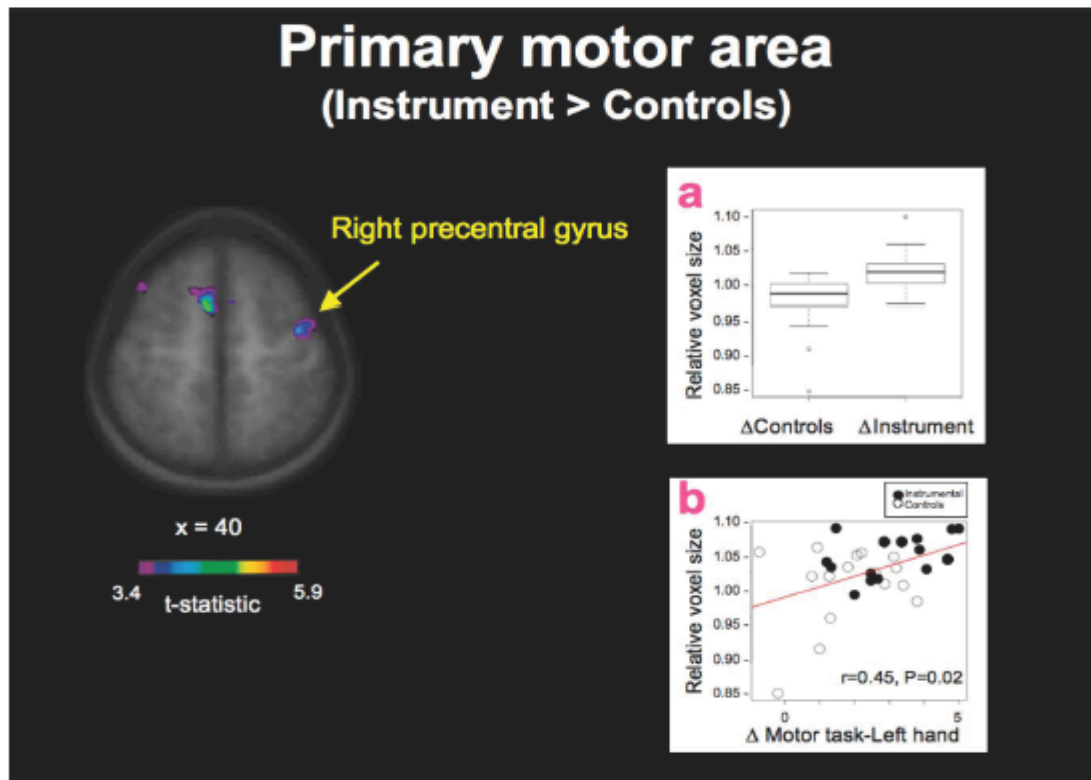
Figure 3.4 (Reprinted with permissions, from Hyde et al., 2007 Cortical thickness in congenital amusia: when less is better than more. *The Journal of Neuroscience*, 27, 13028-13032)

3.6 Conclusion

Evidence shows that the training in a new skill leads toward the changes in the cortical functional activations. In addition, the long-term motor practice, which musicians are exposed to over many years, yields the activations of the motor areas that differ in pattern from those of non-musicians. This further reinforces the notion that musicians represent an excellent example of the effects of the perfected motor skill. The changes in functional activations inevitably lead toward some sort of structural changes indicating the dynamics of neuroplasticity. Similarly, as stated by Duerden and Laverdure-Dupont (2008), some sort of intra-cortical remodeling takes place as a result of changing

functionality. In addition to the implications for education and the skill perfection these changes, which occur due to learning, have clinical implications important for neurorehabilitation measures.

Chapter 4

The present study:

Introduction and Methods

Hypotheses – fMRI method –

Visuomotor study methods – Auditory study methods –

Statistical Analyses – Neuroimaging data

4.1 Hypotheses

The present study aimed to investigate the differences in the functional cortical activations between the musical talents and non-talents, after a short-term practice of a visuomotor and auditory task. Both tasks were created so as not to give an unfair advantage to the musical talents, as will be described in the subsequent sections on methods and results for each of the two studies. The hypothesis for the present investigation was that there will be different patterns of functional activations between the musical talents and non-talents even after the non-talents undergo a short-term practice of the tasks used in the study. The reason for the difference would be the long-term musical practice of the musical talents, which would account for the brain plasticity, resulting in the different information processing in musical talents, not present in non-talents. Further, the direction of the functional activations was predicted to emerge as following: the musical talents would exhibit less activation or activation of the smaller portions of some cortical areas than the non-talents as well as the activation of the different cortical areas than non-talents. As mentioned in the previous chapters, musicians exhibit more activation in the primary motor area than non-musicians in tasks involving motor responses (e.g. Hund-Georgiadis and von Cramon, 1999). Thus, the primary motor cortex (area M1) was taken as a region of interest (ROI), where it is predicted that the talents would exhibit more activation than non-talents in the visuomotor task. The activations in the left inferior frontal gyrus (lIFG) were also hypothesized to differ between the talents (higher activation) and non-talents (lower activation) due to its association with the language processing and given the parallel that

can be drawn between the sight-reading of the musical notation (the language of music) and the written language.

4.2 fMRI method

As we have seen in the previous chapters, the method of functional magnetic resonance imaging (fMRI) is being widely used to investigate brain plasticity, in both functional and structural sense, as well as to investigate the effects of training, including the training in the domain of music (e.g. Haslinger et al., 2004; Schmithorst and Holland, 2003). It is a method which may lead toward the findings that allow us to understand the 'non-rigid' and 'changeable' nature of the brain as well as the mechanisms of learning. As such, it has been utilized in the present study to investigate these mechanisms in musical talents relative to their non-talent cohort.

The fMRI operates on the principle of detecting the blood oxygenation changes, which are presumed to occur as a consequence of the neural activity. The increase in neural activity increases the demand for oxygen delivered to the neurons via the blood. Given that the intensity and/or the amount of neural activity will be accompanied by the amount of oxygen delivery to the neurons, the differences in the blood oxygenation will lead toward the detection of the brain activity in various areas of the brain. More specifically, the changes detected are those in the amount of the deoxyhemoglobin present in the tissue. The increase in neural activity would lead to an increase in all of the physiological parameters on which the amount of deoxuhemoglobin depends (Norris, 2006). This kind of measurement is also known as the blood oxygenation level

dependent (BOLD) imaging, and the response measured is called a BOLD response

(Huettel, Song, and McCarthy, 2004).

4.3 Visuomotor study: Methods

4.3.1. Participants

Forty nine participants underwent an fMRI recording. One participant was

excluded from the analyses due to the incidental finding[1]. Ten participants were excluded

from analyses of the visuomotor task due to the high error rate in this task (M error =

55%, SD = 10%), and 1 participant was excluded due to the image cut-off, leaving N =

37 participants for the visuomotor task. The non-talent participants were randomly

assigned to one of the 2 groups: Non-talents who practiced a visuomotor task and non-

talents who practiced a music task. Talents comprised the third group. All participants

were free of medical and psychiatric illnesses, and were not taking any prescription

medication at the time of testing. As established by the Edinburgh Handedness

Questionnaire, there were 3 left-handed, 29 right-handed, and 15 ambidextrous

participants. Eleven participants (2 male, 9 female), ages 15-18 ($M = 17.88$, $SD = 0.70$)

were musical talents with the average musical instrument practice time of $M = 130.91$

minutes, $SD = 50.69$ minutes a day for the last 2 years to the date of the study, and

comprised an experimental group. Table 4.a. lists the musical instruments played by the

musical talents. Twenty six participants (12 male, 14 female) ages 15-18 ($M = 17.50$, SD

$= 0.81$), who have not played an instrument at least in the last 5 years to the date of the

study, comprised a control group. Twelve participants were in the visuomotor task

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[1] Incidental finding refers to any type of finding by the reviewing physicians that may indicate a possible necessity for the clinical evaluation and follow-up.

practice group and 14 participants were in the auditory task practice group. Table 4.b and

4.c, summarize participant demographics.

All participants signed an informed consent and were provided with the safety

guidelines regarding the MRI scanner. An informed consent was signed by the parents for

the participants under the age of 18. Participants were recruited from the local High

Schools in Bonn, Germany.

Table 4.a Musical Instruments played by the talents

Instrument

	Frequency	Percent
Flute	1	2.7
Flute, Piano	1	2.7
Guitar	1	2.7
Harp	1	2.7
Piano	4	10.8
Piano, Guitar	1	2.7
Piano, Viola, Flute	1	2.7
Violin, Piano	1	2.7
Total	37	100.0

Table 4.b.

	Mean	Standard Deviation
Age	17.61	.80
IQ	108.3	12.1
Error Rate	.21	.11
Average grade	2.26	.54

N = 37

Table 4.c

	N
Gender	Male = 14
	Female = 23
Talent	Yes = 11
	No = 27
Practiced	Auditory = 14
	Visuomotor = 12

4.3.2. Visuomotor task

The task consisted of the 4 x 6 matrix with the left side of the matrix corresponding to the left hand and the right to the right hand. Each of the six column fields of the matrix corresponded to a finger of the hand as following: the left 3 fields corresponding from left to right, to the left ring finger, left middle finger, and left index finger; the right 3 fields corresponding from left to right, to the right index finger, right middle finger, and right ring finger (Figure 4.1). The subjects tapped a sequence defined by the following rules: the order of the tapping was indicated by the rows starting from top to bottom; the frequency of the taps was indicated by three different shapes: circle (tap once), horizontal bar (tap twice), triangle (tap 3 times).

LRF	LMF	LIF		RIF	RMF	RRF
LRF	LMF	LIF		RIF	RMF	RRF
LRF	LMF	LIF		RIF	RMF	RRF
LRF	LMF	LIF		RIF	RMF	RRF

Figure 4.1. Visuomotor task matrix (LRF: left ring finger, LMF: left middle finger, LIF: left index finger; RIF: right index finger, RMF: right middle finger, RRF: right ring finger).

There were combinations of 4 shapes, where any one of the three shapes was presented twice, so that one matrix contained, for example, 2 circles, 1 bar, and 1 triangle (Figure 4.2).

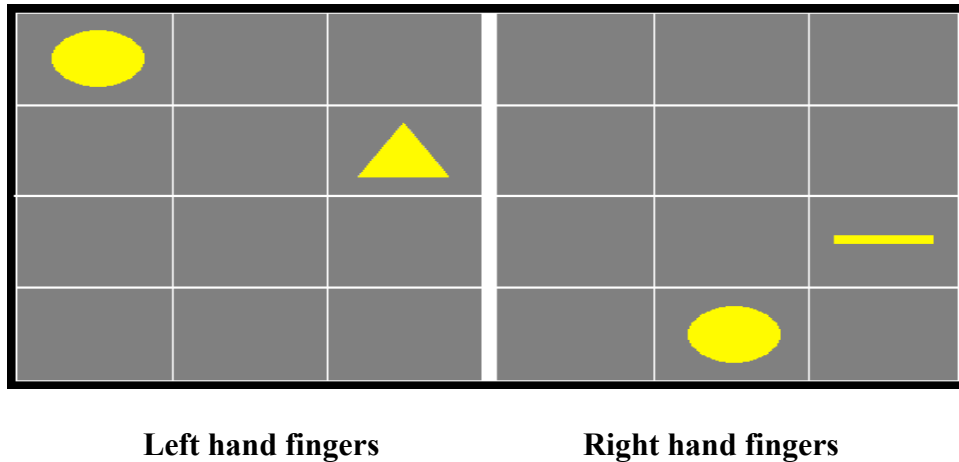**Left hand fingers**   **Right hand fingers**

Figure 4.2. Visuomotor task presentation: the tapping sequence for this example is as follows: 1 tap with the left ring finger, 3 taps with the left index finger, 2 taps with the right ring finger and 1 tap with the right middle finger.[2]

This design for the visuomotor task was used due to it's similarity to the sight-reading in music. While the musical notation dictates the finger movement of the musician on the instrument played, the visuomotor task similarly uses symbols and their specific arrangement as a set of rules, which dictate the specific finger movement (or tapping). In this manner, the rules for the tapping sequence require the "sight-reading" or the visual input from the symbols and reproducing the sequences given by those symbols via the motor response.

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[2] Please see Appendix A for the complete set of instructions given to the subjects for the Visuomotor task.

4.3.3 Procedure

Half of the control group participants practiced the visuomotor task at home for three days prior to the scanning session with the following requirements: achieving 300 correct trials on day 1, 200 correct trials on day 2, and 100 correct trials on day 3. The practice time took approximately 30, 15, and 5 minutes, respectively. The subjects submitted their practice output sheet upon the completion of the practice, to ensure that the practice was performed correctly. The output sheet contained the date, time, and the responses (taps) of the subjects.

All subjects performed the visuomotor task, where only half of the controls practiced the task, while the other half of the control subjects and the experimental group (talents) were briefly familiarized with the task prior to scanning.

