

Katrin Schulze: Neural Correlates of Working Memory for Verbal and Tonal Stimuli in Nonmusicians and Musicians With and Without Absolute Pitch. Leipzig: Max Planck Institute for Human Cognitive and Brain Sciences, 2006 (MPI Series in Human Cognitive and Brain Sciences; 81)

**Neural Correlates of Working Memory for Verbal and Tonal
Stimuli in Nonmusicians and Musicians With and Without
Absolute Pitch**

Neural Correlates of Working Memory for Verbal and Tonal Stimuli in Nonmusicians and Musicians With and Without Absolute Pitch

Von der Fakultät für Biowissenschaften, Pharmazie und Psychologie
der Universität Leipzig
genehmigte

DISSERTATION

zur Erlangung des akademischen Grades
doctor rerum naturalium
Dr. rer. nat.

vorgelegt von
Diplom-Psychologin Katrin Schulze
geboren am 10. September 1977 in Magdeburg, Deutschland

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Tag der Verteidigung: 09.11.06

Acknowledgements

First and foremost, I wish to thank my adviser Dr. habil. Stefan Kölsch for his support, for his guidance and counsel, and for having faith and confidence in me.

I am very thankful to Prof. Dr. Angela D. Friederici for providing me with helpful comments, excellent working conditions and for reviewing this dissertation. I am grateful to Prof. Dr. D. Yves von Cramon for his help during the interpretation of the functional data as well as for the working conditions related to the fMRI environment.

I would like to thank Prof. Dr. Eckart Altenmüller for reviewing this dissertation.

Special thanks go to my colleagues of the music group at the Max Planck Institute for their help and support during all the phases of my dissertation. It has been a pleasure working with them. Special thanks go here to Daniela Sammler and Nikolaus Steinbeis, who read my dissertation and discussed it with me. I thank Dr. Stefan Zysset for the methodological support during data processing.

One experiment of this dissertation was undertaken in the Music and Neuroimaging laboratory in the Beth Israel Deaconess Medical Center/Harvard Medical School in Boston (USA) under the supervision of Prof. Dr. Gottfried Schlaug, whom I thank for giving me the possibility to do neuroscience research in Boston. Nadine Gaab and Katie Overy supported me as friends and colleagues during this time of my research. In this context I would like to thank the German Academic Exchange Council (DAAD) for their financial support during my research stay in Boston.

I wish to express my gratitude to Prof. Dr. Lutz Jäncke, who showed me how fascinating neuroscience is and how intriguing the questions are that we still have to answer.

Many other colleagues and friends helped me in many different ways, thanks to them.

My parents, Kerstin and Wolfgang Schulze, contributed greatly to this. I thank them for always being there for me, listening to me and giving me support.

And Frank, Katja and Suse, thanks for all the encouragement.

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Zusammenfassung der wissenschaftlichen Ergebnisse der Dissertation

Einleitung

Erst vor einigen Jahren wurde begonnen, *Sprache und Musik* unter neurowissenschaftlichen Gesichtspunkten zu untersuchen und zu vergleichen. Ein fundamentaler Mechanismus für komplexe kognitive Funktionen, wie das Hören bzw. „Verstehen“ von Sprache und Musik, ist das *Arbeitsgedächtnis*. Inwieweit sich die kognitive und zerebrale Organisation von Arbeitsgedächtnisprozessen für verbales und tonales Material unterscheidet, ist eine zentrale Fragestellung dieser Dissertation und wurde mittels funktioneller Magnetresonanztomographie (fMRT) untersucht.

Musiker sind Experten für Musik und für Töne. Ausgehend von der Annahme der funktionellen Plastizität, d.h. der Anpassungsfähigkeit des Gehirns an Umweltbedingungen, wie dem verstärkten auditorischen Input während des musikalischen Trainings, wurde erwartet, dass Musiker, wenn sie sich Töne merken, andere Hirnareale beanspruchen als Nichtmusiker. Durch den Vergleich von Nichtmusikern und Musikern wurden potentielle Einflüsse musikalischer Expertise auf die kognitive Architektur und die zugrunde liegenden neuronalen Korrelate des Arbeitsgedächtnisses untersucht.

Eine besondere Gruppe von Musikern bilden die *Absoluthörer*. Als Absolutes Gehör wird die Fähigkeit bezeichnet, Töne der chromatischen Tonleiter ohne externen Referenzton zu benennen. Die Forschungsergebnisse zum Absoluten Gehör sind teilweise uneinheitlich und die der Fähigkeit zugrunde liegenden kognitiven und neuronalen Mechanismen sind nur unzureichend bekannt. Dieser Fragestellung wird in der vorliegenden Dissertation nachgegangen. Weiterhin wurde evaluiert, ob Absoluthörer im gleichen Maße ihr Arbeitsgedächtnis beanspruchen wie Musiker ohne Absolutes Gehör, wenn sie sich Töne merken.

Die wichtigsten Ergebnisse dieser Dissertation wurden in einer Übersicht modellhaft dargestellt und zusammengefasst (siehe Fig. 13.1 in Kapitel 13).

Experimentelle Befunde und Diskussion

Experiment 1

In diesem fMRT-Experiment wurden zerebrale Aktivierungsmuster zwischen Musikern mit ($N = 10$) und ohne ($N = 10$) Absolutes Gehör während einer tonalen Arbeitsgedächtnisaufgabe verglichen, wobei zwischen der Wahrnehmungs- und Arbeitsgedächtnisphase unterschieden wurde. Musiker mit Absolutem Gehör zeigten während der Wahrnehmung der Tonsequenzen eine stärkere Aktivierung im linken Sulcus temporalis superior (STS) im

Vergleich zu Musikern ohne Absolutes Gehör. Aufgrund von Ergebnissen, die demonstrieren, dass dieses Areal bei der Wahrnehmung von verbalem Material stärker involviert ist als bei der Wahrnehmung von tonalem Material, wird dem STS in der Literatur eine wichtige Rolle bei der kategorialen Wahrnehmung zugeschrieben. Demzufolge weist das Ergebnis dieses Experimentes darauf hin, dass Absoluthörer Töne kategorial wahrnehmen, vergleichbar mit der Wahrnehmung von Phonemen. Die Musiker ohne Absolutes Gehör zeigten hingegen während der gesamten Arbeitsgedächtnisaufgabe eine stärkere Aktivierung des rechten superiores Parietallappens, was auf eine Arbeitsgedächtnisstrategie hinweist, möglicherweise eine visuell-räumliche Zuordnung der Töne.

Experiment 2

Um zu untersuchen, ob Absoluthörer, im Gegensatz zu Musikern ohne Absolutes Gehör, Töne kategorial wahrnehmen bzw. verarbeiten wie im Experiment 1 angenommen, wurden in diesem Verhaltensexperiment "Mikrotöne" ($\frac{1}{4}$ Halbtonschritte) präsentiert, die die Versuchspersonen sich merken. Im Gegensatz zu Experiment 1 zeigten die Musiker mit Absolutem Gehör ($N = 16$) keine bessere Verhaltensleistung als die Musiker ohne Absolutes Gehör ($N = 28$). In Experiment 1 entsprachen die Frequenzen der zu vergleichenden Sinustöne den Tönen der chromatischen Tonleiter und die Absoluthörer zeigten eine bessere Verhaltensleistung in dieser tonalen Arbeitsgedächtnisaufgabe als die Musiker ohne Absolutes Gehör. Die Ergebnisse der Experimente 1 und 2 implizieren, dass Absoluthörer sich Töne nur dann besser merken können, wenn sie die Möglichkeit haben, sie einer Kategorie zuzuordnen.

Experiment 3

In dem fMRT-Experiment 3 (bestehend aus den Experimenten 3A – 3C) wurden die Wahrnehmung und Arbeitsgedächtnisprozesse für auditorisches verbales und tonales Material in unterschiedlichen Gruppen (Nichtmusiker, Musiker mit und ohne Absolutes Gehör) analysiert. Dazu wurde eine verbale (Silben) und eine tonale (Sinustöne) Arbeitsgedächtnisaufgabe durchgeführt. Ein Sinuston wurde immer zusammen mit einer gesprochenen Silbe präsentiert. Die Frequenz der Sinustöne entsprach den Tönen der chromatischen Tonleiter, während als verbale Stimuli die Namen der Töne dieser Tonleiter genutzt wurden. Fünf dieser Stimuli (Silbe und Ton) wurden zu einer Sequenz kombiniert. Die Probanden sollten sich, abhängig von der Bedingung, entweder die Töne (tonale Bedingung) oder die Silben (verbale Bedingung) merken. Die Probanden wiederholten die Töne bzw. Silben in der folgenden Stilleperiode (4.2 bis 6.2 s) subvokal (lautlos) und gaben anschließend an, ob ein präsentierter Ton oder eine Silbe bereits in der Sequenz vorkam oder nicht. Demzufolge ist der

auditorische Input in beiden Bedingungen identisch, nur die Bedingung definiert, ob Töne oder Silben wiederholt und wieder erkannt werden sollen. Die Analyse der Ergebnisse über alle Teilnehmer ($N = 41$) ergab, dass der STS stärker während der Wahrnehmung der Silben, verglichen mit der von Tönen, aktiviert war, obwohl die Versuchspersonen immer *beide* Stimuli hörten. In der Literatur wird dieser Aktivierungsunterschied als ein Hinweis auf eine kategoriale Wahrnehmung von Sprache interpretiert. Weiterhin zeigte sich, dass sowohl die verbale als auch die tonale Bedingung deutlich Areale aktivierte, die zu einem Arbeitsgedächtnisnetzwerk gehören (z.B. der mid-dorsolaterale präfrontale Kortex, das Broca-Areal, der prämotorische Kortex, die Insel, parietale und zerebelläre Areale).

Experiment 3A – ging der Frage nach, ob den Arbeitsgedächtnisprozessen für verbales und tonales Material die gleichen neuronalen Korrelate zugrunde liegen. Es wurde mit Nichtmusikern ($N = 17$) durchgeführt, da dies eine stärkere Verallgemeinerung der Daten ermöglicht. Für das verbale und tonale subvokale Wiederholen (kontrastiert gegen eine Kontrollbedingung) wurde ein ähnliches Netzwerk aktiviert, für die tonale Bedingung jedoch deutlich schwächer. Dieses Netzwerk umfasste u.a. inferiore frontale, prämotorische, inferiore parietale und zerebelläre Areale. Während des subvokalen Wiederholens der Silben, verglichen mit dem der Töne, zeigten die Nichtmusiker eine stärkere Aktivierung eines zerebralen Netzwerkes, welches das Broca-Areal, den prämotorischen Kortex beidseitig, und den linken inferioren und superioren Parietallappen umfasste. Dieses Ergebnis betont die spezielle Rolle des Broca-Areals während verbaler Arbeitsgedächtnisaufgaben. Die stärkere prämotorische Aktivierung ist wahrscheinlich auf eine stärkere Assoziation zwischen dem sensorischen Input (auditorisch präsentierte Silbe) und der motorischen Repräsentation der entsprechenden Silbe (die man benötigt, um diese auszusprechen) zurückführbar. Die stärkere Aktivierung des inferioren Parietallappens kann als das neuronale Korrelat des phonologischen Speichers (nach dem Baddeley und Hitch Arbeitsgedächtnismodell) interpretiert werden, der möglicherweise stärker für verbales als für tonales Material genutzt wird. Eine alternative Interpretation betont die Rolle des Parietallappens im motorischen System, was mit der stärkeren Aktivierung im prämotorischen Kortex übereinstimmt. Das subvokale Wiederholen der Töne, verglichen mit dem der Silben, aktivierte den Gyrus cinguli und den linken Gyrus angularis stärker, was auf eine andere Strategie während der tonalen Arbeitsgedächtnisaufgabe hinweist. Zusammengefasst konnte diese Studie zeigen: Trotz der Überlappung der neuronalen Netzwerke für verbales und tonales Material, was auf ein gemeinsames Arbeitsgedächtnissystem hindeutet, gibt es Areale, die stärker bzw. ausschließlich für

verbale (Broca-Areal, inferiorer Parietallappen, prämotorischer Kortex) oder tonale Stimuli (Gyrus angularis) aktiviert sind.