In the scanner, the task was presented in blocks with the approximate duration of 24 seconds and approximately 3 seconds of rest in between blocks. Each block consisted of 6 matrices, with 1 matrix lasting 4 seconds, summing up to 24 seconds per block. The experimental blocks consisted of random tapping finger and shape combination sequences, with the following restrictions: within each matrix two of the same shapes did not appear one next to the other for the same hand; 2 shapes always appeared on the left and 2 on the right side of the matrix indicating left or right hand tapping. Within the block (6 matrices), each shape appeared 8 times, summing up to the 48 taps per block. The control block consisted of the same matrices, however with no variation in shapes, so that each matrix consisted of the 4 instances of only one shape (Figure 4.3)
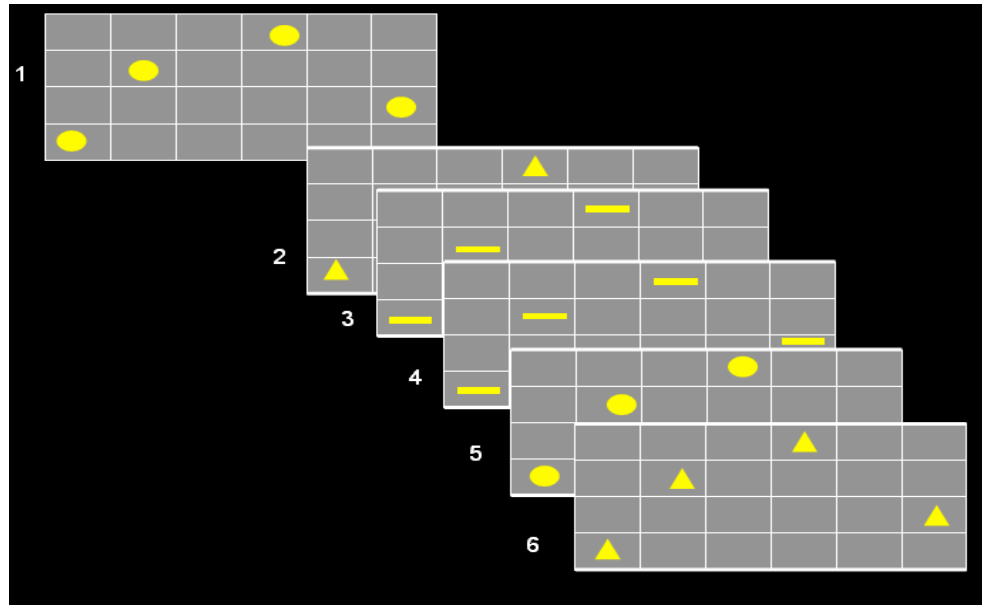
Figure 4.3 Control block trials

4.4. Auditory study: Methods

4.4.1. Participants

The same 49 participants underwent an fMRI recording for the auditory study as for the visuomotor study. One participant was excluded from the analysis of the auditory task due to the aforementioned incidental finding and 1 participant was excluded due to the image cut-off, leaving N = 47 participants in the music task. The assignment of participants was the same as in the visuomotor study. Thirteen participants (4 male, 9 female), ages 15-18 ($M = 17.96$, $SD = 0.68$) were musical talents with the average musical instrument practice time of $M = 131.54$ minutes, $SD = 55.5$ minutes a day for the last 2 years to the date of the study, and comprised an experimental group. Table 4.d lists musical instruments played by the talents who participated in the auditory study. A

control group consisted of 34 participants (19 male, 15 female) ages 15-18 ($M = 17.43$,

$SD = 0.8$), who have not played an instrument at least in the last 5 years to the date of the

study. Sixteen participants were in the visuomotor task practice group and 18 participants

were in the auditory task practice group. Tables 4.e and 4.f show the participant data.

Table 4.d Musical instruments played by the talents

Instrument

	Frequency	Percent
Flute	1	2.1
Flute, Piano	1	2.1
Guitar	1	2.1
Harp	1	2.1
Piano	5	10.6
Piano, Guitar	1	2.1
Piano, Viola, Flute	1	2.1
Trombone	1	2.1
Violin, Piano	1	2.1
Total	47	100.0

Table 4.e

	Mean	Standard Deviation
Age	17.57	.80
IQ	107.40	11.56
Average grade	2.26	.54

N = 47

Table 4.f

	N
Gender	Male = 23
	Female = 24
Talent	Yes = 13
	No = 34
Practiced	Auditory = 18
	Visuomotor = 16

4.4.2 Auditory Task

Auditory task consisted of listening to the 20 seconds long musical clips from the 20th century classical music by Gustav Mahler, Eduard Lalo, and Granville Bantock, and answering questions pertaining to the musical clips heard. Twentieth century classical music was chosen due to the lower popularity than the 18th century classical music such as that of Mozart, Bach, or Beethoven. Auditory task aimed at tackling the perceptual part of music processing, only in terms of auditory perception, rather than the performance as in the visuomotor task.

4.4.3 Procedure

One half of the control group practiced the auditory task for three days prior to the scanning session as following: 15-minute musical clip on day 1, 10-minute on day 2, and 5-minute on day 3. To ensure that the auditory practice took place, 2 seconds long beeps were inserted at random intervals throughout the musical clips as following: 8 beeps in the 15 minute clip, 6 beeps in the 10 minute clip, and 4 beeps in the 5 minute clip. The subjects were asked to report on the number of beeps within each clip. The other half of controls and the experimental group were familiarized with the task for 10 minutes prior to scanning, by listening to a 10-minute long musical clip, as the one given to the practice group on day 2 of practice.

Within the scanner, each block consisted of 20 seconds of auditory material and 3 seconds for answering the questions about the material. Experimental blocks consisted of twenty 20-second musical pieces, followed by the 3-second presentation of the question pertaining to the same musical clip, such as "Have you heard a violin in the previous

clip?". The possible answers for this question were "yes" or "no", which appeared on the screen. "Yes" appeared on the left side of the screen and "no" appeared on the right side of the screen. Depending on the chosen answer, the subjects pressed the left or the right button to indicate "yes" or "no". There were only 3 types of questions and possible answers: "What was the tempo?" with the possible answers of "fast" and "slow"; "What was the emotion" with the possible answers "sad" or "happy"; and "Have you heard a violin/brass/piano/harp/flute/percussion?" with the possible answers "yes" or "no" .[3]

A control block consisted of the 20 seconds of white noise followed by a 3-second presentation of the white square either on the left or on the right side of the screen. The subjects needed to indicate whether the square is on the left or on the right by pressing the left key if the square was on the left and the right key if the square was on the right. The total duration of a block was 23 seconds.

4.5 Statistical analysis.

Behavioral performance differences were tested by a oneway analysis of variance (ANOVA). Furthermore, correlations of experimental task performance and other parameters (task practiced, talent status, IQ, and so on) were analyzed by Pearson's product-moment correlation coefficients (r). The significance level was generally set to α = .05. Behavioral data were analyzed by SPSS (version 17.0.1., German release).

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[3] Please see Appendix A for the complete set of instructions given for the Auditory task

4.6 Neuroimaging data

FMRI data analysis was performed using Statistical Parametric Mapping 5 (SPM5, http://www.fil.ion.ucl.ac.uk/spm/). Preprocessing included realignment with unwarping, slice timing, normalization to an EPI-template and smoothing with a 8 mm Gaussian kernel. The hemodynamic response to each block was modeled by a canonical hemodynamic response function. For modeling, n vectors of stimulus onsets were used (x/y condition) and movement parameters were included as regressors. The onset was defined by the occurrence of the starting stimulus and the modeled block comprised the visuomotor (20 seconds) or auditory task phase (23 seconds). Importantly, at the 1st level analysis the correct trials from the two conditions (experimental and control) were modeled separately from all error trials and the 2nd level analysis only included correct trials to exclude random effects due to error-related processing. Task-related activations were identified by the experimental vs. control condition contrast

Parameter images for the respective contrasts of interest were generated for each subject and were then subjected to a 2nd level random effects analysis using a one-way ANOVA (within subject) as a model. Predefined linear combinations of the group contrast images were then tested with a one-sample t-test against a null hypothesis of no effect. Analyses on the cluster level were done using the Masked Contrast Images (mascoi) tool for SPM (http://homepages.uni-tuebingen.de/matthias.reimold/mascoi/) with a secondary $p = .001$. The MARSeille Boîte À Région d'Intérêt (MarsBaR) extension of SPM (Brett et al., 2002; http://www.nitrc.org/projects/marsbar/) was used to extract the condition-related beta values and for anatomical labeling.

The individual mean corrected beta values for each task condition were determined separately for each task condition in the hypothesized and posthoc region-of-interest (ROI) analyses. The beta values were analyzed via the oneway ANOVA (3 groups: trained non-talents, non-trained non-talents, and talents x true task: experimental vs. control task) and the posthoc Tukey tests for locating the significant interactions among the groups. In addition, the beta values were analyzed via independent samples t-test for detecting the true task activation differences between any two compared groups. Analyses of beta values were performed in SPSS (version 17.0.1, German release)

4.7. fMRI Data Acquisition

For both paradigms, thirty-five axial slices with the matrix size of 64x64 and a field of view of 194x194mm were collected at 1.5T (Avanto, Siemens, Erlangen, Germany). We acquired 500 T2-weighted, gradient echo EPI-scans, with the following parameters: slice-thickness 3mm, interslice gap: 0.3mm, repetition time: 2910ms, echo time: 40ms. In addition, we obtained a sagittal T1-weighted 3D-mprage sequence with 160 slices. There were 20 blocks in the control condition and 20 blocks in the experimental condition, totaling 40 blocks per paradigm. The T1 images were obtained after the first paradigm, followed by a short break, and ending with the second paradigm.

Both fMRI paradigms were in the block design, defined as "the time integrated averaging procedure", where the data is analyzed by way of subtraction method with the idea of comparing the "a task state" with the "control state" (Logothetis, 2008, p. 871). Further, the task state places a specific demand on the brain, which can lead to the

isolation of the specific structures involved in this task when compared to the "control

state" where the same demand on the brain is absent.

      The following chapters explore the results of the two studies and offer a

discussion of the findings.

Chapter 5

Visuomotor study:
Results, Discussion

Behavioral results - Imaging Results - Discussion

5.1. Behavioral Results

The correct responses for the visuomotor task were determined as following: if there were 3 or more correctly tapped matrix sequences in a block, that block was determined as a correct response. If there were only 1-2 correct responses in a block, that block was determined as an error. Thus, the modified number of responses was analyzed for comparison, rather than the total number of responses for each matrix (6 matrices in a block, sums up to 240 matrices total in 40 blocks: 120 for the experimental and 120 for the control blocks). A oneway ANOVA with the groups based on practice (trained nontalents, untrained nontalents and talents) as a between-subject variable and IQ and average grade in school as dependent factors revealed no significant effects. Thus, there were no major or interaction effects of the group factor on IQ and academic achievement. In other words, there is no confounding of the group factor of the IQ, academic achievement, and the error rates in the task. An independent samples t-test revealed no differences in performance between the talents and all nontalents. Thus, the musical talent and/or the music practice can be considered to be the differentiating factors between the 2 groups of non-talents and 1 group of talents in terms of the imaging results, in the absence of behavioral distinction.

5.2 Imaging Results

Table 5.a. provides a list of Talairach coordinates and the areas corresponding to them for the main effect of task (ME of Task) for all of the participants and for the three groups separately. Activated areas for the ME of Task are shown in Fig. 5.1

Between-group (Talents>Nontalents) contrast analyses revealed an activation in the bilateral precuneus (right: BA19, left: BA 7), right middle temporal gyrus (BA 19), and left middle frontal gyrus (BA 6), reflecting the effect of long-term practice in talents. In addition, bilateral precuneus (right: BA 7, left: BA 7), bilateral middle frontal gyrus (right: BA 6, left: BA 6), left precentral gyrus (BA 6), and the right parahippocampal gyrus (BA 30) activation was revealed by the exclusive masking procedure[1] (Fig. 5.2). There were no significant activations in the Nontalents>Talents contrast.

The analyses of the main effect of the short-term practice, referring to the practice of the visuomotor task, and the contrast between the Nontalents who practiced the visuomotor task and Nontalents who practiced the auditory task plus the Talents (trained nontalents > untrained nontalents + Talents), revealed the activations in bilateral precentral gyrus (left: BA 9, right: BA 6), left middle frontal gyrus (BA 47), left superior frontal gyrus (BA 9), shown in Fig. 5.3.

Further between-group contrasts are shown in Table 5.a.

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[1] The exclusive masking procedure reveals the activations significant in one group but not the other, rather than the contrast between the groups. For example, Talents>Nontalents mask reveals the activations significantly present in Talents but not in Nontalents.

Table 5.a.

	Anatomical location/Brodmann area	Talairach coordinates	Voxel cluster Size	Z score
ME of Task (all, N = 37)	Right middle temporal gyrus/BA 19	36, -78, 20	6802	Inf.
	Left medial frontal gyrus/BA 11	-3, 46, -12	862	6.59
	Left frontal lobe/BA 6	-24, 2, 50	121	5.69
	Left precentral gyrus/BA 4	-53, -4, 42	63	4.89
	Left inferior temporal gyrus/BA 2	-59, -9, -15	31	4.77
	Left postcentral gyrus/BA 2	-44, -27, 43	55	4.70
	Right middle frontal gyrus/BA 6	24, -1, 47	52	4.45
ME of Task_untrained nontalents (N=	Right posterior cerebellum	6, -74, -9	2394	5.57
	Left medial frontal gyrus/BA 10	-4, 49, -9	92	4.17
	Left frontal lobe/BA 6	-20, -2, 50	14	3.93
ME of Task_trained nontalents (N = 1.	Left medial frontal gyrus/BA 11	-3, 46, -15	464	5.64
	Left posterior cingulate/BA 30	-9, -52, 14	1494	5.31
	Left middle temporal gyrus/BA 19	-36, -80, 21	178	5.16
	Right cuneus/BA 19	18, -86, 35	152	4.46

Right anterior cingulate/BA 24	6, 32, 9	31	4.31
Left superior frontal gyrus/BA 9	-12, 54, 28	41	4.06
Left precuneus/BA 7	-18, -61, 50	31	3.99
ME of Task_Talents (N = 11)			
Right middle temporal gyrus/BA 19	36, -78, 20	3155	7.24
Left middle frontal gyrus/BA 6	-27, 2, 41	91	5.33
Right middle frontal gyrus/BA 6	27, -1, 44	64	4.98
Right anterior cingulate	0, 32, 1	26	4.09
Left precentral gyrus/BA 4	-53, -4, 42	46	3.99
Right cerebellum (vermis)	0, -71, -22	13	3.93
Right cuneus/BA 18	21, -96, 0	19	3.91
Left parahippocampal gyrus	-27, -32, -1	20	3.56
Left medial frontal gyrus/BA 11	-3, 43, -15	11	3.41

Coordinates are in the standard stereotaxic space (Talairach & Tournoux), z values are uncorrected at $p = 0.000$, voxel threshold = 10