Experiment 3B – mit dieser Studie wurde evaluiert, inwiefern musikalische Expertise einen Einfluss auf die Perzeption und Arbeitsgedächtnisprozesse von verbalem und tonalem Material hat. Dazu wurden zerebrale Aktivierungsmuster von Nichtmusikern ($N = 17$) und professionellen Musikern ohne Absolutes Gehör ($N = 16$) während der Durchführung der verbalen und tonalen Arbeitsgedächtnisaufgabe verglichen. Die Musiker zeigten eine signifikant bessere Performanz für die Töne als die Nichtmusiker, was auf das musikalische Training zurückgeführt wurde. Ein auffallender Unterschied zwischen Musikern und Nichtmusikern war, dass die Stärke der Aktivierungsmuster während der tonalen, verglichen mit der verbalen, Bedingung bei den Musikern keineswegs schwächer war (im Gegensatz zu den Nichtmusikern, siehe Experiment 3A). Auch die Musiker zeigten während der verbalen, verglichen mit der tonalen Bedingung, eine stärkere Aktivierung des Broca-Areals. Dies unterstützt die Interpretation der Ergebnisse aus Experiment 3A, dass das Broca-Areal eine wichtige Struktur für verbale Arbeitsgedächtnisaufgaben darstellt. Die prämotorischen Areale zeigten keine stärkere Involvement während der verbalen (verglichen mit der tonalen) Aufgabe, wieder im Gegensatz zu den Nichtmusikern. Beim subvokalen Wiederholen der tonalen Sequenzen zeigten Musiker eine stärkere Beteiligung des Gyrus supramarginalis, der in Studien als wichtiges Element des Arbeitsgedächtnisses für Töne identifiziert wurde und vor allem bei Musikern, wie diese Studie belegen konnte, eine wichtige Rolle für das tonale Arbeitsgedächtnis spielt. Des Weiteren zeigten Musiker eine stärkere Aktivierung des linken prämotorischen Kortex und des superioren und inferioren Parietallappens während der tonalen Arbeitsgedächtnisaufgabe, verglichen mit Nichtmusikern, was auf das musikalische Training und somit auf funktionelle Plastizität zurückgeführt wurde. Musiker haben wahrscheinlich eine stärkere Assoziation zwischen tonalem auditorischem Input und motorischer Repräsentation (Hören und Spielen des Tones sind stark assoziiert), was sich in der verstärkten Aktivierung des prämotorischen Kortex widerspiegelte. Um den Einfluss musikalischen Trainings detaillierter untersuchen zu können, wurde eine zusätzliche Bedingung implementiert: „key“ Sequenzen (alle Töne gehören zu einer Tonart, drei der Töne formen einen Dreiklang) und „non-key“ Sequenzen (beinhalten keine tonale Struktur). Die Musiker zeigten eine bessere Verhaltensleistung für die key- als für die non-key Sequenzen. Dieser Unterschied spiegelte sich in den funktionellen Daten wider: Während des subvokalen Wiederholens der key-Sequenzen wurden stärker Areale involviert (mid-dorsolateraler präfrontaler Kortex, inferiorer precentraler Sulcus, prämotorischer Kortex), die

in Studien mit strategiebasierten Arbeitsgedächtnisaufgaben beschrieben wurden. Dies impliziert, dass die Musiker ihr musikalisches Wissen genutzt haben, um die tonale Information zu organisieren, zusammenzufassen und sich auf diese Weise besser zu merken.

Experiment 3C – untersuchte den potentiellen Einfluss des Absoluten Gehörs auf tonale Arbeitsgedächtnisprozesse. Die Absoluthörer ($N = 8$) zeigten eine bessere Verhaltensleistung während der tonalen Arbeitsgedächtnisaufgabe als Musiker ohne Absolutes Gehör ($N = 8$). Dies kann höchstwahrscheinlich darauf zurückgeführt werden, dass die Frequenzen der verwendeten Töne denen der chromatischen Tonleiter entsprachen. Die Ergebnisse der Experimente 1, 2 und 3C führten zu der Schlussfolgerung, dass sich Absoluthörer Töne dann besser merken können, wenn diese einer Kategorie zugeordnet werden können. Um zusätzliche Informationen über die kognitiven und neuronalen Grundlagen des Absoluten Gehörs zu sammeln, wurde eine weitere Bedingung eingeführt: Einige der Sequenzen waren kongruent, d.h. die Namen der Töne waren die gleichen wie die gesprochenen Silben, während dies in der inkongruenten Bedingung nicht der Fall war. Da eine gängige Hypothese über das Absolute Gehör davon ausgeht, dass Absoluthörer die Töne automatisch benennen, wurde bei den Absoluthörern eine schlechtere Leistung für die inkongruenten Sequenzen erwartet. Die Musiker mit absolutem Gehör erinnerten tendenziell Töne aus kongruenten Sequenzen besser, verglichen mit inkongruenten Sequenzen, was die Theorie unterstützt, dass Absoluthörer die Töne automatisch benennen. Allerdings implizieren die Ergebnisse weiterhin, dass die Absoluthörer diese Strategie weniger anwenden, je besser ihr Absolutes Gehör ist. Die Perzeption der inkongruenten Tonsequenzen aktivierte den STS und den Gyrus temporalis superior beidseitig stärker. Dies deutet auf ein frühes Erkennen der Inkongruenz und auf die Beeinflussung von Wahrnehmungsprozessen durch das Absolute Gehör hin. Während der Perzeption der Töne zeigten die Absoluthörer eine signifikant stärkere Beteiligung des linken STS als die Musiker ohne Absolutes Gehör. Damit wurde die These der kategorialen Wahrnehmung gestützt (Experiment 1). Der Vergleich der tonalen Arbeitsgedächtnisaufgabe zwischen Musikern mit und ohne Absolutes Gehör zeigte Aktivierungsunterschiede, die auf unterschiedliche Arbeitsgedächtnisprozesse für Töne zwischen beiden Gruppen hinweisen.

Chapter 1

Language, Music, Working Memory and Musicians – An Introduction

“La musique, c’est du bruit qui pense.” Victor Hugo

The main purpose of this dissertation was to investigate the perception and processing of verbal and tonal material in nonmusicians and musicians with and without absolute pitch (see Fig. 1.1). This chapter gives an overview of the various aims of this study while embedding them into a broader context.

There are many open questions concerning the link between *language and music*. Language and music are described as characteristics of the human species. While the former – from an

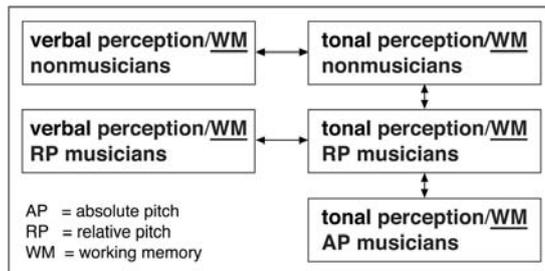


Fig. 1.1: Perception and WM Processes for verbal and tonal Material (focus on WM) was investigated in Nonmusicians, RP and AP musicians

evolutionary perspective – has evolved for the sake of communication, the question why music has emerged is still a matter of debate. There are theories that propose music could have developed as a sexual selection system, that music might facilitate group cohesion and some even believe that music has no

adaptational function at all (for an overview see Hauser & McDermott, 2003). However, it is important to note that human musical abilities might have played an important phylogenetic role in the evolution of human language (Koelsch, 2005). The fact that non-human mammals still communicate using tonal auditory signals (Gray et al., 2001), which are characterised by frequency and amplitude differences and modulations, would support such a view. Furthermore, Trehub (2003) reported, that there are surprisingly few differences concerning the music perceptual skills between infants prior to their language acquisition and adult participants, who have been exposed to music for years. Mothers all over the world sing to their babies, providing them with prelinguistic information. Even when they speak to their children, they use a more melodious voice (Trehub, 2003), so that children can use the prosody to learn the meaning of the words. These observations indicate that music might also play an important ontogenetical role for language acquisition (Koelsch, 2005; Trehub, 2003).

Nonetheless, in neuroscience researchers have emphasised mainly the investigation of language, only recently beginning to explore the neural correlates of music perception and processing. Patel (2003; p. 674) described the relevant question as follows: “What is the cognitive and neural relationship of language and music? Are they largely separate ‘modular’ brain systems that operate in fundamentally different ways, or is there significant overlap?” Because there are differences and similarities in the perception (Binder et al., 2000; Jancke, Wustenberg, Schulze, & Heinze, 2002; Zatorre, Evans, Meyer, & Gjedde, 1992) and processing of language and music (Koelsch et al., 2004; Maess, Koelsch, Gunter, & Friederici, 2001) it was considered necessary to investigate the perception and working memory (WM) processes for tonal and verbal stimuli. Considering the issues raised above, the question arises whether the processing of tonal stimuli might be based on phylogenetically older neural structures than that of verbal stimuli, although it is not the purpose of this dissertation to answer this question. Nevertheless, the (potential) overlap concerning the neural correlates of verbal and tonal stimuli might allow to draw conclusions about the similarity and/or difference between language and music.

Because music and language unfold over time, the already heard auditory information needs to be maintained to build up a context, so that subsequent stimuli can be integrated into this context in order to understand or appreciate it. Therefore, *working memory (WM)* seems to be fundamental to language and music processing. According to the pioneering model of Baddeley and Hitch (1974) “[...] working memory refers to a brain system that provides temporary storage and manipulation of the information necessary for [...] complex cognitive tasks [...]” (Baddeley, 1992, p. 556). This model defines WM as a basic mechanism for executive functions, which is necessary for processes like attentional control, sequential planning, implementation and monitoring of intermediate results, and therefore essential for complex cognitive tasks, like language comprehension, reasoning and learning. To conclude, WM is one of the most fundamental aspects of human cognition. Because the cognitive and neural relationships between language and music are still not fully understood, the knowledge we have of WM for verbal material cannot be generalised to the musical domain. Therefore, the potential differences or similarities between the neural networks underlying WM for tonal and verbal stimuli have remained elusive. Consequently, this dissertation investigated the similarities and differences between the organisation and the underlying neural networks of WM for verbal and tonal material. In other words, this dissertation analysed to what extent tonal information is subserved by a different WM system compared to verbal information.