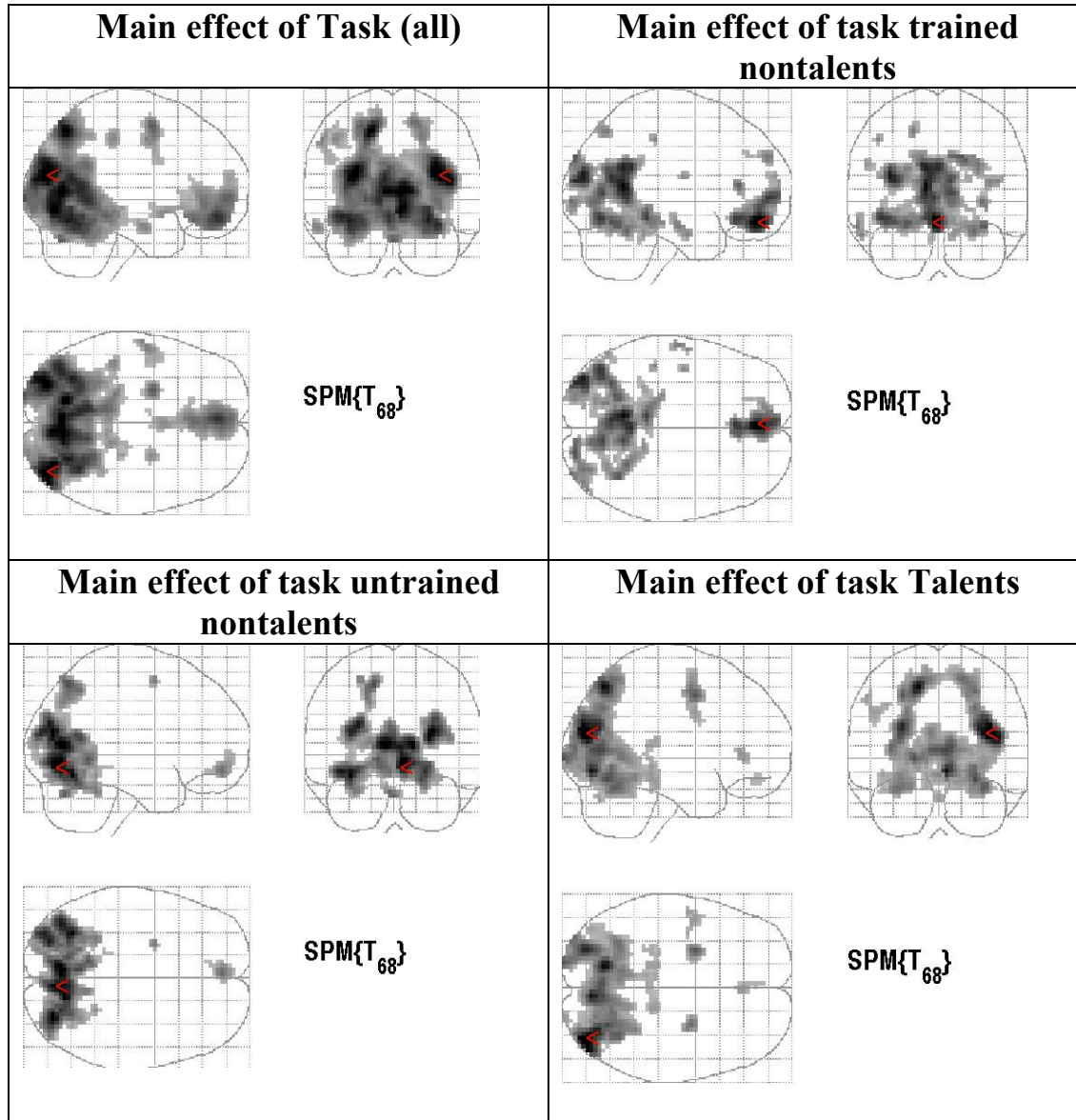| Main effect of Task (all)	Main effect of task trained nontalents
SPM{T_{68}}	SPM{T_{68}}
Main effect of task untrained nontalents	**Main effect of task Talents**
SPM{T_{68}}	SPM{T_{68}}

Fig. 5.1 (Main effect of the visuomotor task in the entire sample, in trained nontalents, untrained nontalents and Talents)

T > NT

SPM{T$_{68}$}
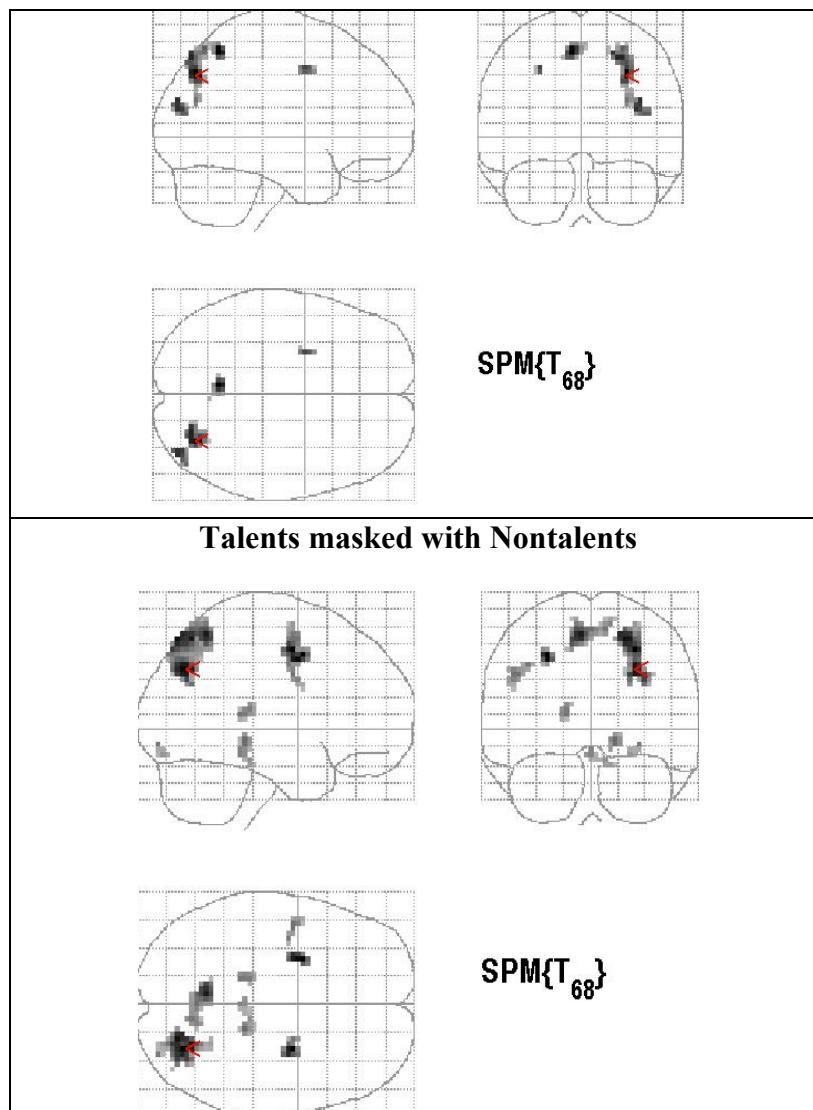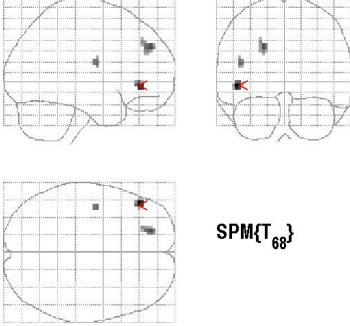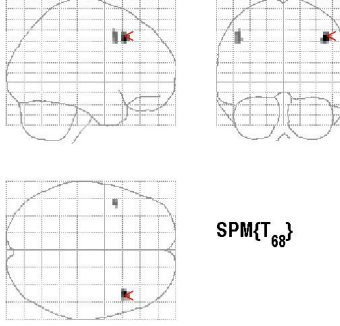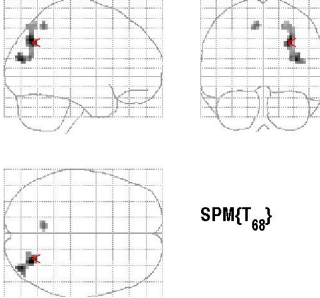
Talents masked with Nontalents
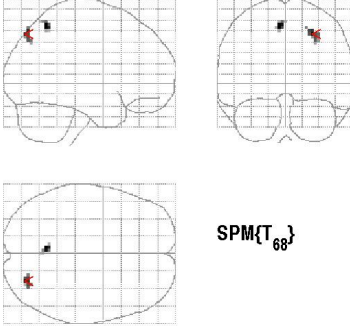
SPM{T$_{68}$}

Fig. 5.2 Between-group analyses: Talents > Nontalents

Table 5.b.

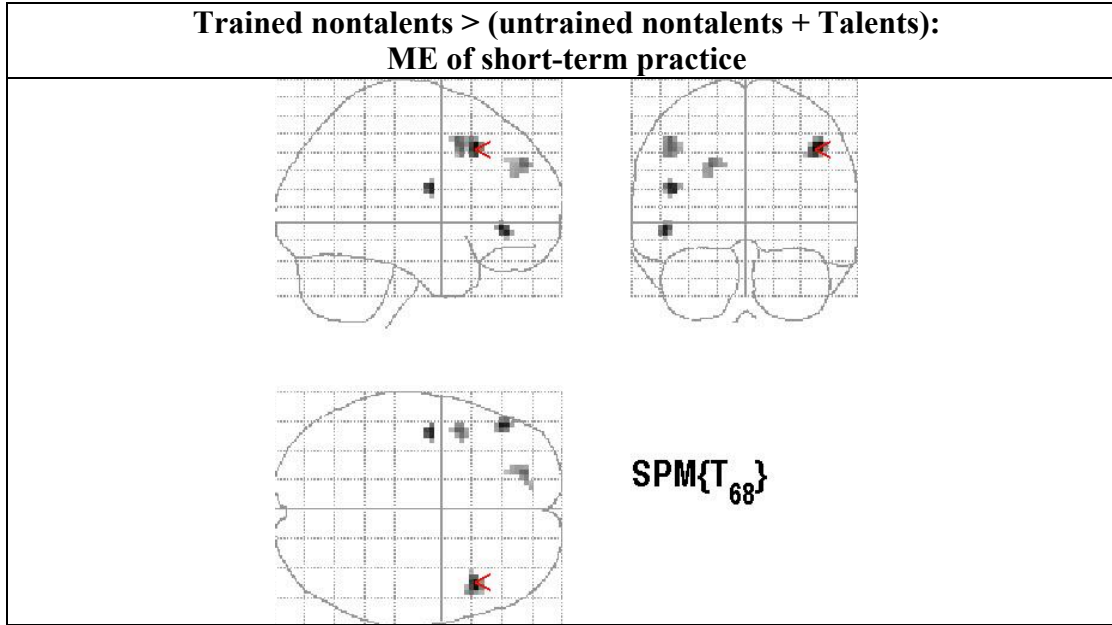|	**Trained nontalents**	**Untrained nontalents**	**Talents**
Trained nontalents vs.		 SPM{T$_{68}$} Left middle frontal gyrus (BA 47) Left superior frontal gyrus (BA 9) Left Insula (BA 13)	 SPM{T$_{68}$} Bilateral middle frontal gyrus (BA 8)
Untrained nontalents vs.	NO effect		NO effect
Talents vs.	 SPM{T$_{68}$} Bilateral precuneus (BA 7)	 SPM{T$_{68}$} Right superior parietal lobule (BA 7) Left precuneus (BA 7)	

Fig. 5.3 The main effect of short-term practice

5.3. Region of interest (ROI) and posthoc analyses

The ROI analyses for the main effect of task in the bilateral M1 revealed significant activations in the left M1, uncorrected $p = 0.000$. Oneway ANOVA analyses of the beta values, revealed the non-significant main effect trend of the extent of activation in the three groups, $F(2, 36) = 3.01$, $p = 0.063$. Posthoc Tukey also revealed the non-significant interaction trend between the untrained Nontalents and the Talents, $p = 0.064$. Further analyses of the ROI beta values in the left M1 between the Talents and Non-talents, revealed moderately significant differences in the extent of activation in Talents and Non-talents, $t(35) = -2.45$, $p = 0.019$. Fig. 5.4 illustrates these results, as well as the bar graph representing the beta values for the left M1 activations.
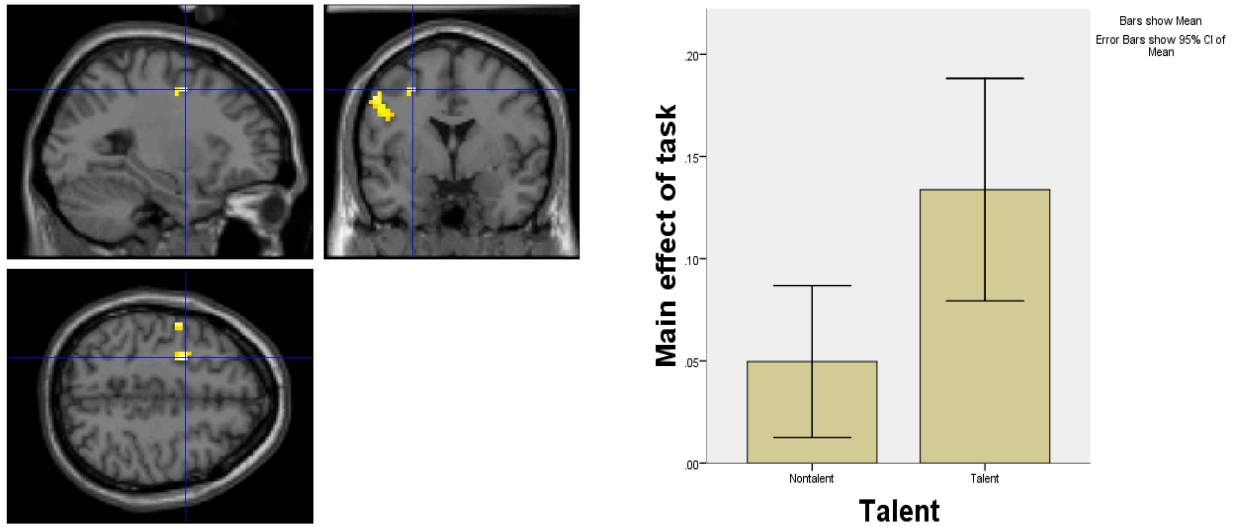
Fig. 5.4 ROI analyses: Main effect of task in the left M1

As a posthoc analyses, additional areas were identified from the activations

extracted by the exclusive masking procedure with the focus on the cerebellum as

following: anterior lobe of the right cerebellum (Talairach coordinates 15, -39, -16) (Fig.

5.5), where the oneway ANOVA revealed a main effect of activation in this area among

the three groups, F (2, 36) = 4.73, p = 0.015, and the interaction between the untrained

nontalents and trained nontalents group, posthoc Tukey, p = 0.011. Further analysis

revealed a significant difference in activation between the trained nontalents and

untrained nontalents group, t (24) = 2.94, p = 0.007; the anterior lobe of the left

cerebellum (Talairach coordinates -21, -37, -13) (Fig. 5.6) with the oneway ANOVA

revealing a non-significant main effect of activation trend, F (2, 36) = 3.02, p = 0.062,

with the non-significant interaction trend between the trained nontalents and Talents

group, posthoc Tukey, p = 0.050, and further analysis showing a significant difference

between the trained nontalents and Talents group, t (24) = -2.67, p = 0.014; and the

posterior lobe of the left cerebellum (Talairach coordinates -36, -56, -15) (Fig. 5.7),

where a oneway ANOVA revealed a marginally significant main effect of activation, F $(2, 36) = 3.61$, $p = 0.038$, with the non-significant interaction trend between trained nontalents and Talents group, posthoc Tukey, $p = 0.059$, and further analysis showing the significant difference in the extent of activation in this area between these 2 aforementioned groups, $t(21) = 2.73$, $p = 0.013$.
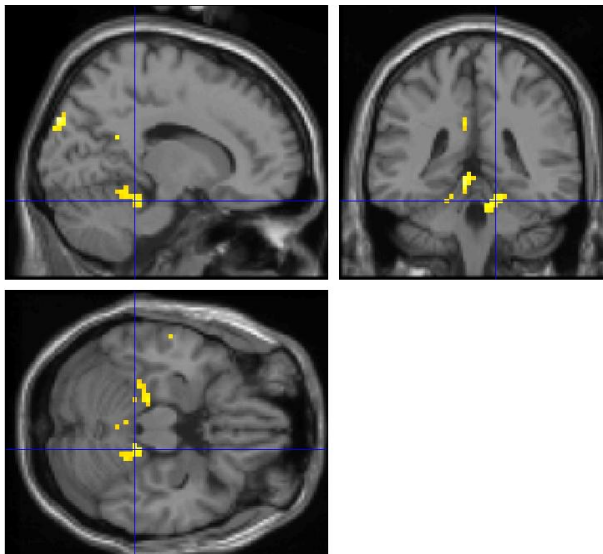

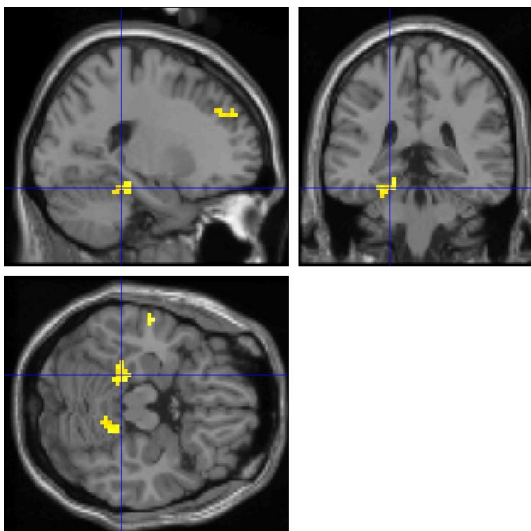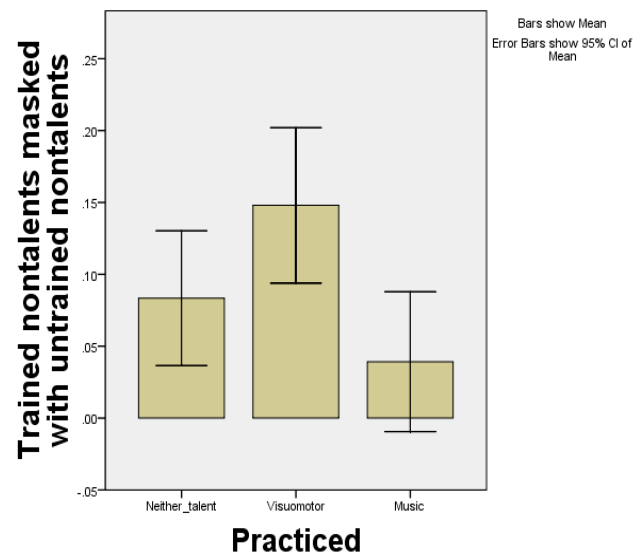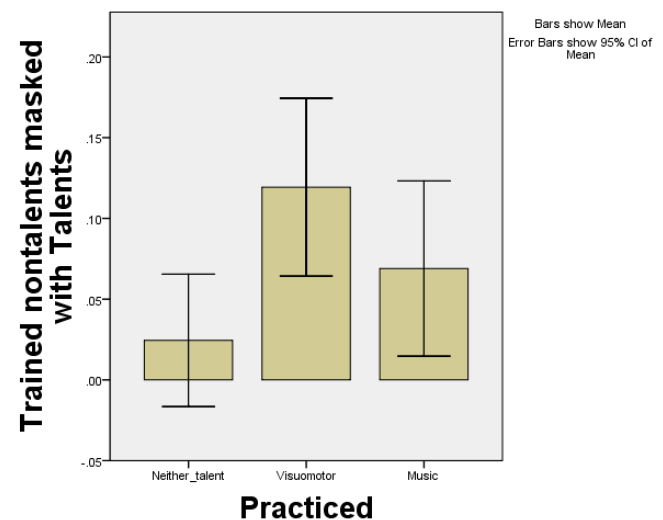Fig. 5.5 Anterior lobe of the right cerebellum.

Fig. 5.6 Anterior lobe of the left cerebellum.
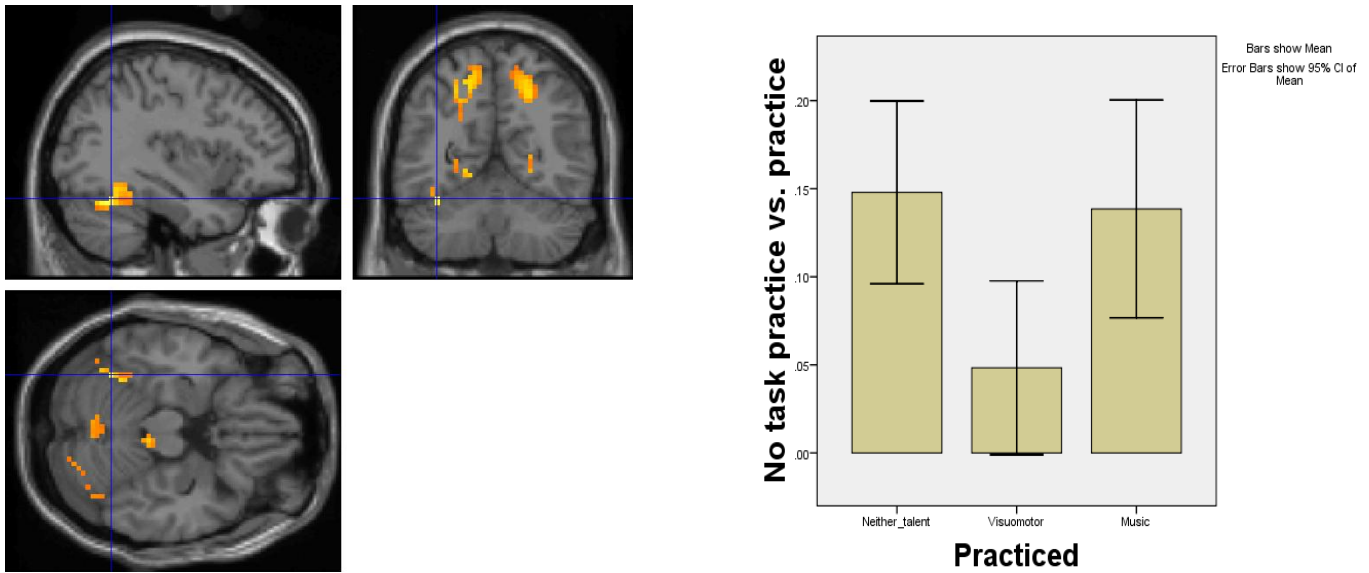
Fig. 5.7 Effect of no practice on the task in the posterior lobe of the left cerebellum.

As hypothesized, the left inferior frontal gyrus (lIFG) was also analyzed as a region of interest (ROI). The detracted portion of the lIFG was the only one found to be significantly activated only in the "short-term practice > no practice + long-term musical practice" contrast: Trained nontalents > untrained nontalents + Talents. The oneway ANOVA revealed a significant main effect of activation in lIFG , $F (2, 36) = 7.08$, $p = 0.003$, and posthoc Tukey showed the interaction between the trained and untrained nontalents group, $p = 0.002$ (Fig. 5.8).

Fig. 5.8 Short-term practice effect in the left inferior frontal gyrus (lIFG). The greatest difference in the extent of activation is shown between the trained and untrained nontalents.
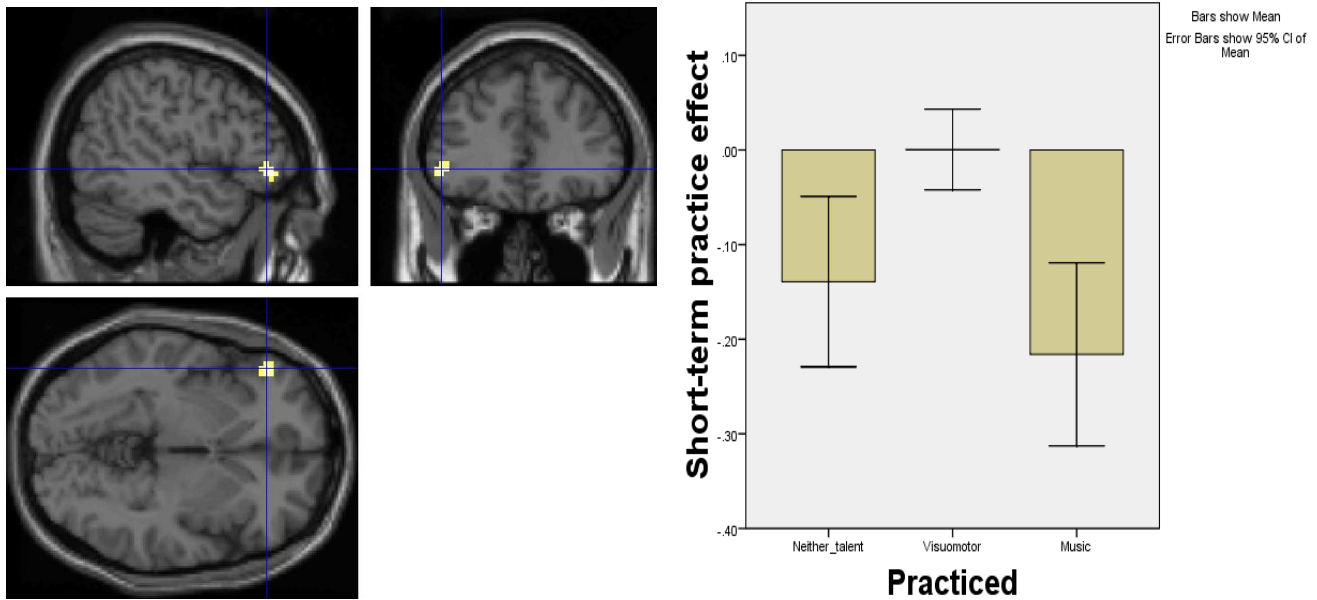
5.4. Discussion

The present study investigated the differences in functional activation between the talents, non-talents trained in the task and non-talents untrained in the task. The hypothesized decreased activation in the same areas and/or activation of the smaller portions of the same cortical areas in talents and non-talents were not confirmed. Instead, bilateral precuneus, right middle temporal gyrus, and left middle frontal gyrus emerged as the structures activated in talents in response to the visuomotor task, but not in non-talents. Consequently, it is likely that these cortical structures can be associated with the long-term musical practice in support of the visuomotor task processing. Interestingly, the activation of precuneii was present in non-talents who practiced the task, however it wasn't evident when comparing this group to the other two groups of subjects while by

the same token, precuneii emerged as activated when subtracting the activations of either

of the non-talent groups from the talents. Precuneii have been suggested to be involved in

memory retrieval (Petersson, Elfgren, and Ingvar, 1999), and thus may indicate that

talents may rely more on the visuomotor memory from the short familiarization with the

task than the non-talents do. This may be the result of the strategy developed due to the

long-term visuomotor practice.

In the absence of behavioral differences in performance among the three groups,

the cortical activation differences could be ascribed to the talent. It is also possible that

the plastic changes as a consequence of the long-term training in talents, lead toward

differences, however subtle, in processing of the visuomotor task. In fact, Shadmehr and

Holcomb (1997) showed that even though the performance didn't change after practice of

the motor task, new brain regions were recruited to perform a task, specifically moving

from the prefrontal to the posterior parietal and cerebellar regions. According to the

authors, while the task performance was not affected, the reorganization that ensued may

have contributed to the motor skill stability. While the posterior areas in the present

visuomotor task were not favored after practice, the post-hoc analyses revealed

significant differences in the anterior lobe of the right cerebellum and the left primary

motor cortex (precentral gyrus).

Doyon et al. (1998) suggest that striatum and cerebellum are involved in the late

stages of motor learning when the task becomes automatized. Shadmehr and Holcomb

suggest that as the task becomes automatized, cerebellum takes on a greater role and

might be "the site of motor memory" (p. 823). Viewed from the angle of plasticity, it has

been shown that the larger cerebellar volume in male musicians correlates with the

lifelong motor practice (Hutchinson, Lee, Gaab, and Schlaug, 2003). Further, the

synapses in Purkinje cells, the cells found in the cerebellar cortices, become remodeled

(Seeds, Williams, and Bickford, 1992) and more numerous (Anderson, Alcantara, and

Greenough, 1996) in rats after the motor practice.

Diverging evidence came from the study by Flament et al. (1996), which showed

the activation of the cerebella in the initial stages of motor learning, rather than in the

consolidation stages. In yet another study, Tracy et al. (2001) showed the involvement of

cerebellum in both early and late stages of motor learning. In the present study, the

increased cerebellar activation was associated with the extent of practice. In other words,

both talents and trained non-talents had a higher cerebellar activation as opposed to the

untrained non-talents. Thus, in the present study, the higher activation in the anterior lobe

of the right cerebellum is associated with the consolidation, rather than initial stages of

visuomotor learning. In addition, although new to the task, talents exhibited higher

cerebellar activation than the untrained non-talents. The activation in question occurred in

the right cerebellum, which is consistent with the findings by Koeneke et al. (2004) in

terms of the right cerebellar activation in musicians in response to the bimanual

movement, thus possibly showing faster motor learning consolidation.