This question was examined in different groups of participants: nonmusicians and relative pitch (RP) musicians. Many *musicians* start their musical training at a very early age. This extensive musical practise results in an increased auditory, visual and somatosensory input, as well as in intensive training of motor functions. Thus, musicians are excellent participants to investigate to what extent the environment can shape the brain (Munte, Altenmuller, & Jancke, 2002; Schlaug, 2001). Because for reasons outlined below musical expertise was expected to be a moderating factor in WM processes for tonal stimuli, which was investigated in this dissertation¹.

Some musicians possess *absolute pitch* (AP), i.e. they can name every tone of the Western musical scale without a reference tone (Takeuchi & Hulse, 1993). One aim of this work was to explore the involved perceptual and/or cognitive mechanisms and the underlying neural correlates of this rare ability. Because there are still contradictory results concerning the degree of WM involvement in pitch memory tasks in AP musicians (Crummer, Walton, Wayman, Hantz, & Frisina, 1994; Hirose et al., 2002; Klein, Coles, & Donchin, 1984; Wayman, Frisina, Walton, Hantz, & Crummer, 1992), it was investigated if the ability of AP has an influence on the cognitive processes (degree of involvement) and the neural organisation of WM for tonal stimuli by comparing AP musicians to RP musicians. The exploration of the phenomenon of AP is also relevant to understand workings of the auditory system. Saffran and Griepentrog (2001) observed that 8-month old infants, while performing a tone-sequence learning task, preferred to use absolute pitch cues, in contrast to adult participants, which preferred relative pitch cues. Therefore, the authors hypothesised that infants are born with an initial focus on absolute pitch cues. When infants acquire language and music skills, for which relative pitch cues are more important (e.g., melodies), this might cause a shift from the usage of absolute to relative pitch cues (Saffran & Griepentrog, 2001; Takeuchi & Hulse, 1993). This implies that a better knowledge of AP not simply explains a very rare ability, but also helps to understand human auditory perception and processing in more general.

¹ The neural networks underlying verbal WM were not compared between RP musicians and nonmusicians in the present dissertation for two reasons: (i) the focus was to compare tonal WM between both groups (because RP musicians are experts for tones) and (ii) no behavioural differences were observed between RP musicians and nonmusicians in the verbal WM task.

Chapter 2

Auditory Perception and Processing – Music and Language

Music and language are considered as human universals. While language has received much research attention, the interest in music investigation has started to grow only recently. According to Patel (2003) one fundamental issue in neuroscience research concerns the question about the cognitive and neural relationship between music and language, and whether music and language are processed in separate (brain) systems.

The aim of this chapter is to introduce the relevant literature on music and language perception and processing. Two models, for understanding the perception and processing of language (Friederici, 2002) and music (Koelsch & Siebel, 2005), will be exemplarily introduced. It is important to note that the main focus of this dissertation lies on the perception and processing of tonal material. Findings on language perception and processing serve here as a model to understand and interpret findings concerning the perception and processing of tonal information.

2.1 Language

Based on electrophysiological and neuroimaging data, Friederici (2002) suggested a neurocognitive model of auditory sentence comprehension, which includes a temporal (when is this process taking place) and a spatial dimension (which part of the brain is involved in this process). The model consists of three phases (see Fig. 2.1). During the first 100-300 ms word category is identified to build an initial syntactic structure of the auditory input (phase 1). Subsequently, in phase 2 (300-500 ms) morphosyntactic and lexical-semantic processing occurs. Finally, during the last step (phase 3, 500-1000 ms) the integration of the different types of extracted information takes place.

The processing of language regularities, the syntax (see also Chapter 2.3.1), has been shown to be subserved by the left anterior superior temporal gyrus (STG), Broca's area (BA²44), as well as the deep frontal operculum (Caplan, Alpert, & Waters, 1998; Friederici, Opitz, & von Cramon, 2000; Inui et al., 1998). However, in these studies the factors 'syntactic complexity' and 'WM' involvement were most often confounded. A study that disentangled these two components showed that the activation of Broca's area was due to increased WM demands

² BA = Brodmann area

rather than to enhanced syntactic complexity (Fiebach, Schlesewsky, & Friederici, 2001; Fiebach, Schlesewsky, Lohmann, von Cramon, & Friederici, 2005). Electrophysiological experiments indicated that different steps of structure building are reflected by different event-related potential (ERP) components. An early left-anterior negativity (ELAN, 200 ms; Friederici, Pfeifer, & Hahne, 1993) is thought to reflect the detection of a violation of phrase structure (syntax processing in language is described in more detail in Chapter 2.3.1). The slightly later left-anterior negativity (LAN, 300-500 ms) (Gunter, Friederici, & Schriefers, 2000) has been described most often in association with the processing of morphosyntactic violations. Whereas the N400 (a negative ERP component with a latency of 400 ms after the onset of a word, predominant over centro-parietal electrodes) is thought to reflect the processing of meaning (Kellenbach, Wijers, & Mulder, 2000; Kutas & Federmeier, 2000; Kutas & Hillyard, 1980; see Chapter 2.3.2).

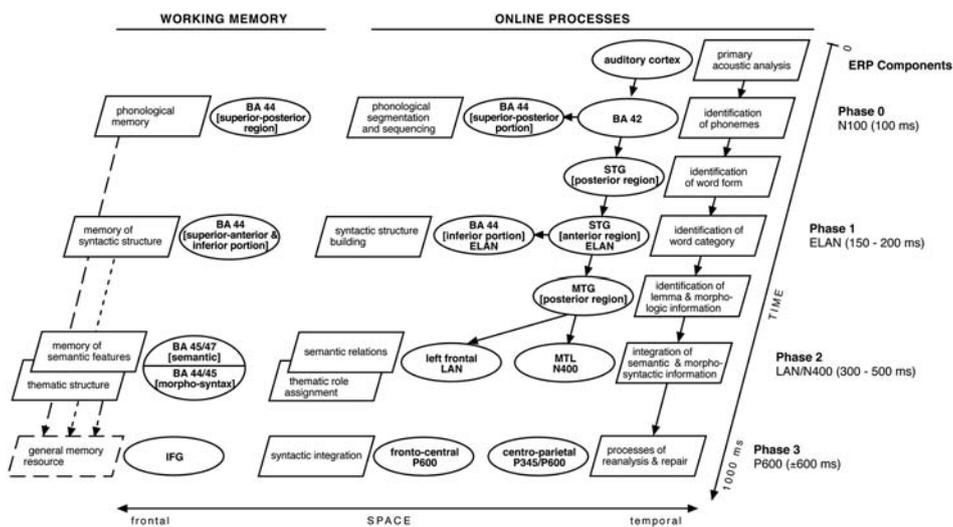


Fig. 2.1: The neurocognitive Model of auditory Sentence Processing developed by Friederici (2002). Processes are visualised by Boxes, whereas the neural Structures are indicated by Ellipses.

Finally, a late centro-parietal positivity was observed, the P600 (Kaan, Harris, Gibson, & Holcomb, 2000), which occurs between 600-1000 ms, and is assumed to correlate with the processing of syntactic violations that require the processing of syntactically complex sentences and syntactic revision.

Neuroimaging studies indicated that semantic processes (categorisation and selectional restriction), that is the processing of meaning, are supported by a neural network including the left middle temporal gyrus (MTG), the angular gyrus, and the left inferior frontal gyrus

(IFG, BA 45/47) (Demonet et al., 1992; Price, Moore, Humphreys, & Wise, 1997; Wise et al., 1991). On an electrophysiological level semantic processes are reflected by the N400, which is observed if a word is not semantically related to the established context (Kellenbach et al., 2000; Kutas & Federmeier, 2000; Kutas & Hillyard, 1980; see Chapter 2.3.2).

Furthermore, temporal structures are thought to underlie the processing and identification of word category and meaning, which are presumably encoded in the mental lexicon (Friederici, 2002). The prosodic information is hypothesised to be processed in the right prefrontal cortex (at a segmental level) (Zatorre, Mondor, & Evans, 1999), whereas violations of pitch for lexical elements in a tonal language correlated with increased activation in the left frontal operculum (Gandour et al., 2000). The processing of pitch, if pitch is a marker for syntax (suprasegmental level), seems to engage the right hemisphere, namely the right STG as well as the right fronto-opercular cortex (Meyer, Alter, Friederici, Lohmann, & von Cramon, 2002).

In summary, the model by Friederici (2002) describes the neural network underlying auditory sentence comprehension as a bilateral temporo-frontal network. Whereas the left temporal regions are involved in processing phonetic, lexical and structural features, the left frontal cortex plays an important role in sequencing and the formation of structural, semantic and thematic relations. In addition, the right temporal region is described as the underlying neural structure for processes of the analysis of prosodic information, and the right frontal cortex is thought to support the processing of sentence melody.

2.2 Music

Similar to language, music perception and processing seems to involve a broad neural network, including a multitude of cerebral structures. Koelsch and Siebel (2005) proposed a model of music perception and processing (see Fig. 2.2). They stated that the primary (and secondary) auditory cortices are involved in the extraction of acoustic properties, namely of pitch height, pitch chroma, timbre, intensity, and roughness (e.g., Kaas, Hackett, & Tramo, 1999; Tramo, Shah, & Braida, 2002; Warren, Uppenkamp, Patterson, & Griffiths, 2003). The exact locations within the auditory cortex, where these attributes are processed, are still not fully explored, however, the processing of these features is accompanied by electrophysiological correlates (e.g., ERP components P1 and N1). After the extraction of the auditory attributes, the auditory information is used to form auditory Gestalts (see Fig. 2.2). This process includes the grouping according to melodic, rhythmic, timbral and spatial patterns, which follows Gestalt principles. These Gestalt principles, such as similarity,

proximity and continuity, are known from the visual domain. The auditory Gestalt formation includes partly the auditory scene and the stream segregation, e.g., one part of the auditory Gestalt analysis is the processing of the melodic contour, which is thought to rely on the right (posterior) STG (e.g., Liegeois-Chauvel, Peretz, Babai, Laguitton, & Chauvel, 1998). Closely linked to Gestalt formation, a fine-grained analysis of intervals takes place, including the processing of the pitch relations of tones in a melody or chords as well as the analysis of temporal intervals. However, temporal and melodic intervals are analysed separately. This more detailed analysis of interval information is hypothesised to involve the anterior as well as the posterior areas of the supratemporal cortex bilaterally (e.g., the planum temporale (PT) is especially engaged in processing pitch intervals and sound sequences and therefore plays an important role during the auditory scene analysis and stream segregation) (Patterson, Uppenkamp, Johnsrude, & Griffiths, 2002; Zatorre, Evans, & Meyer, 1994). The next step comprises the structure building in music, which includes the analysis of the musical syntax (see Fig. 2.2). This process appears to be quite automatic and is reflected in ERP components like the early-right anterior negativity (ERAN; Koelsch, 2005; Koelsch, Gunter, Wittfoth, & Sammler, 2005; Koelsch & Siebel, 2005). The processing of musical syntax will be discussed in further detail below (see Chapter 2.3.1). In general, during the structure building processes, single elements are organised into a rhythmic, harmonic, temporal and timbral structure. Parallel to syntactic processing, but also already during earlier stages, the analysis of meaning and emotional processes takes place (Koelsch & Siebel, 2005).