The post-hoc analyses, revealed the activation of the left primary motor cortex

(M1 or precentral gyrus), which has reached moderate significance when all Nontalents

(both trained and untrained) were compared to Talents. This indicates that the difference

in the left M1 activation, consistent with the contralateral dominant hand movement,

since most of the subjects were right-handed, can be viewed as an apparent effect of the

long-term practice, potentially leading toward different strategies for visuomotor

learning. Thus, the talents exhibited a stronger activation of the M1, likely indicating the

the extent of the ability to exert an effort via the M1, when learning a new visuomotor

task. As with the cerebellum, M1 appears to respond differently in different stages of

motor learning. Karni et al. (1998) indicate that M1 activation decreases in the initial

stages of learning, and increases in the later stages, though their investigation did not

include musicians. Based on these findings, the talents in the present study already

exhibited an increase in M1 activation during the initial stage of learning, thus possibly

reflecting the effect of the long-term musical practice. This pattern occurred in a study by

Hund-Georgiadis and von Cramon (1999), where the piano players recruited larger M1

areas already in the early stages of motor learning. The authors go further to suggest that

this pattern of activation in the M1 of musically trained individuals reflects the plastic

changes due to the long-term motor experience.

      Further support for the plastic changes in the M1 emerged from the investigation

by Amunts et al. (1997). The findings in this study indicated that musicians exhibited a

greater left-right symmetry of the precentral gyrus (M1), which additionally correlated

negatively with the age of onset of musical learning. Much of the evidence thus points to

the claim that "Motor cortex physiology is highly sensitive to motor experience" (Kleim

et al., 2006, p. 735).

      As language has been compared to music in terms of the information processing

(Sergent, et al., 2007; Limb, 2006), the significant activation differences among the three

groups found in the posthoc analyses, in the left inferior frontal gyrus (lIFG), area

supporting the language functions, may explain the possible sub-vocal task performance.

The trained non-talents were trained well enough in the task that the sub-vocal assistance

for performing the task was not necessary, hence less activation of the lIFG in this group; the untrained non-talents had a greater need for the sub-vocal following of the task (such as verbally thinking about the positions of the fingers and the meaning of the shapes), thus exhibited higher activation in lIFG; and the talents fell in the middle, possibly exhibiting lesser reliance on the sub-vocal performance, however still incorporated it somewhat into their strategy for performing the present visuomotor task.

The visuomotor task paradigm in the present study is high in complexity and a demand for the bimanual movement coordinated by the visual stimuli. It is thus possible, that the results showing the recruitment of additional areas in talents versus non-talents rather than less or smaller areas in talents occurred due to the task complexity. As such, the task would require more attentional resources and varying strategies in performing it successfully. Consequently, the talents' cortical structures might have resorted to the use of additional areas to accommodate the learning of the new visuomotor task with the different strategy than that of non-talents.

Chapter 6

Auditory study:
Results, Discussion

Behavioral results - Imaging results - Discussion

6.1. Behavioral Results

The correct responses for the auditory task were determined according to the number of correctly answered questions about the musical excerpts. A oneway ANOVA with the groups based on practice (trained nontalents, untrained nontalents, and talents) as a between-subject variable and IQ and average grade in school as dependent factors revealed no significant effects. As for the visuomotor task, there were no major or interaction effects of the group factor on IQ and academic achievement. An independent samples t-test revealed no differences in performance between the talents and all nontalents. Behavioral results possibly reveal a ceiling effect for the performance, whereby no group exceeded the other groups in correctness of responding.

6.2 Imaging Results

The main effect of task (ME of Task) revealed the activation in the right superior temporal gyrus (BA 22), left superior temporal gyrus (BA 41), right middle frontal gyrus (BA 46), left inferior frontal gyrus (BA 9), left medial frontal gyrus (BA 6), bilateral inferior parietal lobule (BA 40), and left lingual gyrus (BA 17). Table 6.a. provides a list of Talairach coordinates and the areas for the main effect of Music task in the whole sample and individual groups. Activated areas for the ME of Task are shown in Fig. 6.1.

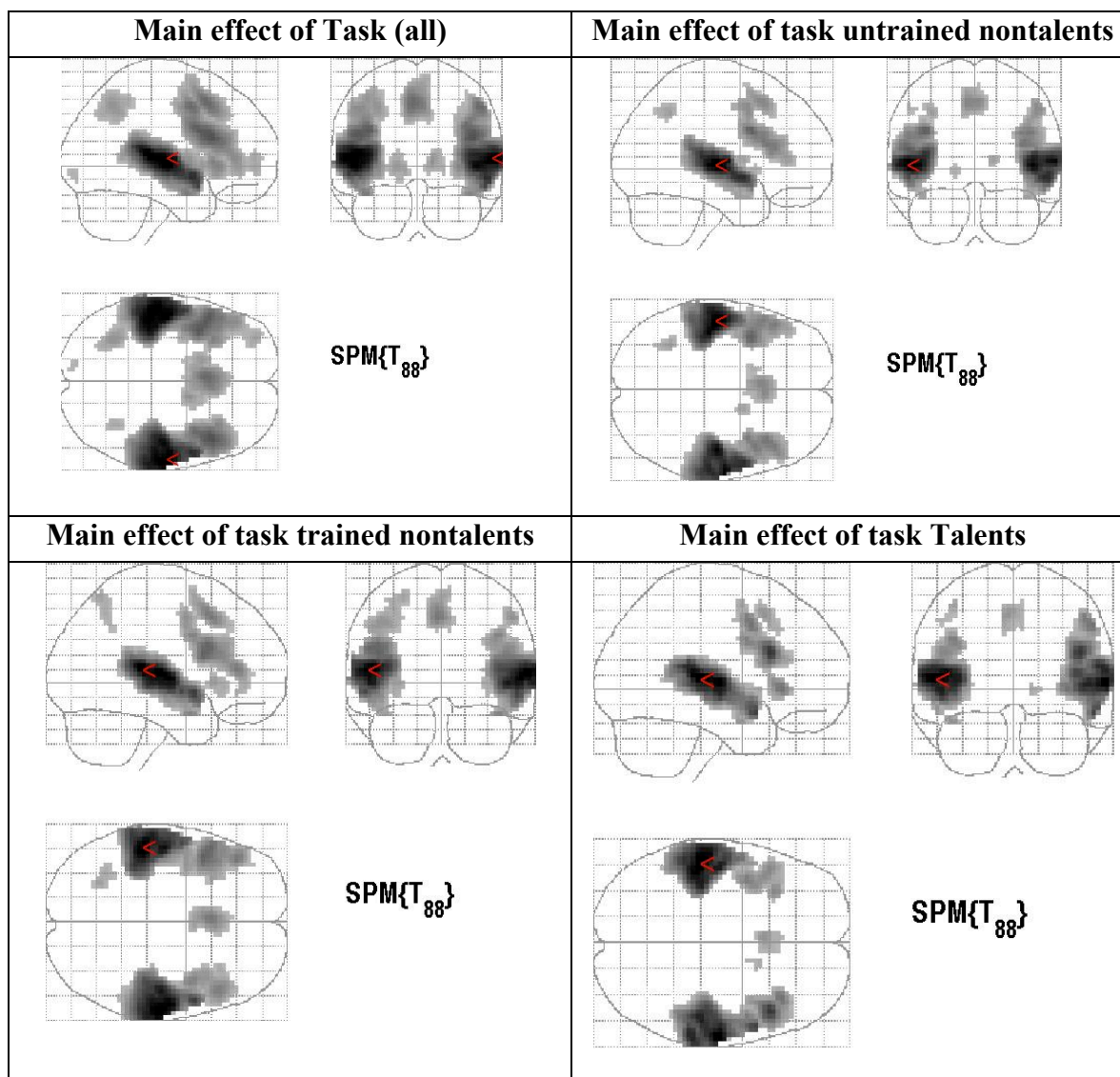| Main effect of Task (all)	Main effect of task untrained nontalents
SPM{T₈₈}	SPM{T₈₈}
Main effect of task trained nontalents	**Main effect of task Talents**
SPM{T₈₈}	SPM{T₈₈}

Figure 6.1. Main effect of task in the entire sample, and the three sub-groups.

Table 6.a.

	Anatomical locations/Brodmann area	Talairach coordinates	Voxel cluster size	Z score
ME of Task (all, N = 47)				
	Right superior temporal gyrus/BA 22	59, -14, 6	1527	Inf
	Left superior temporal gyrus/BA 41	-50, -29, 10	1463	Inf
	Right middle frontal gyrus/BA 46	44, 21, 18	987	Inf
	Left inferior frontal gyrus /BA 9	-44, 16, 21	1411	7.72
	Left medial frontal gyrus /BA 6	-3, 17, 43	450	7.14
	Left inferior parietal lobule/BA 40	-33, -53, 44	226	5.28
	Right inferior parietal lobule/BA 40	33, -54, 36	40	4.07
	Left lingual gyrus/BA 17	-12, -87, -1	16	3.68
ME of Task_trained nontalents (N = 18)	Left superior temporal gyrus/BA 41	-50, -29, 10	1056	Inf
	Right superior temporal gyrus/BA 22	62, -20, 6	1162	Inf
	Left Insula/BA 13	-44, 13, 19	655	6.00
	Left cingulate gyrus/BA 32	-3, 19, 40	208	5.35
	Right inferior frontal gyrus/BA 45	47, 24, 18	412	5.15
	Left superior parietal lobule/BA 7	-27, -58, 58	76	4.03

	Right inferior frontal gyrus/BA 47	39, 26, -4	44	3.73
ME of Task_untrained nontalents (N = 16)	Left superior temporal gyrus/BA 22	-50, -17, 4	996	Inf
	Right Insula/BA 13	44, -17, 4	1008	Inf
	Left Inferior frontal gyrus/BA 9	-39, 10, 24	494	5.94
	Left medial frontal gyrus/BA 8	0, 20, 46	184	4.78
	Left inferior parietal lobule/BA 14	-33, -50, 41	45	4.10
	Left precentral gyrus/BA 6	-50, -4, 42	13	3.85
ME of Task_T (N = 13)				
	Left superior temporal gyrus/BA 41	-50, -26, 7	922	7.63
	Right superior temporal gyrus/BA 22	62, -14, 3	1006	7.52
	Right middle frontal gyrus/BA 46	44, 18, 21	378	6.28
	Right inferior frontal gyrus/BA 47	36, 26, -1	78	4.98
	Left inferior frontal gyrus/BA 9	-41, 4, 30	231	4.64
	Left medial frontal gyrus/BA 6	-3, 17, 43	77	4.11

Coordinates are in the standard stereotaxic space (Talairach and Tournoux), z values are uncorrected at $p = 0.000$, voxel threshold = 10.

The contrast (Talents + trained nontalents > untrained nontalents) investigating the effect of practice, both short (trained nontalents) and long-term (Talents), yielded significant activations in the region of the right inferior frontal gyrus (rIFG). (Fig. 6.2). Oneway ANOVA of the beta values for each group in the aforementioned significantly activated region of the rIFG revealed a main effect of practice, $F(2, 46) = 6.69$, $p = 0.003$, where the posthoc Tukey test revealed an interaction between the Talents and untrained nontalents, $p = 0.002$ (Fig. 6.3).
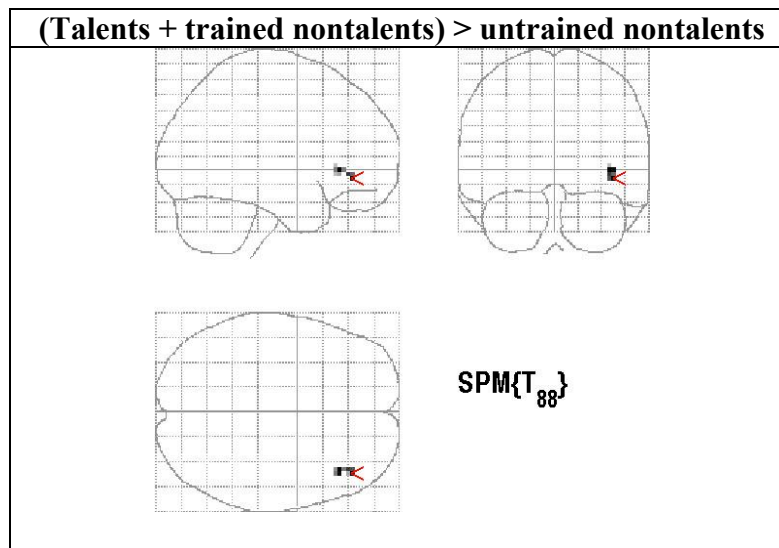

Fig. 6.2. The effect of long and short-term music practice vs. no practice showing activations in the region of the rIFG.
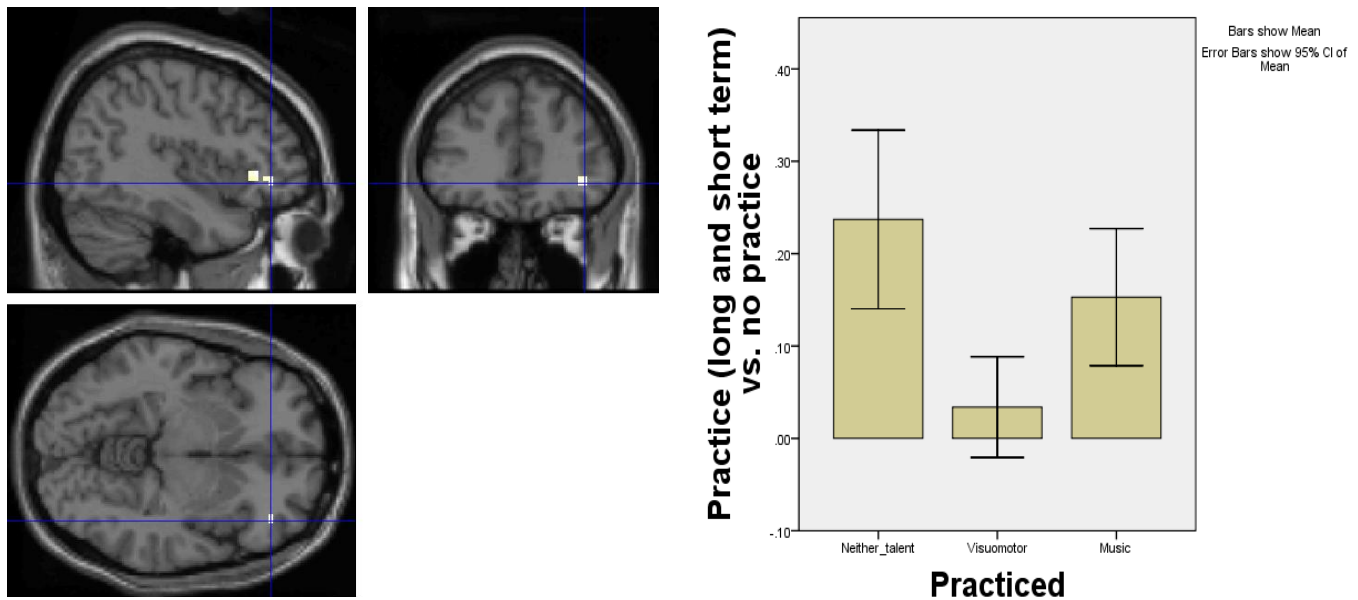
Fig. 6.3. Between-subject analyses of the rIFG.