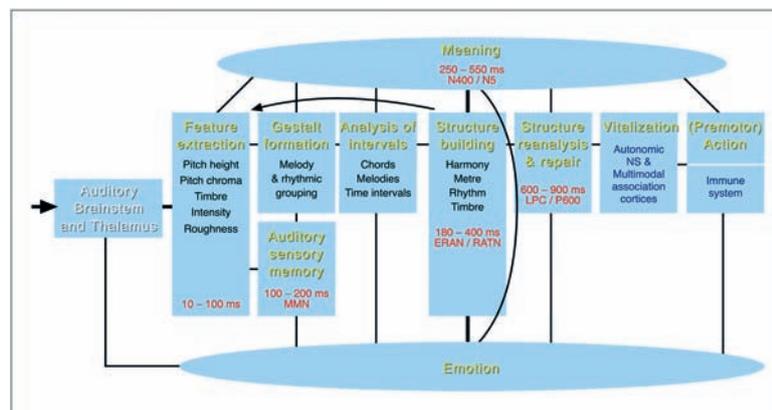


Fig. 2.2: The neurocognitive Model of Music Perception developed by Koelsch and Siebel (2005)

It is furthermore important to note that the processes of the single stages are more or less closely linked to WM functions (Berti & Schroger, 2003) as well as to long-term memory formations (Näätänen, Tervaniemi, Sussman, Paavilainen, & Winkler, 2001). E.g., the

building of a structure, the extraction of meaning or emotion, rely on WM processes as well as on long-term representations including, for example, the implicit knowledge of the regularities of the Western tonal system (Koelsch & Siebel, 2005). The model furthermore describes the reaction and action processes, which might follow music perception and might be linked to the autonomic nervous and the premotor and motor system (Koelsch & Siebel, 2005).

It is important to keep in mind that some of these relationships are still speculative and need further empirical validation.

2.3 Comparison Between Music and Language

Studies which compared the underlying networks of language and music have gathered contradictory results. Lesion studies showed that amusia (an impairment of music processing) can occur without aphasia (an impairment of language processing) and vice versa, indicating a functional and neural dissociation between music and language processing (Brust, 2001; Patel, 2003; Peretz & Coltheart, 2003).

Nonetheless, these results are contradictory to those gained by electrophysiological and neuroimaging studies, which observed analogous ERP components and similar activation patterns (Koelsch, 2005) for language and music perception and processing. As an explanation, Patel (2003) suggested that the comprehension problems in patients with Broca's aphasia, which are related to syntax, impair language exclusively, but also influence music perception unnoticed. He furthermore suggested that music and language have different, e.g. syntactic, representations (long-term structural knowledge), but share the operations performed on these representations. These factors could lead to differences between neuroimaging and lesion studies.

For example, when comparing verbal and tonal perception neuroimaging studies showed that the verbal perception activated the STG and the superior temporal sulcus (STS) more strongly (e.g., Binder et al., 2000; Dehaene-Lambertz et al., 2005; Jancke et al., 2002; Mottonen et al., 2006; Specht, Rimol, Reul, & Hugdahl, 2005). Therefore, it has been concluded that the STS might play an important role during the perception and processing of phonemic (possibly categorical) perception of verbal material (Liebenthal, Binder, Spitzer, Possing, & Medler, 2005; Mottonen et al., 2006). In contrast, the IFG seems to be engaged during the processing of verbal as well as tonal information, although with different hemispheric weighting. Language activates predominantly the left IFG (Friederici, 2002), whereas a more bilateral/right IFG activation was observed during tonal processing (Koelsch, 2005; Maess et al., 2001;

Tillmann, Janata, & Bharucha, 2003; Zatorre et al., 1992). The involvement of the IFG in music perception and processing might be due to the analysis of the musical syntax (Koelsch, 2005; Koelsch, Fritz, Schulze, Alsup, & Schlaug, 2005; Koelsch, Gunter et al., 2002; Maess et al., 2001; Tillmann et al., 2003), the involvement of WM for tonal material (Gaab, Gaser, Zaehle, Jancke, & Schlaug, 2003) or to lexico-semantic access (Platel et al., 1997).

In order to give an example of the similarities and differences in the perception and processing of both domains, studies which have investigated the underlying structures of processing semantics and syntax in language and music are described below.

2.3.1 Syntax in Music and Language

Perceptually single elements of language, as well as music, are arranged according to certain regularities. This rule-based structure of music and language is termed syntax (e.g., Friederici, 2002; Patel, 2003). The (implicit) knowledge about this structure is usually acquired effortlessly by growing up with a certain language or music system (e.g., Western music; Tillmann, Bharucha, & Bigand, 2000). Therefore, people are familiar with the regularities of language and music. The violation of such regularities in language, as well as in music, elicits a particular ERP component, with the same latency, polarity, and frontal scalp distribution, but with a different hemispheric weighting.

Koelsch, Gunter, Friederici, and Schroger (2000) investigated in an electroencephalography (EEG) experiment the neural mechanisms associated with the processing of musical information, including the establishment of a musical context and the detection of musical irregularities. Nonmusicians listened to five-chord sequences. Half of the sequences contained a Neapolitan chord, which violated the musical predictions based on the musical context that had been built up. It is important to note that a Neapolitan chord alone is a consonant chord (such as the tonic chord), which appears irregular merely due to the previously established context. The Neapolitan chords elicited an early ERP component over frontal electrodes with right-hemispheric predominance, which was termed ERAN (onset at around 150 ms). It is thought to reflect the detection of violation of a musical structure and is therefore associated with the processing of musical rules, i.e. the musical syntax (Koelsch, Schroger, & Gunter, 2002; for an overview see Koelsch & Siebel, 2005).

The violation of a syntactic structure in the language domain (e.g., the phrase structure of a German sentence is violated when a preposition is followed by a participle instead of a noun) elicits a similar early ERP component, the ELAN (Friederici, 2002).

Using magnetoencephalography (MEG), Maess et al. (2001) explored the neural generators of the ERAN. The results implicated that the processing of musical structure or syntax takes

place in the pars opercularis (BA 44) of the IFG bilaterally. Importantly, the left pars opercularis (Broca's area) is known to be involved in the processing of linguistic syntax (Friederici, 2002; Friederici, Meyer, & von Cramon, 2000). The results obtained by Maess et al. (2001) indicated that Broca's area and the homologous area in the right hemisphere might be engaged not only in the processing of linguistic syntax, but its function includes also the processing of musical syntax.

This led to the hypothesis that similar brain areas are involved in the processing of structure in language and music, but with different hemispheric predominance. This was supported by functional magnetic resonance imaging (fMRI) studies, which showed a right/bilateral involvement of the pars opercularis in the processing of musical structure (it was stronger activated when comparing the processing of irregular with regular chords (Koelsch, 2005; Koelsch, Fritz et al., 2005; Koelsch, Gunter et al., 2002; Tillmann et al., 2003)). The pars opercularis, with a more left-hemispheric weighting has also been shown to be involved during the processing of linguistic syntax (Friederici, 2002).

Taken together, these studies showed that the processing of syntax in language and music is reflected in similar ERP components and that similar brain areas are engaged for both functions, indicating the involvement of similar processes in both domains.

2.3.2 Semantics in Music and Language

The term semantic is equatable with meaning and is usually used for language (Friederici, 2002). The N400, a negative ERP component with a latency of 400 ms after the onset of a word, is measured over centro-parietal electrodes as an electrophysiological correlate of the processing of meaning, as known from language studies (e.g., Kellenbach et al., 2000; Kutas & Federmeier, 2000; Kutas & Hillyard, 1980). Because the amplitude of this component depends (inversely) on the semantic fit between two verbal stimuli, that is the better a word can be integrated into a context, the smaller the N400, it serves therefore as an electrophysiological index of semantic priming (Friederici, 2002; Koelsch et al., 2004; Kutas & Federmeier, 2000).

Koelsch et al. (2004) examined the ability of music to prime the meaning of words using EEG. Sentences and musical excerpts, which were either related or unrelated to target words, were used as primes. It was observed that an N400 was elicited if target words were not semantically related to the preceding sentence. The same effect was observed if musical stimuli were used as primes: An N400 was observed if the target words were not semantically associated to the previous musical pieces. Importantly, the N400 elicited by verbal or musical

primes differed neither in terms of latency, amplitude or scalp distribution, nor in terms of location, orientation, strength, time point of maximum or variance. The results obtained by this experiment indicate (i) that music and language can prime the meaning of words and (ii) that music is able to communicate meaning to a higher degree than previously believed.

2.4 Summary

Electrophysiological and neuroimaging studies showed that there are considerable similarities between the processing of music and language, e.g., the processing of syntax and semantics in music evoked electrophysiological responses similar to those observed during the perception of syntax and semantics in language (e.g., Koelsch, 2005; Koelsch et al., 2004; Maess et al., 2001; Tillmann et al., 2003). On the contrary, other studies reported that, despite such similarities, differences exist in the underlying neural correlates between music and language, e.g., verbal perception and processing showed stronger activation of the STG and STS compared to tonal perception and processing (e.g., Binder et al., 2000; Dehaene-Lambertz et al., 2005; Jancke et al., 2002; Specht et al., 2005). Potential differences and similarities in the neural pattern underlying language and music processing, especially for WM processes, have remained elusive.

Chapter 3

The Phonological Loop – A Component of Working Memory

This chapter attempts (i) to introduce the Baddeley and Hitch (1974) working memory model, (ii) to give an overview of behavioural studies providing insights into the mechanisms and the organisation of WM and (iii) to summarise the results of electrophysiological and neuro-imaging data on the underlying networks of WM processes.

3.1 The Baddeley and Hitch Working Memory Model

In 1974 Baddeley and Hitch developed one of the most influential WM models. To date, many studies have supported their model (for an overview see Baddeley, 2003). According to this model “[...] working memory refers to a brain system that provides temporary storage and manipulation of the information necessary for [...] complex cognitive tasks [...]” (Baddeley, 1992, p. 556) like learning, comprehension and reasoning (Baddeley, 1998). There are different stages of the WM system: encoding, which is the registration of the information, storage, which refers to the maintenance of information over time (phonological store and articulatory rehearsal process³) and also includes the manipulation of information, and retrieval, that is recall or recognition (Baddeley, 2002).

The Baddeley and Hitch WM model (Baddeley, 1992; Baddeley & Hitch, 1974) consists of an attentional control system, the central executive, that operates in conjunction with two slave systems: the visuospatial sketchpad and the phonological loop (see Fig. 3.1).

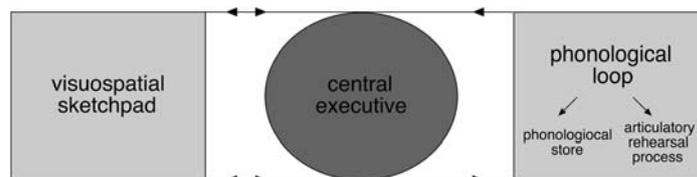


Fig. 3.1: The Baddeley and Hitch WM Model (modified after Baddeley, 1992, 2003).

The visuospatial sketchpad is concerned with the storage and manipulation of visual and spatial information. The other slave system, the phonological loop, processes auditory and speech-based information, and consists of a phonological store, which holds memory traces

³ Articulatory rehearsal process and phonological rehearsal process are used synonymously in this dissertation.

for a few seconds (between 1 and 2 seconds; Baddeley, 1992), and an articulatory (phonological) rehearsal process that is analogous to subvocal speech (Baddeley, 2003). The focus of this dissertation was on the phonological loop.

Behavioural (Baddeley, 1966; Baddeley, Thomson, & Buchanan, 1975; Conrad & Hull, 1964), neuropsychological (Vallar & Baddeley, 1984) and neuroimaging (e.g., Awh et al., 1996; Gruber & von Cramon, 2003; Paulesu, Frith, & Frackowiak, 1993) studies support the assumption of the functional independence of the phonological store and the rehearsal mechanism. Auditory information is stored in the phonological store when the articulatory rehearsal process is operating at full capacity, e.g., if there is continuous auditory stimulation while the auditory material should be maintained (Baddeley, 1992, 2003). Material in the phonological loop can be refreshed by means of subvocal rehearsal.

Behavioural research has discovered several mechanisms of the phonological loop, which have provided information about the underlying mechanisms of this system.

1. *The phonological similarity effect* – Participants showed inferior performance for phonologically similar sequences of consonants during immediate memory tasks, compared to sequences of phonologically different sounding consonants (Conrad & Hull, 1964). This might indicate that the phonological loop, and especially the articulatory rehearsal process, operates using a phonological code and is therefore comparable to subvocal speech (Baddeley, 2003).
2. *The word length effect* – Participants showed a greater memory span for short words than for long words (Baddeley et al., 1975). They could memorise as many words as they could pronounce in two seconds, indicating an inverse relation between the number of items that could be remembered and the time it took to pronounce a word (Baddeley, 1986, 1992). This effect reveals that the phonological rehearsal process repeats verbal material in real time.
3. *The articulatory suppression* – The articulatory suppression is a reduction of the verbal WM function caused by additional, competing processes, which are disturbing the articulatory rehearsal process of the phonological loop (Baddeley, 1992, 2003; Gruber & von Cramon, 2003). This articulatory suppression prevents the phonological loop from rehearsing the words, and therefore participants rely only on the phonological store in order to perform the task.
4. *The irrelevant sound effect* – When participants were presented visually with items they were asked to remember, they showed a decrease in performance when they heard simultaneously irrelevant speech (e.g., a foreign language) (Colle, 1980). This effect

could not be explained by simple distraction, because noise bursts did not have the same effect (for an overview see Baddeley, 1992, 2003). This effect was interpreted as a consequence of the fact that spoken material accesses the phonological store, which causes interference with the verbal material to be remembered (Baddeley, 1992). However, some studies questioned this interpretation and suggested that the irrelevant speech effect could be due to a disturbance of storage of serial order (Jones & Macken, 1995; Jones, Macken, & Nicholls, 2004).

Although, the Baddeley and Hitch (1974) three-component WM model accounts for these effects, there are some phenomena that cannot be explained by this model (for an overview see Baddeley, 2000). Therefore, this model is still under development. At the moment the existence of an episodic buffer is discussed in the literature (Baddeley, 2000).

3.2 A Slave System for Musical Stimuli (Tonal Loop)?

The phonological loop was mainly investigated under the aspect of language. It was described as a ‘language learning device’ (Baddeley, Gathercole, & Papagno, 1998), responsible for holding speech-based information (Baddeley, 1998). It was furthermore suggested that the phonological loop evolved in order to facilitate the acquisition of language by storing new phoneme sequences in the phonological store and to enhance learning by rehearsing new verbal material in the articulatory rehearsal process (Baddeley, 2003). However, as already discussed in Chapter 2, there are differences and similarities in the perception (Binder et al., 2000; Jancke et al., 2002; Zatorre et al., 1992) and processing (Koelsch et al., 2004; Maess et al., 2001) of language and music. Therefore, the question arises, whether the phonological loop is also concerned with the processing of tonal and musical material, or if this is done by another comparable system. Pechmann and Mohr (1992) suggested the existence of a tonal loop, similarly Berz (1995) proposed a music memory loop. There have been some behavioural studies that investigated this issue by comparing WM processes for tonal and verbal material. Deutsch (1970) presented participants with two standard tones, and then asked them to indicate whether these tones were same or different in terms of pitch. Participants showed a good performance, if there was a 6 seconds lasting period of silence between these two standard tones. But, if participants were presented with eight intervening tones instead of a silent period, performance dropped rapidly, even when participants were instructed to ignore the intervening tones (Deutsch, 1970). This shows that the memory trace of pitch height decays quickly and is influenced by the production of other tones. In contrast, when instead of the intervening tones (Deutsch, 1970) auditory verbal material (e.g.,

numbers) was presented, the participants showed a better performance. Deutsch (1970) argued that these results point to the conclusion that the intervening tones interfered more strongly with the pitch memory task, because of the interference *within* a specialised system. As a consequence the performance of this system decreased, which was reflected in the diminished memory for the pitch heights. Because the verbal stimuli did not cause such a striking performance decrease, this might indicate that verbal auditory stimuli are processed in a system different from that for tonal stimuli. This experiment therefore suggested two separate WM systems for auditory verbal and tonal material.

Semal, Demany, Ueda, and Halle (1996) questioned the results and interpretations obtained by Deutsch (1970). Their criticism was that the frequency relations between the standard tones and the intervening verbal material was not controlled in Deutsch's study, which might have explained the missing interference between the standard tones and the intervening verbal material. Semal et al. (1996) showed in their behavioural experiment that the pitch similarity of the intervening stimuli (words or tones) had a greater effect on the performance rate than the modality of the intervening stimuli (verbal or tonal), indicating that both types of stimuli, verbal and tonal, are processed in the same WM system.

Nonetheless, results by other studies supported the assumption of two independent WM systems for verbal and tonal stimuli. For example, Salame and Baddeley (1989) investigated the effect of music on verbal WM. Silence and noise showed almost no influence on verbal WM performance, but instrumental music caused a performance decrease, which was however not as large as that caused by the unattended speech. Lange (2002) compared verbal and tonal stimuli in a WM experiment and showed that musical tasks were relatively undisturbed by additional verbal tasks. Therefore, the processing of tonal WM tasks in the phonological loop needs to be questioned.

In contrast, Chan, Ho, and Cheung (1998) reported that adults, who started their musical training before the age of 12, showed a better verbal WM span. Conversely, there was no difference between the performances in a visual memory task for both groups. These results might indicate that the same WM slave system processes verbal and tonal information, or that both types of stimuli are processed by partly overlapping systems. This assumption was supported by Iwanaga and Itoh (2002). Additionally, Pechmann and Mohr (1992) introduced another dimension by showing that musical experience has an influence on the potential of stimuli to interfere with the performance during a tonal WM task. In musicians only tones interfered with the tonal WM task, whereas the performance in the tonal WM task in nonmusicians was also affected by the verbal conditions and the visual-attended condition.

Nevertheless, as already mentioned, not many studies compared tonal and verbal WM systems. Based on these contradictory results (Chan et al., 1998; Deutsch, 1970; Lange, 2002; Salame & Baddeley, 1989; Semal et al., 1996) and the additional influence of musicianship (Pechmann & Mohr, 1992), this dissertation aimed to investigate if there are differences concerning the underlying neural networks subserving tonal and verbal stimuli.

3.3 Neural Correlates of the Phonological Loop

The first indication of a locus of the anatomical structures involved in WM came from animal studies. For example, Goldman-Rakic (1992) showed that monkeys with a lesion in the lateral prefrontal cortex failed to continue to represent the information where the experimenter put the food over a very short period of time, which indicates the involvement of the prefrontal cortex for WM.

The knowledge we have about the anatomical substrate of WM in humans was gained by (a) clinical studies in patients with auditory-verbal span impairment and (b) by neuroimaging studies which investigated verbal WM.

3.3.1 Lesion Studies

Lesions in the left temporo-parietal region were observed to cause selective impairments in auditory-verbal memory span (Vallar, Di Betta, & Silveri, 1997; for an overview see Vallar & Papagno, 2002). Vallar et al. (1997) examined two patients with auditory-verbal span impairment, however with different left-sided lesions. Whereas the localisation of the lesion in patient L.A. comprised the inferior parietal lobe (IPL), superior and middle temporal gyri, the patient T.O. showed a lesion in subcortical premotor and rolandic regions as well as in the anterior insula. Behavioural assessment displayed that L.A. was unable to maintain verbal material in the phonological store, whereas he showed normal performance in tasks requiring the articulatory rehearsal process (e.g., phonological judgement). In patient T.O. the researchers observed an impairment related to the articulatory rehearsal process, conversely T.O. showed no decreased performance in tasks associated with the phonological store. This reported double dissociation led to the conclusion that the two components of the phonological loop are subserved by separate anatomical structures.

More evidence came from patients with conduction aphasia. These patients, with a lesion in the left posterior parietal area, showed the inability of repeating verbal stimuli. This deficit was independent of the delay, therefore a lack of rehearsal cannot be the main underlying cause, and this impairment was limited to verbal material (for an overview see Smith & Jonides, 1998). This supports the assumption that the IPL is the neural correlate of the

phonological store. But this interpretation was already questioned by a study from Cohen (1992), who observed that patients with conduction aphasia have other phonological problems in addition, indicating the possibility that the IPL might be involved in phonological processing and not only subserving the phonological memory store.

3.3.2 Neurophysiological and Neuroimaging Studies

Neural correlates of WM – The P300 describes a positive ERP component with a latency of 300-500 ms that occurs over parieto-occipital brain areas (Polich & Kok, 1995). This component is thought to be associated with WM processes (Donchin, 1981; Klein et al., 1984), although some results suggested that this component is rather related to attentional processes than to WM (Portin et al., 2000). The amplitude of the P300 was reported to increase with the WM load (Ruchkin, Johnson, Grafman, Canoune, & Ritter, 1992), although other studies have shown the opposite: The amplitude of the P300 component decreased with increasing information load (McEvoy, Smith, & Gevins, 1998) or increasing task difficulty (Hantz, Crummer, Wayman, Walton, & Frisina, 1992). This WM related P300 component was localised in the superior parietal lobe/intraparietal sulcus (SPL/IPS; Moores et al., 2003). One of the first neuroimaging studies that investigated the underlying neural correlates of the phonological loop of WM in humans was conducted by Paulesu et al. (1993) using positron emission tomography (PET). Their results supported the assumption that the left IPL subserves the phonological store, whereas Broca's area is supposed to play a crucial role during the phonological rehearsal process. Subsequent verbal WM studies (for an overview see Baddeley, 2003), which used either PET or fMRI, supported that the passive storage component is subserved by superior and inferior parietal areas (Awh et al., 1996; Chen & Desmond, 2005; Crottaz-Herbette, Anagnoson, & Menon, 2004; Gruber, 2001; Gruber & von Cramon, 2003; Henson, Burgess, & Frith, 2000; Jonides et al., 1998; Kirschen, Chen, Schraedley-Desmond, & Desmond, 2005; Paulesu et al., 1993; Ravizza, Delgado, Chein, Becker, & Fiez, 2004), whereas the active rehearsal is mainly supported by Broca's area and the premotor areas (Awh et al., 1996; Chen & Desmond, 2005; Fiez et al., 1996; Gruber, 2001; Gruber & von Cramon, 2003; Paulesu et al., 1993; Ravizza et al., 2004), the insular cortex (Bamiou, Musiek, & Luxon, 2003; Paulesu et al., 1993) and the cerebellum (Chen & Desmond, 2005; Kirschen et al., 2005; Ravizza et al., 2004) (see Fig. 3.2).