6.3. Posthoc and ROI analyses

Posthoc ROI analyses for the bilateral IFG at the uncorrected significance level of $p = 0.05$, revealed a significant activation for the contrast between Talents and Non-talents in the rIFG. The analyses of the beta values for these activations in the rIFG revealed a significant difference between the talents and non-talents, $t(45) = 2.45$, $p = 0.005$ (Fig. 6.4).

Similarly the posthoc analyses of the beta values in the left inferior frontal gyrus lIFG portion, between Talents and Nontalents, emerging from the exclusive masking of Non-talents who practiced the auditory task with Talents, revealed a non-significant trend, $t(45) = 2.1$, $p = .041$ (Fig. 6.5).
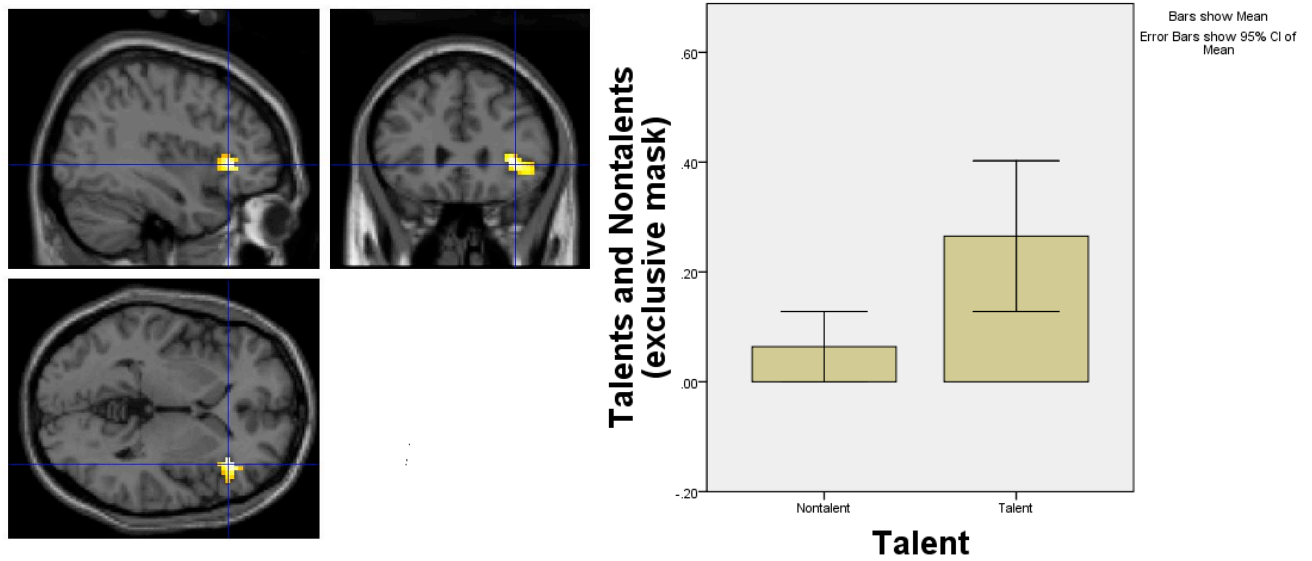
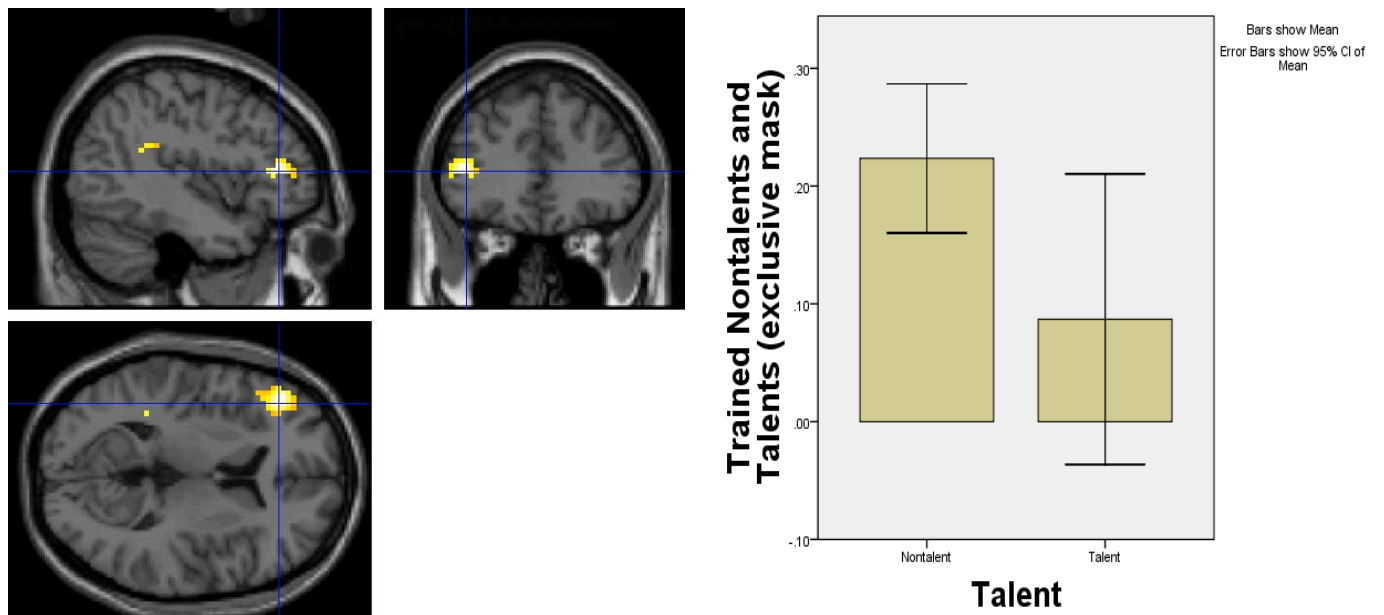Fig. 6.4. Between-group (Talents and Non-talents) differences in the rIFG.

Figure 6.5. lIFG activation differences in Talents and Non-talents.

6.4 Discussion

The present study investigated differences in the cortical activation patterns in response to an auditory task with the hypothesis claiming the differences between the talents and non-talents in terms of the activation of the same areas, but with the different intensity. In addition the investigation aimed at finding the differences in cortical activations between the trained and the non-trained subjects indicating the effect of neural plasticity as a consequence of practice. Not unexpectedly, bilateral superior temporal gyri were activated in the main effect of task due to their auditory properties, as well as the necessity for the auditory attention for answering the questions about the presented musical excerpts. Superior temporal gyri have been previously found to be activated in response to melodic processing (Schmithorst and Holland, 2003), as well in correlation to the musical training (Koelsch et al., 2005).

Both the short-term practice and Talent exhibited effects on the right inferior frontal gyrus (rIFG). In other words, the activations in the rIFG were higher in talents than in non-talents as well as higher in trained nontalents than in the untrained nontalents. The right hemisphere counterpart of the left inferior frontal gyrus (lIFG) or the site of language processing, the rIFG may be more activated either in response to the melodic language (pitch, rhythm, timbre) or as a result of the music listening practice. Given the likely, and desired, unfamiliarity of the subjects with the musical excerpts presented in the study, it is possible that the unexpected sequences in them resulted in the pattern of the rIFG activation. The connection between the musical violations and unexpected events in music and the inferior frontal regions has been shown previously (Tilmann et al., 2006; Koelsch et al., 2005). In addition, the structural studies show that individuals

who are amusic have a reduced white matter in the rIFG (Hyde et al., 2007). The patterns

of activation in the rIFG in the present study clearly point toward the relationship with

the musicality and the extent of musical practice. In addition, although the practice of the

non-talents entails some familiarity with the type of the musical excerpts presented, the

musical structure of the 20th century classical music, as the one used in the present study,

may exhibit musical violations as compared to the more familiar classical music of the

earlier centuries.

The opposite pattern of activation in the lIFG, where the talents exhibited less

activation than the non-talents may reflect the suppression of the verbal processing or the

possible subvocal rehearsal (Logie et al., 2003) in talents in order to allocate attentional

resources onto the music processing. At the same time, the non-talents may have less

control over the ability to suppress verbal processing as a result of no musical training

and may conduct subvocal rehearsal of the answer that they were required to give to a

question at the end of each musical excerpt. On the other hand, the non-talents may be

accessing the melody in terms of its lexico-semantic properties (pitch, rhythm, timbre),

hence exhibiting higher activation in the lIFG, as shown previously (Hyde et al., 1997).

The existence of the shared properties between language and music has been mentioned

before (Chartrand, Peretz, and Belin, 2008).

Chapter 7

General Discussion

"It is reasonable to assume that plasticity is a characteristic of the nervous system that evolved for coping with changes in the environment. Understanding changes in brain structure as a result of learning and adaptation is pivotal in understanding the characteristic flexibility of our brain to adapt"

Draganski et al.
(Temporal and spatial dynamics of brain structure changes during extensive learning, 2006, p. 6317)

General discussion – Future studies – Conclusion

7.1. General Discussion

In broad terms, the present study aimed to investigate the neural plasticity via assessing the long-term musical practice (talents) and short-term task practice (trained non-talents) as well as no practice (untrained non-talents) effects on the functional cortical activation. The emerging effects were supposed to have occurred due to the brain plasticity as a result of practice, either long or short-term. At present, the method of neuroimaging via the functional magnetic resonance presents the best tool for investigating neural plasticity in human subjects in vivo.

The absence of behavioral differences in terms of the lack of differences in correct responding in both tasks, among the three groups or between any two groups leads toward the conclusion that there were no practice effects on performance, although some have emerged in the imaging data. One possible interpretation is that the practice on both tasks exerted the use of different, but not necessarily better strategies in completing the tasks. Furthermore, the hypothesized effect of reduced activation in talents of the same cortical areas as that of non-talents, as well as the activation of different cortical areas was not strongly supported in the present study. Rather, the most significant effects emerged for the specific regions of interest in both the visuomotor and auditory study. The lack of effect may be contained in the lack of power and the need for the higher number of subjects. Though, the effects don't lack in the studies on musical experts mentioned in the previous chapters, even with the lower number of participants than in the present study, the question of expertise arises in terms of age. In the present study, the subjects were teenagers between 15 and 18 years of age. It is possible that the development of expertise (though not in prodigies) requires additional developmental

maturity of the brain and additional plastic changes, which occur as a result of maturation. As mentioned in the previous chapters, synaptic pruning does occur at a very early age however, it is feasible to assume that there is a second level synaptic pruning, which occurs as a result of practice and the development of expertise, taking place at a later age. In fact, while it is known that myelination is most rapid during the first 2 years of life, it has been suggested that it continues into early adulthood (Klingberg et al., 1999), at least until the age of 20 (Klingberg, 2006), hence opening the possibility of further "straightening" of the structural component, likely influenced by the environmental factors, such as the skill acquisition. Furthermore, long-term practice may produce a " 'cleaner' functional map of the cognitive process of interest…as extraneous processes are "whittled away" to yield essential functional anatomy of that process" (Garavan et al., 2000, p. 56). Musicians nevertheless represent an ideal group for investigating the specialized functional maps and neural plasticity. Developing projective maps of neuroplasticity due to practice is not only contributing to the understanding of talent, but also to the development of treatment methods for the individuals who suffered any kind of brain injury and/or cerebral insults (Draganski and May, 2008).

Visuomotor tasks are a good method of investigating differences between the musical talents and non-talents as they mimic music performance (musical notation sight-reading and the motor performance), however do not give an unfair advantage to the musical talents. In addition, the present auditory study utilized the wholesome music experience by using the excerpts of the orchestral performances, rather than single tones. Such experience may hold a great importance in terms of detecting the actual attentional properties of the music perception, which in the present study appears to call upon the

extension of the ascribed properties of the inferior frontal gyri, to incorporate active

"music appreciation" and perception.

7.2. Future studies

Currently presented significant activations in the primary motor cortex and

inferior frontal gyri, as well as the cerebella, may indicate the necessity for the more

local, rather than global approach to the investigation of plasticity in young talents.

According to Raichle et al., "functional anatomical measurements through time are

essential" (1994, p. 23), thus closer monitoring of changes brought on by practice should

be done through time via longitudinal studies to create a better picture of the course of the

plastic changes due to the skill acquisition.

While the present investigation did not yield remarkable activations in the

striatum, a longer practice of the tasks, as well as the multiple recordings might have

yielded striatal activations, due to the supposed necessity of the "long-lasting potentiation

of glutamatergic transmission in the striatum" (Yin et al., 2009, p. 338) for learning a

skill. Hence, future studies may utilize longer practice and use striatum as a region of

interest to detect changes brought on by practice.

Although not investigated in the current study, as related to the factor of mere

talent, without the consideration of the practice effects, the question of the already

present baseline activation in different subjects remains open (Hoppe et al., Manuscript in

preparation), thus the resulting effects might become questionable in terms of whether

they occurred in relation to baseline or as a true response to the task. Nevertheless, it is an

important aspect of detecting the "true" functional activations as a result of the task-

related information processing. While the method of functional imaging continues to be an anchor for investigating the structural and functional properties of the brain, future studies should also exercise special caution in terms of the potential effect of the changes in tissue properties with age, on the technical procedures in MRI investigations (Salat et al., 2009). Thus parallels of the previous investigations on the similar tasks with different age groups might not be drawn with ease. Rather, careful cross-sectional analyses of the effect of practice on neuroplasticity, may yield a more accurate picture.

It has already been suggested that gifted individuals are more vulnerable to autoimmune disorders, and seem to exhibit a slowed growth of the left hemisphere; in addition, it has been suggested that musicians exhibit anomalous language dominance in comparison to the non-talents (Hassler and Gupta, 1993). Future studies may further expand the focus of talent and plasticity research to incorporate these biological and genetic factors, including the investigation of the potential inherited musicality within the families.