A number of studies showed that increased WM load was positively correlated with increased activation of Broca's area (Braver et al., 1997; Chen & Desmond, 2005; Fiebach et al., 2005; Ravizza et al., 2004; Smith & Jonides, 1998; Xue, Dong, Jin, & Chen, 2004) as well as with stronger activation of the IPL (Braver et al., 1997; Chen & Desmond, 2005; Kirschen et al.,

2005; Ravizza et al., 2004). Klingberg, Forssberg, and Westerberg (2002) investigated the development of WM capacity and the underlying neural activity in participants aged 9 to 18. They observed that older children showed a better WM performance, which in turn was positively correlated (amongst other structures) with an increased bilateral activation of the IPS.

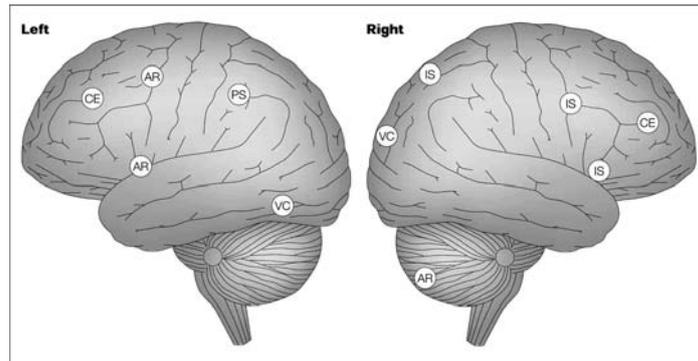


Fig. 3.2: Overview over the neural Correlates of verbal and spatial WM (Baddeley, 2003)
(AR = Articulatory Rehearsal, CE = Central Executive, PS = Phonological Store, IS = Inner Scribe (spatial Rehearsal), VC = Visual Cache (visual Store))

Although the importance of Broca's area for the internal verbal rehearsal was supported by many studies (e.g., Baddeley, 2003; Gruber & von Cramon, 2003; Paulesu et al., 1993), the existence of the phonological store in the IPL is still discussed controversially. The parietal lobe is known as an association area, subserving numerous functions e.g., attention, orientation, spatial localisation, reaching and grasping, processing of shape, spatial and non-spatial WM, mental imagery, tasks switching, mental rotation, alertness, calculation, pain processing and meditation (for an overview see Cabeza & Nyberg, 2000; Culham & Kanwisher, 2001). Therefore, it is a challenge to investigate the specific function of the IPL and SPL, especially because the parietal cortex is involved in attention (Corbetta & Shulman, 2002), which plays a role in a multitude of cognitive tasks. As a consequence the existence and/or the location of the phonological store is still highly controversial: Many studies supported the notion of the existence of the phonological loop in the IPL (Awh et al., 1996; Gruber & von Cramon, 2003; Henson et al., 2000; Jonides et al., 1998; Paulesu et al., 1993; Ravizza et al., 2004), whereas other studies reported opposite results (Fiez et al., 1996; Hickok, Buchsbaum, Humphries, & Muftuler, 2003; Jones et al., 2004).

The mid-dorsolateral prefrontal cortex (DLPFC) – Another important structure is the DLPFC. Goldman-Rakic (1987) showed in primates that lesions of area 46 (DLPFC) impaired the ability to maintain information, which are not physically presented any longer. It was concluded that the DLPFC is involved in producing and creating internal representations

of sensory information. Further studies showed that the DLPFC in monkeys and humans was active during a delay period, when items had to be remembered (for an overview see Curtis & D'Esposito, 2003).

Based on the similarity in terms of their cytoarchitectonic characteristics, parts of BA 9 and BA 46 in the posterior middle frontal gyrus are often termed mid-DLPFC (area 9/46 according to Petrides, 2000a, 2000b, 2005). Petrides, Alivisatos, Meyer, and Evans (1993) conducted a verbal WM experiment, which consisted of three different conditions. In the first condition (control condition) participants were asked to count aloud, in the second condition they said randomly a number between 1 and 10 (self-ordered task), and in the third condition they were presented with a spoken sequence of numbers and their task was to detect the omitted number (externally-ordered task). The self-ordered task and the externally ordered task required enhanced WM involvement compared to the control task. The authors observed activation in the mid-DLPFC (area 9/46), which was related to the performance in the self- and externally-ordered task (Petrides, Alivisatos, Meyer et al., 1993). In another study Petrides, Alivisatos, Evans, and Meyer (1993) applied a similar design, but used spatial stimuli. Again, the mid-DLPFC was observed to be involved in increased WM demands.

Whereas some experiments emphasised mainly the role of the mid-DLPFC (e.g., Goldman-Rakic, 1987; Petrides, 2000a, 2000b; Petrides, Alivisatos, Evans et al., 1993; Petrides, Alivisatos, Meyer et al., 1993), other studies showed a strong involvement of the ventrolateral prefrontal cortex (VLPFC), including Broca's area, during WM task (Awh et al., 1996; Fiez et al., 1996; Gruber, 2001; Ravizza et al., 2004). According to Petrides (2000a) this is due to the different demands in WM tasks. In the studies by Petrides et al. (Petrides, Alivisatos, Evans et al., 1993; Petrides, Alivisatos, Meyer et al., 1993) participants had to manipulate information and to monitor their performance in order to solve the task, whereas in other WM experiments, the only task was to maintain the information (e.g., Gruber & von Cramon, 2003; Paulesu et al., 1993). When a WM task requires manipulation of the information and monitoring of the performance, then the mid-DLPFC is activated, whereas during the pure maintenance of information the ventrolateral prefrontal cortex is involved (Petrides, 2000a). According to Petrides (2005) the mid-DLPFC is primarily important to monitor the ongoing WM process, but this area is also engaged in the manipulation of the material to be maintained. Another important aspect is that the mid-DLPFC has connections to hippocampal and parahippocampal regions via the retrosplenial cortex, which might be the anatomical basis of the control and monitor function of the mid-DLPFC during WM processes (for an overview see Petrides, 2005). The results concerning the influence of memory load on

mid-DLPFC activity are contradictory. Whereas some studies state that memory load influences DLPFC activity (Druzgal & D'Esposito, 2003; Linden et al., 2003; Rypma, Berger, & D'Esposito, 2002), other studies could not support this assumption (Jha & McCarthy, 2000; Rypma & D'Esposito, 1999). These contradictory results could be due to the fact that encoding strategies (e.g., chunking) might also influence activation in the mid-DLPFC.

Subdivisions of WM – Since the WM model of Baddeley and Hitch (1974) assumed two slave systems, studies have tried to separate the neural correlates underlying visual and verbal WM (see Fig. 3.1)⁴. E.g., Gruber and von Cramon (2003) investigated verbal and visuospatial WM, both under single-task conditions and under suppression. Their results showed that verbal and visuospatial WM are represented by different networks in the human brain and that there are (partly) different networks subserving verbal rehearsal (left-lateralised premotor-parietal network) and verbal storage (bilateral anterior prefrontal and inferior-parietal network). These findings raise the question, whether there might be a further dissociation within the WM system, e.g. for verbal and tonal material. To date, only a sparse investigation of tonal WM, especially the comparison between tonal and verbal WM processes, has been undertaken. In an fMRI study Stevens (2004) compared the WM processes involved during the processing of voices, words and tones, using a two-back WM task. WM for words, compared to tones, activated stronger left superior and middle temporal gyrus, left superior frontal gyrus (SFG), left anterior cingulate gyrus and right superior temporal gyrus compared to tones, whereas WM processes related to the tonal condition activated more the IPL bilaterally, the left inferior temporal gyrus (ITG), the left insula and the right inferior frontal gyrus than the word condition. Because this comparison was not the main issue addressed by this study, the conditions were not well matched in terms of stimulus complexity (pure tones vs. nouns). However, the obtained results indicate (partly) functionally dissociable WM processes and structures for verbal and tonal WM.

During a pitch memory task Gaab, Gaser et al. (2003) showed the involvement of the supramarginal gyrus, posterior dorsolateral frontal regions, superior parietal regions and dorsolateral cerebellar regions during tonal WM. But the neural correlates underlying WM for basic tonal and verbal material have not been compared so far. This dissertation investigated whether there are different organisational systems and/or different neural correlates for verbal and tonal WM.

⁴ For an overview of the neural correlates of spatial WM and the central executive see Baddeley (2003).

3.4 Summary

The Baddeley and Hitch WM model is supported by numerous behavioural, neuropsychological and neuroimaging studies (e.g., Awh et al., 1996; Baddeley, 1966, 2003; Baddeley et al., 1975; Conrad & Hull, 1964; Gruber & von Cramon, 2003; Paulesu et al., 1993; Vallar & Baddeley, 1984). The phonological loop, one part of the model, is thought to consist of (at least) two components: the phonological rehearsal process, which is neurally implemented by Broca's area and the premotor areas (Awh et al., 1996; Fiez et al., 1996; Gruber, 2001; Ravizza et al., 2004), whereas the phonological store seems to rely on superior and inferior parietal areas (Awh et al., 1996; Gruber, 2001; Henson et al., 2000; Jonides et al., 1998). However, there are contradictory results concerning the existence and location of the phonological store in the IPL (Corbetta & Shulman, 2002; Culham & Kanwisher, 2001; Fiez et al., 1996; Hickok et al., 2003; Jones et al., 2004). The mid-DLPFC is also involved in WM tasks, as soon as monitoring of the performance and manipulation of the information is required (Petrides, 2000a, 2005). Though, there is still a lack of studies, which investigated the underlying neural components of tonal WM respectively compared the neural correlates underlying verbal and tonal WM.

Chapter 4

Learning, Plasticity and Musicians

When musicians learn to play an instrument, they train to associate auditory and visual input and to use this information to coordinate the highly complex movements necessary to make music. But how does the brain learn and how is this process reflected in the brain? The aim of Chapter 4 is to introduce what is known about learning and the correlated changes in the brain.

4.1 The Discovery of Plasticity

Learning and memory were defined as the ability to acquire new information and retain it over time (Gazzaniga, Ivry, & Mangun, 1998). For a long time it was not clear how the brain acquires new knowledge and how it adapts to the environment. In the early 1980's numerous studies showed that cortical representations and connectivity in the adult brain are only partially determined by genetics, and therefore can be modified and changed by experience and by the environment (e.g., Kelahan & Doetsch, 1984; Merzenich et al., 1984; Robertson & Irvine, 1989). Neuroimaging studies started to investigate sensory cortical maps in the visual, auditory, and somatosensory cortex, which are organised in a topographic manner, that is adjacent cortical regions respond to adjacent skin areas (somatotopic), basilar membrane areas (tonotopic) and retinal areas (retinotopic).

4.1.1 Functional Plasticity in Different Modalities

Merzenich et al. (1984) showed in an experiment with monkeys that the cortical representation of the fingers in the *somatosensory cortex* is altered by amputation. The cortical areas, which before the amputation responded only to the skin of the amputated surfaces, responded to touch of adjacent fingers or to the palm after 2-8 months. This result was replicated in numerous studies with different animals (e.g., Kelahan & Doetsch, 1984; Pons et al., 1991). Ramachandran, Rogers-Ramachandran, and Stewart (1992) examined two human patients after amputation. The patient felt his left hand when he was touched on the cheek, although his left arm had been amputated. Therefore, touch stimulation revealed the large-scale functional reorganisation after amputation. The authors suggested that, because of the spatial closeness of the cortical map representing the hand and the face area, the somatosensory input from the face areas 'intruded' on the cortical representation of the hand. The phantom limb pain is associated to, and might even be a consequence of the cortical

reorganisation in the somatosensory cortex (Flor et al., 1995). Training-induced plasticity was examined by Jenkins, Merzenich, Ochs, Allard, and Guic-Robles (1990): They trained adult monkeys to hold one or two fingertips on a revolving grooved disk, which caused heavy stimulation. After a few months of training the primary somatosensory area, which subserves the stimulated fingertips, was enlarged. The finding of a reorganisation in somatosensory cortex was supported by subsequent animal studies (Recanzone, Jenkins, Hradek, & Merzenich, 1992; Wang, Merzenich, Sameshima, & Jenkins, 1995). In a human MEG study Pascual-Leone and Torres (1993) analysed the cortical somatosensory maps subserving the hand in Braille readers. The recorded potentials were observed to be enlarged over the cortical representation for the right index finger, compared to non-Braille readers.

Studies demonstrated this potential to reorganise for the *auditory cortex* as well. An early study of the auditory cortex of guinea pigs showed that one month after cochlear lesion the cortex responded to tone frequencies next to the frequency damaged by the lesion (Robertson & Irvine, 1989). Recanzone, Schreiner, and Merzenich (1993) trained monkeys for several weeks in a frequency discrimination task. After the training the cortical representations for the trained frequencies were enlarged and this was accompanied by a better behavioural performance. Studies that altered the acoustic environment, e.g., raising rats in an environment that provided additional complex sounds (Engineer et al., 2004) or presented continuous, moderate-level noise (Chang & Merzenich, 2003), also reported reorganisation in the auditory cortex. In an MEG study, Cansino and Williamson (1997) trained three human participants with a frequency discrimination task to see if the results obtained by Recanzone et al. (1993) were transferable to humans. When the performance was correct in more than 75%, the spatial pattern of the magnetic fields differed significantly between correct and incorrect responses during the first 70 ms, indicating a training effect, which was accompanied by functional reorganisation. In an MEG study (Pantev, Wollbrink, Roberts, Engeli, & Lutkenhoner, 1999) participants listened for three hours on three consecutive days to modified music (one frequency was missing). They observed that the cortical representation for the missing frequency band was significantly diminished. The finding of cortical reorganisation in auditory cortex after auditory training has been replicated in subsequent studies (e.g., Jancke, Gaab, Wustenberg, Scheich, & Heinze, 2001; Pantev et al., 2003).

In order to investigate the *visual cortex*, Kaas et al. (1990) lesioned a part of the retina in adult cats. Weeks after the lesion recordings showed that the area, that had responded previously to the lesioned part of the retina, was now responding to retina areas that were

surrounding the lesion. This potential of the visual cortex to reorganise was also reported for humans (Baseler, Morland, & Wandell, 1999; Ross, Olson, & Gore, 2003).

However, the ability of functional reorganisation or plasticity is not a unique attribute of primary sensory areas. It has been demonstrated in many studies that the *motor cortex* shows this trait as well. Karni et al. (1995) reported that several weeks of training of a complex finger tapping task in humans improved the behavioural performance and led to functional reorganisation in motor cortex. The area of the cortex activated by the trained sequence was enlarged, compared to the untrained sequence. This study indicated training-induced plasticity in the primary motor cortex, which is presumably the underlying mechanism for acquiring new motor skills. This finding of a reorganisation in motor cortex was supported by later studies (e.g., Pascual-Leone et al., 1995).

4.1.2 Anatomical Plasticity – Morphometric Studies

Environmental factors do not only change functional representations, but also influence brain morphometry in all stages of life. In non-human mammals influences on the brain anatomy have been usually investigated by rearing rats in enriched (EC) and impoverished (IC) conditions. While EC rats lived in groups of 6-12 in large cages with stimulating objects (such as toys, boxes, ladders), social interaction, sensory and physical manipulations, as well as learning opportunities, IC rats were housed without any toys and mostly individually in normally sized cages. It was observed in these studies that an enriched environment increased the brain weight, cortical thickness, the number of glia cells, the glia to noise ratio, neural cell body, nucleus size, dendritic branching, dendritic spine density, and the number of discontinuous synapses (e.g., Cummins, Walsh, Budtz-Olsen, Konstantinos, & Horsfall, 1973; Freire & Cheng, 2004; Pascual-Leone et al., 1995; for an overview see Schrott, 1997). It was shown that the induction of synaptic plasticity, for example by stimulation, can alter the numbers or the shape of spines (for an overview see Lamprecht & LeDoux, 2004) or that sensory deprivation drives structural plasticity in dendrites (Lendvai, Stern, Chen, & Svoboda, 2000).

In a human study, Maguire and colleagues (2000) investigated the brain morphometry of London taxi drivers using voxel-based morphometry (VBM). They reported an increased grey matter volume in taxi drivers, compared to a control group, in the right and left hippocampus. Furthermore, they observed a significant positive correlation between right hippocampal grey matter volume and the number of months that the participants had worked as taxi drivers. Therefore, the authors argued that the observed changes in the right hippocampus, and

probably also in the left hippocampus, were acquired during their time working as taxi drivers.

In summary, research showed that cortical maps and cortical structures in the adult brain are not determined, as has been believed for a long time, but that instead these maps can be modified within certain limits (Buonomano & Merzenich, 1998). This ability of the brain to adapt to the environment or to be shaped by experience is called plasticity and is believed to underlie learning.

4.1.3 Neural and Molecular Correlates of Plasticity

As pointed out by Buonomano and Merzenich (1998), the present view is that cortical reorganisation and plasticity is a consequence of synaptic plasticity. In this context long-term potentiation (LTP) plays an essential role in modifying the strength of the connection between two neurons. Hebb (1949) postulated the rule that a modification in the strength of the connection between two synapses is based on activation of the pre- and post-synaptic neurons. If two connected neurons are activated simultaneously, their connection is strengthened by physiological and molecular processes. This so called Hebbian plasticity plays an important role in the cortical development and cortical reorganisation, even in adult animals and humans.

Bliss and Lomo (1973) first described LTP. They stimulated the excitatory perforant pathway of the hippocampus in the rabbit. The consequence of this stimulation was a long-term increase in the amplitude of excitatory postsynaptic potentials, so the strength of the synapses increased after stimulation. This phenomenon was termed long-term potentiation (LTP) and can be explained by Hebb's rule (Hebb, 1949). Other studies supported the finding of LTP in the hippocampus (e.g., Sastry, Goh, & Auyeung, 1986).

The N-methyl-D-aspartate (NMDA) receptors play an important role in LTP and are located at the dendritic spines of postsynaptic neurons. Glutamate is one of the important excitatory transmitters in the hippocampus. This transmitter can use NMDA and non-NMDA receptors. If the NMDA receptors are chemically blocked, for example by 2-amino-5-phosphonopentanoate, no LTP occurs. If glutamate binds to NMDA receptors and if in addition the membrane is depolarised, the blocking ions (magnesium ions) can be ejected, so that calcium ions (Ca²⁺) can enter the cell (Gazzaniga et al., 1998). The influx of calcium into the postsynaptic neuron is the decisive event in Hebbian plasticity (for an overview see Lamprecht & LeDoux, 2004). Calcium serves as an intracellular messenger, which activates additional signalling pathways, which activate enzymes, which in turn initiate gene transcription and protein synthesis. This leads to structural alterations at the postsynaptic

membrane. That way, changes in excitatory synaptic transmission are stabilised over hours and days, which might be the prerequisite for anatomical and functional plastic changes and therefore for learning.

4.2 Plasticity and Musicians

Brain mechanisms, receptive fields and even anatomical structures can be shaped by experience. This was primarily investigated in animal studies, due to obvious reasons (lesion studies, elaborate training studies, etc.). However, the studies described in Chapter 4.1 show the great potential of the brain to adapt to environmental changes.

Practising and performing music entails increased somatosensory and auditory input (Pantev, Engelien, Candia, & Elbert, 2001). Besides, musicians practise their motor abilities. Making music demands the simultaneous integration of this sensory and motor information, as well as the online supervision of the performance. Considering that average professional musicians start to play their musical instrument at a very early age, when their brain is still developing, and practise for several hours each day over years (long-term, intense training), they provide a perfect model to investigate plasticity (Munte et al., 2002; Pantev, Engelien et al., 2001; Schlaug, 2001).

4.2.1 Anatomical Differences Between Musicians and Nonmusicians

Schlaug, Jancke, Huang, Staiger, and Steinmetz (1995) reported an enlarged anterior part of the corpus callosum (CC) in musicians, compared to nonmusicians, especially in musicians that started their musical training before the age of 7. Because the anterior part of the CC consists predominantly of crossing motor fibres, the authors interpreted this finding in terms of a requirement for increased inter-hemispheric communication due to complex bimanual motor tasks (to make music) in musicians. Thus, this anatomical difference could be due to musical training associated with enhanced bimanual finger motor performance. This anatomical difference between musicians and nonmusicians was also reported in other studies (Lee, Chen, & Schlaug, 2003; Schmithorst & Wilke, 2002). Hutchinson, Lee, Gaab, and Schlaug (2003) found a significant difference in cerebellar volume between male musicians and nonmusicians. In addition, the cerebellar volume relative to the whole brain volume correlated positively with the intensity of lifetime musical training in male musicians. Amunts et al. (1997) compared the structure of motor cortex between right-handed keyboard players and nonmusicians. As an indicator of the size of the motor area they used the intrasulcal length of the posterior wall of the precentral gyrus bordering the central sulcus (intrasulcal length of the precentral gyrus = ILPG) and observed a pronounced left-larger-than-right

asymmetry in nonmusicians, whereas keyboard players showed a more symmetrical ILPG. Besides, the size of the ILPG was negatively correlated with the age of musical commencement. It can be assumed that asymmetry in the motor cortices is reduced as a consequence of the decreased asymmetry between hand dexterity (Jancke, Schlaug, & Steinmetz, 1997).

By using VBM, Gaser and Schlaug (2003) found that different cerebral areas showed an increase of grey matter volume in musicians compared to nonmusicians, including the perirolandic regions, primary and somatosensory areas, premotor areas, anterior superior parietal areas, the left inferior temporal gyrus bilaterally, the left cerebellum, the left Heschl's gyrus and the left IFG. They concluded that these differences are a result of musical experience, e.g., the SPL might be involved in visual-spatial processing. Another structural peculiarity was reported by Schneider et al. (2002), who showed that professional musicians have an increased grey matter volume of the anteromedial portion of Heschl's gyrus (primary auditory cortex) compared to nonmusicians. This increased grey matter volume was correlated with musical aptitude.