7.3. Conclusion

The present investigation revealed that the practice of the visuomotor and auditory tasks resulted in the use of some different cortical areas and possibly strategies among the three groups, however did not reveal the effect of practice or talent on the behavioral outcome. While the imaging results are in line with some previous studies, as reported, due to the lack of behavioral differences, they should be interpreted with caution. The future direction of the present investigation should include talented subjects with the longer average instrument practice time, as the time offered in the present study

may not have been sufficient. In addition, the short-term practice time of the visuomotor task may be longer, as the floor effect may have occurred for all subjects indicating that the task might be too difficult to master via the practice of 600 trials. Furthermore, the auditory task may not have been sufficiently difficult to result in behavioral differences, thus indicating a ceiling effect.

The study contributes to a limited extent to our understanding of the changes over time in the brain function and structure, as well as to our acceptance of the non-rigid nature of the brain. Musical talents present an ideal group for isolating specific cortical functional properties as a result of long-term practice that may subsequently be attributed to neuroplastic changes. Pinpointing these changes leads toward acknowledging the possibility of rehabilitation after the brain injury and stroke. Furthermore, "acquired" neuroplasticity via the skill acquisition and/or any kind of environmental influence may lead toward a better understanding of the resulting information processing and intellectual enrichment or impoverishment.

References

1. Abraham, W.C. (2008). Metaplasticity: tuning synapses and networks for plasticity. *Nature Reviews Neuroscience*, 9, 387-399.

2. Anderson, B.J., Alcantara, A.A., & Greenough, W.T. (1996). Motor-skill learning: changes in synaptic organization of the rat cerebellar cortex. *Neurobiology of Learning and Memory*, 66, 221-229.

3. Anderson, B.J., Eckburg, P.B., & Relucio, K.I. (2002). Alterations in the thickness of motor cortical subregions after motor-skill learning and exercise. *Learning & Memory*, 9, 1-9.

4. Bangert, M., & Altenmüller, E.O. (2003). Mapping perception to action in piano practice: a longitudinal DC-EEG study. *BMC Neuroscience*, 4, 1-14.

5. Bangert, M. & Schlaug, G. (2006). Specialization of the specialized in features of external human brain morphology. *European Journal of Neuroscience*, 24, 1832-1834.

6. Bavelier, D. & Neville, H.J. (2002). Cross-modal plasticity: where and how? *Nature Reviews Neuroscience*, 3, 443-451.

7. Beauchamp, M.H., Dagher, A., Aston, J.A.D., & Doyon, J. (2003). Dynamic functional changes associated with cognitive skill learning of an adapted version of the Tower of London task. *Neuroimage*, 20, 1649-1660.

8. Berlucchi, G. & Buchtel, H.A. (2009). Neuronal plasticity: historical roots and evolution of meaning. *Experimental Brain Research*, 192, 307-319.

9. Bhattacharya, J. & Petsche, H. (2005). Phase synchrony analyses of EEG during music perception reveals changes in functional connectivity due to musical expertise. *Signal Processing*, 85, 2161-2177.

10. Brecht, M. & Schmitz, D. (2008). Rules of Plasticity. *Science*, 319, 39-40.

11. Brust, J.C.M. (2003). Music and the Neurologist: a historical perspective. In Peretz, I. & Zatorre, R.J.(Eds.). *The Cognitive Neuroscience of Music* (pp. 181-191). New York, NY: Oxford University Press.

12. Buonomano D.V. & Merzenich, M.M. (1998). Cortical plasticity: from synapses to maps. *Annual Review of Neuroscience*, 21, 149-186.

13. Büchel, C., Coull, J.T., & Friston, K.J. (1999). The predictive value of changes in effective connectivity for human learning. *Science*, 283, 1538-1541.

14. Chartrand, J.P., Peretz, I., & Belin, P. (2008). Auditory recognition expertise and domain specificity. *Brain Research*, 1220, 191-198.

15. Cheeran, B., Talleli, P., Mori, F., Koch, G., Suppa, A., Edwards, M., Houlden, H., Bhatia, K., Greenwood, R., & Rothwell, J.C. (2008). A common polymorphism in the brain-derived neurotrophic factor gene (BDNF) modulates human cortical plasticity and the response to rTMS. *Journal of Physiology*, 586, 5717-5725.

16. Clem, R.L., Celikel, T., & Barth, A.L. (2008). Ongoing in vivo experience triggers synaptic metaplasticity in the neocortex. *Science*, 319, 101-104.

17. Collignon, O., Voss, P., Lassonde, M., & Lepore, F. (2009). Cross-modal plasticity for the spatial processing of sounds in visually deprived subjects. *Experimental Brain Research*, 192, 343-358.

18. Cramer, S.C. (2008). A window into the molecular basis of human brain plasticity. *Journal of Physiology*, 586, 5601.

19. Douglas, K.M. & Bilkey, D.K. (2007). Amusia is associated with deficits in spatial processing. *Nature Neuroscience*, 10, 915-921.

20. Doyon, J., Laforce, R., Bouchard, G., Gaudreau, D., Roy, J., Poirier, M., Bedard, P.J., Bedard, F., & Bouchard, J.P. (1998). Role of the striatum, cerebellum and frontal lobes in the automatization of a repeated visuomotor sequence of movements. *Neuropsychologia*, 36, 625-641.

21. Doyon, J., Song, A.W., Karni, A., Lalonde, F., Adams, M.M., & Ungerleider, L.G. (2002). Experience-dependent changes in cerebellar contributions to motor sequence learning. *PNAS*, 99, 1017-1022.

22. Draganski, B., Gaser, C., Busch, V., Schuierer, G., Bogdahn, U., & May, A. (2004). Changes in grey matter induced by training. *Nature*, 427, 311-312.

23. Draganski, B., Gaser, C., Kempermann, G., Kuhn, H.G., Winkler, J., Bücher, C., & May, A. (2006). Temporal and spatial dynamics of brain structure changes during extensive learning. *The Journal of Neuroscience*, 26, 6314-6317.

24. Draganski, B. & May, A. (2008). Training-induced structural changes in the adult human brain. *Behavioural Brain Research*, 192, 137-142.

25. Duerden, E.G. & Laverdure-Dupont, D. (2008). Practice makes cortex. *The Journal of Neuroscience*, 28, 8655-8657.

26. Elbert, T., Pantev, C., Wienbruch, C., Rockstroh, B., & Taub, E. (1995). Increased Cortical Representation of the Fingers of the Left Hand in String Players. *Science*, 270, 305-307.

27. Elbert, T. & Rockstroh, B. (2004). Reorganization of the human cerebral cortex: the range of changes following use and injury. The Neuroscientist, 10, 129-141

28. Flament, D., Ellermann, J.M., Kim, S.G., Ugurbil, K., & Ebner, T.J. (1996). Functional magnetic resonance imaging of cerebellar activation during the learning of a visuomotor association task. *Human Brain Mapping*, 4, 210-226.

29. Fletcher, P., Büchel, C., Josephs O., Friston, K., & Dolan, R. (1999). Learning-related neuronal responses in prefrontal cortex studied with functional neuroimaging. *Cerebral Cortex*, 9, 168-178.

30. Frakowiak, R.S.J. (1999). Imaging investigations of human brain plasticity. In. J. Grafman & Y. Christen (Eds.), *Neuronal plasticity: building a bridge from the laboratory to the clinic* (pp. 141-156). Heidelberg, Germany: Springer-Verlag.

31. Garavan, H., Kelley, D., Rosen, A., Rao, S.M., & Stein, E.A. (2000). Practice-related functional activation changes in a working memory task. *Microscopy Research and Technique*, 52, 54-63.

32. Gaser, C. & Schlaug, G. (2003). Brain structures differ between musicians and non--musicians. *The Journal of Neuroscience*, 23, 9240-9245.

33. Grafman, J. & Litvan, I. (1999). Evidence for four forms of neuroplasticity. In. J. Grafman & Y. Christen (Eds.), *Neuronal plasticity: building a bridge from the laboratory to the clinic* (pp. 131-139). Heidelberg, Germany: Springer-Verlag.

34. Haslinger, B., Erhard, P., Altenmueller, E., Hennenlotter, A., Schwaiger, M., Graefin von Einsiedel, H., Rummeny E., Conrad, B., Ceballos-Baumann, A.O. (2004). Reduced recruitment of motor association areas during bimanual coordinaton in Concert pianists. *Human Brain Mapping*, 22, 206-215.

35. Hebb, D.O. (1949). Chapter 4: The first stage of perception: growth of the assembly. *The Organization of Behavior: A Neuropsychological Theory*. Chapter 4, 60-78, McGraw-Hill: New York, NY

36. Hempel, A., Giesel, F.L., Caraballo, N.M.G., Amann, M., Meyer, H., Wuestenberg, T., Essig, M., & Schroeder, J. (2004). Plasticity of cortical activation related to working memory during training. *American Journal of Psychiatry*, 161, 745-747.

37. Ho, Y., Cheung, M., & Chan, A.S. (2003). Music training improves verbal but not visual memory: cross-sectional and longitudinal explorations in children. *Neuropsychology*, 17, 439-450.

38. Huettel, S.A., Song, A.W., & McCarthy, G. (2004). Functional magnetic resonance imaging. Sinauer Associates, Inc., Sunderland, MA.

39. Hund-Georgiadis, M. & von Cramon, D.Y. (1999). Motor-learning-related changes in piano players and non-musicians revealed by functional magnetic-resonance signals. *Experimental Brain Research*, 125.

40. Hutchinson, S., Lee, L.H.L., Gaab, N., & Schlaug, G. (2003). Cerebellar volume of musicians. *Cerebral Cortex*, 13, 943-949.

41. Hyde, P., Price, C., Baron J-C., Wise, R., Lambert, J., Frackowiack, R.S.J., Lechevalier, B., & Eustache, F. (1997). The structural components of music perception: a functional anatomical study. *Brain*, 120, 229-243.

42. Hyde, K.L., Lerch, J.P., Zatorre, R.J., Griffiths, T.D., Evans, A.C., & Peretz, I. (2007). Cortical thickness in congenital amusia: when less is better than more. *The Journal of Neuroscience*, 27, 13028-13032.

43. Hyde, K.L., Lerch, J., Norton, A., Forgeard, M., Winner, E., Evans, A.C., & Schlaug, G. (2009). Musical training shapes structural brain development. *The Journal of Neuroscience*, 29, 3019-3025.

44. Jacobs, B., Schall, M., & Scheibel, A.B. (1993). A quantitative dendritic analysis of Wernicke's area in humans. II. Gender, hemispheric and environmental factors. *Journal of Comparative Neurology*, 327, 97-111.

45. Jäncke, L., Shah, N.J., & Peters, M. (2000). Cortical activations in primary and secondary motor areas for complex bimanual movements in professional pianists. *Cognitive Brain Research*, 10, 177-183.

46. Johnson, J.K., Petsche, H., Richter, P., von Stein, A., & Filz, O. (1996). The dependence of coherence estimates of spontaneous EEG on Gender and Music Training. *Music Perception*, 13, pp. 563-582.

47. Jones, S. V., Choi, D.C., Davis, M., & Ressler, K.J. (2008). Learning-dependent structural plasticity in the adult olfactory pathway. *The Journal of Neuroscience*, 28, 13106-13111.

48. Jonides, J. (2004). How does practice make perfect? *Nature Neuroscience*, 7, 10-11.

49. Kaas, J.H., Krubitzer, L.A., Chino, Y.M., Langston, A.L., Polley, E.H., & Blair N. (1990). Reorganization of the retinotopic cortical maps in adult mammals after lesions of the retina. *Science*, 248, 229-231.

50. Kaas, J.H. (2004). The reorganization of sensory and motor maps after injury in adult mammals. In Gazzaniga, M.S. (Ed.). *The Cognitive Neurosciences III (3rd ed.)* (pp. 223-236). Cambridge, MA: MIT Press.

51. Karni, A., Meyer, G., Rey-Hipolito C., Jezzard, P., Adams, M.M., Turner, R., & Ungerleider, L.G. (1998). The acquisition of skilled motor performance: fast and slow experience-driven changes in primary motor cortex. *PNAS*, 95, 861-868.

52. Kassubek, J., Schmidtke, K., Kimmig, H., Lücking, C.H., & Greenlee, M.W. (2001). Changes in cortical activation during mirror reading before and after training: an fMRI study of procedural learning. *Cognitive Brain Research*, 10, 207-217.

53. Kelly, A.M.C. & Garavan, H. (2005). Human functional neuroimaging of brain changes associated with practice. *Cerebral Cortex*, 1-14.

54. Kelly, C., Foxe, J.J., & Garavan, H. (2006). Patterns of normal human brain plasticity after practice and their implications for neurorehabilitation. *Archives of physical medicine and rehabilitation*, 87, s20-s29.

55. Kelly A.M.C., Hester, R., Foxe, J.J., Shpaner, M., & Garavan, H. (2006). Flexible cognitive control: effects of individual differences and brief practice on a complex cognitive task. *Neuroimage*, 31, 866-886.

56. Kleim, J.A., Chan, S., Pringle, E., Schallert, K., Procaccio, V., Jimenez, R., & Cramer, S.C. (2006). BDNF val66met polymorphism is associated with modified experience-dependent plasticity in human motor cortex. *Nature Neuroscience*, 9, 735-737.

57. Klingberg, T., Vaidya, C.J., Gabrieli, J.D.E., Moseley, M.E., & Hedehus, M. (1999). Myelination and organization of the frontal white matter in children: a diffusion tensor MRI study. *Neuroreport*, 10, 2817-2821.

58. Klingberg, T. (2006). Development of a superior frontal-intraparietal network for visuo-spatial working memory. *Neuropsychologia*, 44, 2171-2177.

59. Koelsch, S., Schmidt, B-H., Kasok, J. (2002). Effects of musical expertise on the early right anterior negativity: an event-related brain potential study. *Psychophysiology*, 39, 657-663.

60. Koelsch, S. & Friederici, A.D. (2003). Toward the neural basis of processing structure in music: comparative results of different neurophysiological investigation methods. *Annals of the New York Academy of Sciences*, 999, 15-28

61. Koelsch, S., Kasper, E., Sammler, D., Schulze, K., Gunter, T., & Friederici, A.D. (2004). Music, language and meaning: brain signatures of semantic processing. *Nature Neuroscience*, 7, 302-307.

62. Koelsch, S. (2005). Neural substrates of processing syntax and semantics in music. *Current Opinion in Neurobiology*, 15, 207-212.

63. Koelsch, S., Fritz, T., Schulze, K., Alsop, D., & Schlaug, G. (2005). Adults and children processing music: an fMRI study. *Neuroimag*e, 25, 1068-1076.

64. Koelsch, S. & Siebel, W.A. (2005). Towards a neural basis of music perception. *Trends in Cognitive Sciences*, 9, 578-584.

65. Koeneke, S., Lutz, K., Wuestenberg, T., & Jaencke, L. (2004). Long-term training affects cerebellar processing in skilled keyboard players. *Neuroreport*, 15, 1279 1282.

66. Kolb, B. (1999). Towards an ecology of cortical organization: Experience and the changing brain. In. J. Grafman & Y. Christen (Eds.), *Neuronal plasticity: building a bridge from the laboratory to the clinic* (pp. 17-34). Heidelberg, Germany: Springer-Verlag.

67. Kourtzi, Z., Betts, L.R., Sarkheil, P., & Welchman, A.E. (2005). Distributed neural plasticity for shape learning in the human visual cortex. *PLoS Biology*, 3, 1317-1327.

68. Landau, S.M., Schumacher, E.H., Garavan, H., Druzgal, T.J., & D'Esposito, M. A functional MRI study of the influence of practice on component process of working memory. Neuroimage, 22, 211-221.

69. Lappe, C., Herholz, S.C., Trainor, L.J., & Pantev, C. (2008). Cortical plasticity induced by short-term unimodal and multimodal musical training. *The Journal of Neuroscience*, 28, 9632-9639.

70. Limb, C. (2006). Structural and functional neural correlates of music perception. *The Anatomical Record Part A*, 288 A, 435-446.

71. Logie, R.H., Venneri, A., Della Sala S., Redpath, T.W., & Marshall I. (2003). Brain activation and the phonological loop: the impact of rehearsal. *Brain and Cognition*, 53, 293-296.

72. Logothetis, N.K. (2008). What we can and what we cannot do with fMRI. *Nature*, 453, 869-877.

73. Mahncke, H.W., Connor, B.B., Appelman, J., Ahsanuddin, O.N., Hardy, J.L., Wood, R.A., Joyce, N.M., Boniske, T., Atkins, S.M., & Merzenich, M.M. (2006). Memory enhancement in healthy older adults using a brain plasticity based training program: a randomized, controlled study. *Proceedings of the National Academy of Sciences*, 103, 12523-12528.

74. Martin, K.C., Bartsch, D., Bailey, C.H., & Kandel, E.R. (2004). In Gazzaniga, M.S. (Ed.). *The Cognitive Neurosciences III (3rd ed.)* (pp. 121-137). Cambridge, MA: MIT Press.

75. Meister, I., Krings, T., Foltys, H., Boroojerdi, B., Mueller, M., Toepper, R., & Thron, A. (2005). Effects of long-term practice and task complexity in musicians and nonmusicians performing simple and complex motor tasks: implications for cortical motor organization. *Human Brain Mapping*, 25, 345-352.

76. Münte, T.F., Altenmüller, E., & Jäncke, L. (2002). The musician's brain as a model of neuroplasticity. *Nature Reviews Neuroscience*, 3, 473-478.

77. Nakashima, A.S. & Dyck, R.H. (2008). Enhanced plasticity in zinergic, cortical circuits after exposure to enriched environments. *The Journal of Neuroscience*, 28, 13995-13999.

78. Neville, H.J. & Bavelier, D. (2004). Specificity and plasticity in neurocognitive development in humans. In Gazzaniga, M.S. (Ed.). *The Cognitive Neurosciences III (3rd ed.)* (pp.83-98). Cambridge, MA: MIT Press.

79. Norris, D.G. (2006). Principles of magnetic resonance assessment of brain function. *Journal of Magnetic Resonance Imaging*, 23, 794-807.

80. Ohnishi, T., Matsuda, H., Asada, T., Aruga, M., Hirakata, M., Nishikawa, M., Katoh, A., & Imabayashi, E. (2001). Functional anatomy of musical perception in musicians. *Cerebral Cortex*, 11, 754-760

81. Olesen, P.J., Westerberg, H., & Klingberg, T. (2003). Increased prefrontal and parietal activity after training of working memory. *Nature Neuroscience*, 7, 75-79.

82. Peretz, I. & Zatorre, R.J. (2005). Brain organization for music processing. *Annual Revue of Psychology*, 56, 89-114

83. Petersen, S.E., van Mier, H., Fiez, J.A., & Raichle, M.E. (1998). The effects of practice on the functional anatomy of task performance. *PNAS*, 95, 853-860.

84. Petersson, K.M., Elfgren, C., & Ingvar, M. (1999). Dynamic changes in the functional anatomy of the human brain during recall of abstract designs related to practice. *Neuropsychologia*, 37, 567-587.

85. Poldrack, R.A. (2000). Imaging brain plasticity: conceptual and methodological issues – A theoretical review. *Neuroimage*, 12, 1-13.

86. Raichle, M.E., Fiez, J.A., Videen, T.O., Macleod, A.M.K., Pardo, J.V., Fox, P.T., & Petersen, S.E. (1994). Practice-related changes in human brain functional anatomy during nonmotor learning. *Cerebral Cortex*, 4, 8-26.

87. Rauschecker, J.P. (1995). Developmental plasticity and memory. *Behavioural Brain Research*, 66, 7-12.

88. Rauschecker, J. P. (1999). Auditory cortical plasticity: a comparison with other sensory systems. *Trends in Neuroscience*, 22, 74-80.

89. Rauschecker, J.P. (1999). Auditory cortical plasticity and sensory substitution. In. J. Grafman & Y. Christen (Eds.), *Neuronal plasticity: building a bridge from the laboratory to the clinic* (pp. 53-63). Heidelberg, Germany: Springer-Verlag.

90. Ridding, M.C., Brouwer, B., & Nordstrom, M.A. (2000). Reduced interhemispheric Inhibition in musicians. *Experimental Brain Research*, 133, 249-253.

91. Rosenzweig, M.R. & Bennett, E.L. (1995). Psychobiology of plasticity: effects of training and experience on behavior. *Behavioural Brain Research*, 78, 57-65.

92. Salat, D.H., Lee, S.Y., van der Kouwe, A.J., Greve, D.N., Fischl, B., & Rosas, H.D. (2009). Age-associated alterations in cortical gray and white matter signal intensity and gray to white matter contrast. *Neuroimage*, 48, 21-28.

93. Schlaug, G., Jäncke, L., Huang, Y., Steinmetz, H. (1995). In vivo evidence of structural brain assymetry in musicians. *Science*, 267, 699-701.

94. Schlaug, G., Jäncke, L., Huang, Y., Staiger, J.F., & Steinmetz, H. (1995a). Increased corpus callosum size in musicians. *Neuropsychologia*, 33, 1047-1055

95. Schlaug, G. (2003). The Brain of Musicians. In Peretz, I. & Zatorre, R.J.(Eds.). *The Cognitive Neuroscience of Music* (pp. 367-381). New York, NY: Oxford University Press.

96. Schmithorst, V.J. & Holland, S.K. (2003). The effect of musical training on music processing: a functional magnetic resonance imaging study. *Neuroscience Letters*, 348, 65-68.

97. Schneider, P., Sluming, V., Roberts, N., Scherg, M., Goebel, R., Specht, H.J., Dosch, H.G., Bleeck, S., Stippich, C., & Rupp, A. (2002). Structural and functional asymmetry of lateral Heschl's gyrus reflects pitch perception reference. *Nature Neuroscience*, 8, 1241-1247.

98. Schön, D., Magne, C. & Besson, M. (2004). The music of speech: music training facilitates pitch processing in both music and language. *Psychophysiology*, 41, 341-349.

99. Seeds, N.W., Williams, P.C., & Bickford, P.C. (1995). Tissue plasminogen activator induction in Purkinje neurons after cerebellar motor learning. *Science*, 270, 1992-1994.

100. Sergent, J., Zuck, E., Terriah, S., & MacDonald, B. (2007). Distributed neural network underlying musical sight-reading and keyboard performance. *Science*, 257, 106-109.

101. Shadmehr, R. & Holcomb, H.H. (1997). Neural correlates of motor memory consolidation. *Science*, 277, 821-825.

102. Shahin, A.J., Roberts, L.E., Chau, W., Trainor, L.J., & Miller, L.M. (2008). Music training leads to the development of timbre-specific gamma band activity. *Neuroimage*, 41, 113-122.

103. Sluming V., Brooks, J., Matthew, H., Joseph, D.J., & Neil R. (2007). Broca's area supports enhanced visuospatial cognition in orchestral musicians. *The Journal of Neuroscience*, 27, 3799-3806.

104. Spierer, L., Tardif, E., Sperdin, H., Murray, M.M., & Clarke, S. (2007). Learning-Induced plasticity in auditory spatial representations revealed by electrical neuroimaging. *The Journal of Neuroscience*, 27, 5474-5483.

105. Spolidoro, M., Sale, A., Berardi, N., & Maffei, L. (2009). Plasticity in the adult brain: lessons from the visual system. *Experimental Brain Research*, 192, 335--341.

106. Stein, D.G. & Hoffman, S.W. (2003). Concepts of CNS plasticity in the context of brain damage and repair. *Journal of Head Trauma Rehabilitation*, 18, 317-341.

107. Tilmann, B., Koelsch, S., Escoffier, N., Bigand, E., Lalitte, P., Friederici, A.D., & von Cramon, D.Y. (2006). Cognitive priming in sung and instrumental music: activation of inferior frontal cortex. *Neuroimage*, 31, 1771-1782.

108. Tracy, J.I., Faro, S.S., Mohammed, F., Pinus, A., Christensen, H., & Burkland, D. (2001). A comparison of 'Early' and 'Late' stage brain activation during brief practice of a simple motor task. *Cognitive Brain Research*, 10, 303-316.

109. Wieloch, T. & Nikolich, K. (2006). Mechanisms of neural plasticity following brain injury. *Current Opinion in Neurobiology*, 16, 258-264.

110. Yin, H.H., Mulcare, S.P., Hilario, M.R.F., Clouse, E., Holloway, T., Davis, M.I.,
Hansson, A.C., Lovinger, D.M., Costa, R.M. (2008). Dynamic reorganization
of striatal circuits during the acquisition and consolidation of a skill. *Nature
Neuroscience*, 12, 333-341.

111. Zatorre, R.J., Chen, J.L., Penhune, V.B. (2007). When the brain plays music:
auditory--motor interactions in music perception and production. *Nature Reviews
Neuroscience*, 8, 547-558.

112. Zielinski, K. (2006). Jerzy Konorski on brain associations. *Acta Neurobiologiae
Experimentalis*, 66, 75-90.

Appendix A

Hier ist das graue Feld, mit 6 Spalten und 4 Zeilen.
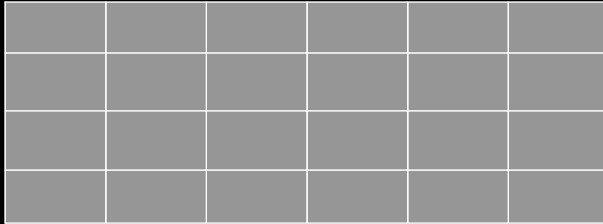
Die waagerechten Zeilen des grauen Feldes entsprechen der Reihenfolge von oben nach unten

Start

4-5 s

Ziel

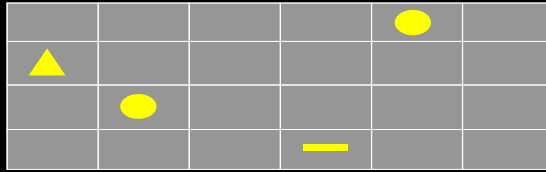| 1					
2					
3					
4					
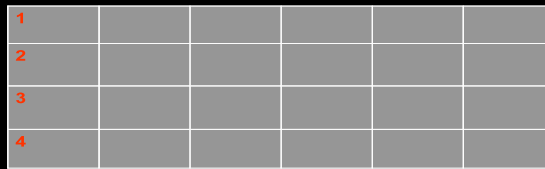
Die senkrechten Spalten des grauen Feldes entsprechen den Fingern bzw. den Tasten.
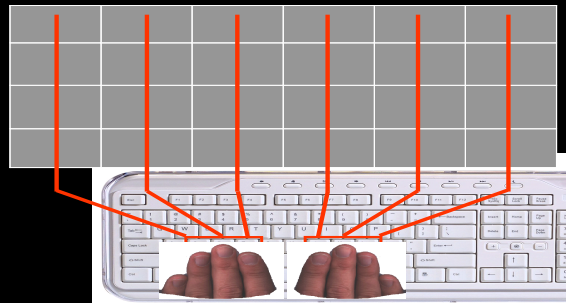
Im grauen Feld erscheinen gelbe Zeichen:

Reihenfolge

Finger

Die Form der gelben Zeichen zeigt an, wie oft Sie eine Taste drücken sollen!
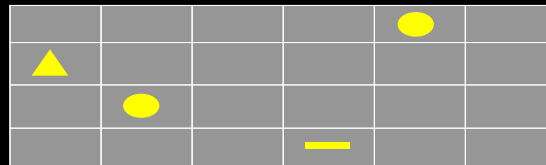
ein Kreis! → 1 x Tippen
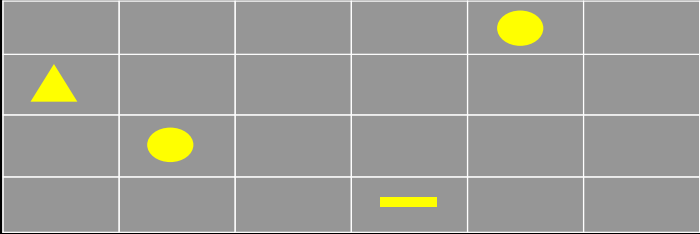
zwei Enden! → 2 x Tippen

drei Ecken! → 3 x Tippen

Test: Wie müssen Sie hier also tippen?

Figure A.1. The instructions for the Visuomotor task practice (in the scanner, the keyboard was replaced with the 2, 4-button boxes where 3 buttons were used from each box to correspond to the three right-hand and three left-hand fingers)

Figure A.2. The instructions for the Auditory (Music) task

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