4.2.2 Functional Differences Between Musicians and Nonmusicians

In a longitudinal EEG study, Altenmüller, Gruhn, Parlitz, and Kahrs (1997) investigated music learning (recognition of specific structural elements) and the associated neural activation pattern. One group was instructed verbally, one group was instructed musically, and one group served as a control group and was not instructed at all. The authors reported an increase of activation of the frontotemporal brain regions (in the group that had been verbally instructed) and an enhancement of activation of the right frontal and of bilateral parietal lobes (in the group that had received musical instructions) after learning. They concluded that musical training influences the neural activation pattern during a music decision task and that these activations are furthermore dependent on the applied instructions or strategies.

Pantev et al. (1998) used functional magnetic source imaging to record auditory evoked fields (AEF) in order to investigate the cortical representation of piano tones and pure tones in the *auditory cortex* of musicians and nonmusicians. The dipole moments for piano tones were enhanced about 25% in musicians, compared to nonmusicians. This was not observed for the pure tones. The fact that the enlargement was correlated with the age of musical commencement indicates that these differences are a consequence of musical training and that use-dependent functional reorganisation has taken place. In a further experiment, Pantev, Engelen et al. (2001) presented tones with different timbre (trumpet and violin) to trumpet and violin players. Musicians showed increased dipole moments for tones that were played by

their instrument. This suggested an experience-dependent effect, which is a result of musical training and the altered acoustic environment (Pantev, Roberts, Schulz, Engelien, & Ross, 2001).

Studies described different components of *event-related potentials* (ERPs) to be different in musicians and nonmusicians. Schneider et al. (2002) reported, in an MEG study, that the amplitude of an ERP component evoked in primary auditory cortex (A1) was increased in professional musicians compared to nonmusicians (19 ms to 30 ms after stimulus onset). This difference was not observed for the late N100 component. The anatomical (increased grey matter volume of the anteromedial portion of Heschl's gyrus in professional musicians) and the functional finding (increased early auditory cortical responses in professional musicians) were highly correlated with musical aptitude. Koelsch, Schroger, and Tervaniemi (1999) presented violinists and nonmusicians with major chords and single tones. Some of the chords were slightly impure, leading to an MMN in musicians, an ERP component that reflects a cerebral automatic change-detection response. The component was present even during an ignore condition when musicians were reading a book. In contrast, this component was not observed in nonmusicians. Therefore, this study reported the first indication for superior pre-attentive auditory processing in musicians. In a subsequent experiment, Koelsch, Schmidt, and Kansok (2002) showed that the amplitude of the ERAN, as a response to music syntactic processing, was larger in musicians, as compared to nonmusicians. Because musicians have explicit and implicit knowledge about musical structures, their expectations are more specific and the violations of the musical structure are more obvious to them, which might have led to the larger amplitude in the ERAN. Differences in electrophysiological correlates observed during auditory tasks between musicians and nonmusicians have been reported by many studies in adults (Besson, Faita, & Requin, 1994; Pantev et al., 2003; Tervaniemi, Just, Koelsch, Widmann, & Schroger, 2005) and even in children (Shahin, Roberts, & Trainor, 2004).

Using fMRI, Gaab and Schlaug (2003) compared cerebral activation during a pitch memory task between musicians and nonmusicians, who were matched for behavioural performance in this pitch memory task. For musicians they reported more activation of the PT (more right-sided), the supramarginal gyrus (SMG), and the SPL bilaterally. Nonmusicians employed more areas known to be involved in pitch discrimination (e.g., Heschl's gyrus) and regions known to subserve memory functions (e.g., hippocampal gyrus). This study indicated perception and processing differences for tonal WM between musicians and nonmusicians that are not due to performance differences. Koelsch et al. (2005) reported that the strength of activation of the IFG (BA 44) during listening to irregular chords (contrasted against regular

chords) was correlated with musical training. The IFG is an area, which is thought to be involved during music syntactic processing (see Chapter 2.3.1).

Because of the increased *motor training*, which is associated with musical training, researchers investigated the functional representations in musicians and compared them to nonmusicians. Nonetheless, the results gained for the potential functional reorganisation in the motor domain are still contradictory. Some studies reported an increase and some a decrease of activation associated with an increase in motoric dexterity. Krings et al. (2000) compared four right-handed piano players with matched nonmusicians, while participants performed a complex motor task with the dominant hand. Accuracy did not differ between the two groups. Surprisingly, although piano players showed a faster performance (increased dexterity), authors observed a lesser degree of activation. Musicians and nonmusicians were evaluated by Hund-Georgiadis and von Cramon (1999) while they performed a complex finger tapping task for 35 min during an fMRI session. All subjects improved their tapping frequency. The learning process in piano players was accompanied by increased activation in the contralateral primary motor hand area, in secondary motor areas, in premotor and somatosensory as well as cerebellar cortices. In contrast, nonmusicians involved more ipsi- and bilateral primary and secondary motor regions, while the activation of primary motor cortex (M1) decreased during the trainings session. In another fMRI study, Jancke, Shah, and Peters (2000) investigated two piano players and two matched controls during a finger tapping task. They observed that musicians involved primary and secondary motor areas to a lesser degree compared to nonmusicians. The authors suggested that the musical training resulted in an increased hand dexterity, which is coupled with greater efficiency. This greater efficiency is reflected in the cerebral activation pattern by decreased activations. They proposed a ‘degree of freedom’ theory: Nonmusicians used a more voluntary motor control of their movements in this task, while musicians used an automatic strategy to control their movements. Therefore, fewer neurons were necessary for musicians to conduct their movements, compared to nonmusicians.

The increased motor training while playing a musical instrument necessarily entails enhanced somatosensory input. The first study that showed differences in the *somatosensory* organisation between musical experts and novices was conducted by Elbert, Pantev, Wienbruch, Rockstroh, and Taub (1995). Using magnetic source imaging, they found that the representations of the fingers of the left hand in musicians were increased, compared to those in nonmusicians. Furthermore, the size of the cortical representation correlated negatively with the age of musical commencement. Therefore, this study showed an use-dependent

plasticity in the somatosensory cortex induced by musical training. Ragert, Schmidt, Altenmüller, and Dinse (2004) reported that professional pianists showed significantly reduced tactile discrimination thresholds, induced by musical training. In a follow-up experiment they attempted to improve tactile discrimination performance in pianists by using a Hebbian learning protocol: By coactivating a skin area of the tip of the right index finger (Hebb rule) they elicited synchronous neural activity. The improvement in spatial discrimination was larger in musicians than in nonmusicians, and was furthermore correlated with the amount of daily practise during the years of intense musical training. The authors concluded that these results indicate superior learning abilities in musicians, which are accompanied by the ability of plastic reorganisation, indicating 'meta-plasticity' in musicians.

This large amount of findings that describe anatomical and functional cerebral differences between musicians and nonmusicians points to the conclusion that these changes are a result of, and not a prerequisite for, musical training. For example, the correlation with the years of musical training with an the anatomical size of an investigated structure or a physiological response (Amunts et al., 1997; Elbert et al., 1995; Ragert et al., 2004) or differences between musicians playing different instruments (Munte, Nager, Beiss, Schroeder, & Altenmüller, 2003; Pantev, Roberts et al., 2001) suggest that these differences are the result of musical training. Thus, a very specific environment seems to lead to very specific changes in the brain.

4.3 Training, Plasticity and Working Memory

There are only a few studies, which have looked at the influence of training on the neural pattern of WM organisation (Jansma, Ramsey, Slagter, & Kahn, 2001; Olesen, Westerberg, & Klingberg, 2004). Jansma et al. (2001) used a Sternberg paradigm in order to investigate practise effects on verbal WM. Participants practised one task, whereas a similar task was not practised. In their behavioural pretests the authors described a shift from a controlled to an automatic processing in the practised task, which was accompanied by a decrease of reaction time (RT) and error rate. They observed that this shift (controlled to automatic processing) was reflected in an overall decrease of activation in WM related brain areas (DLPFC bilateral, right superior frontal cortex and right frontopolar area, and the supplementary motor area (SMA)). There was no area observed, which showed more activation when the practised task was compared with the unpractised task.

Three participants trained a visuospatial WM task for 20, 24 and 30 days in an experiment conducted by Olesen et al. (2004). Before and after the training period, an fMRI scan was

conducted while participants performed the task. An increase after WM training in the following brain regions was reported: right middle frontal gyrus, right IPL and in the IPS bilaterally. In a follow-up experiment the authors trained participants in a more challenging visuospatial WM task, and they were scanned five times during the training period. During the training the participants improved their behavioural performance. The following structures, among others, showed an increase in activity over the course of the WM training: the SPL bilaterally, the right IPS and the IPL bilaterally. Therefore, the authors concluded that this WM training induced changes in brain activation pattern, mostly related to frontal and parietal regions. These studies showed that after the training of WM processes the underlying neural correlates change.

4.4 Summary

The large amount of plasticity studies (e.g., Kaas et al., 1990; Merzenich et al., 1984; Pascual-Leone et al., 1995; Ramachandran et al., 1992; Recanzone et al., 1993; Schrott, 1997) and the numerous studies, which described plasticity in musicians (e.g., Amunts et al., 1997; Koelsch et al., 1999; Munte et al., 2002; Pantev, Roberts et al., 2001; Schlaug, 2001; Schneider et al., 2002) showed that musicians are excellent human participants to study brain plasticity. In addition, potential training-induced alterations in the brain activation pattern related to WM are still not fully understood. This dissertation explored the potential effect of training on WM processes and their underlying neural correlates.

Chapter 5

Absolute Pitch

5.1 Definition

Absolute pitch (AP) is defined as the ability to identify any pitch of the Western musical scale without an external reference tone (Miyazaki, 1988; Takeuchi & Hulse, 1993). The AP ability has to be distinguished from relative pitch. Relative pitch (RP) is defined as the ability to identify the standard tonal intervals (Siegel & Siegel, 1977) and is usually possessed by professional musicians.

Although AP has fascinated researchers for many decades, we do not fully understand the underlying perceptual and/or cognitive mechanisms, the neural correlates or the relative contributions of genetic and non-genetic factors that are important for the AP phenotype (e.g., Drayna, Manichaikul, de Lange, Snieder, & Spector, 2001; Keenan, Thangaraj, Halpern, & Schlaug, 2001; Profita & Bidder, 1988; Schlaug, Jancke, Huang, & Steinmetz, 1995; Takeuchi & Hulse, 1993).

5.2 Phenotype

AP is an automatic and effortless ability, qualifying it as a form of perceptual expertise (Levitin & Rogers, 2005). However, there is evidence that AP does not necessarily contribute to a better musical performance. This is due to the fact that relative pitch cues are very important for music, but AP musicians tend to use absolute cues, even if this is disadvantageous, e.g., while identifying intervals (Miyazaki, 1993) or transposed melodies (Miyazaki, 2004). In addition, studies have shown that there are certain limitations of the AP ability. For example, the unique quality of the sound of a specific instrument is defined by the timbre (Takeuchi & Hulse, 1993). Absolute pitch identification is usually better for piano tones than for pure tones, because AP possessors are able to use the additional timbre information (Miyazaki, 1989; Takeuchi & Hulse, 1993). Furthermore, AP possessors identify pitches faster and with more accuracy in central pitch registers (Miyazaki, 1989; Takeuchi & Hulse, 1993), a phenomenon which has been termed the ‘effect of pitch register’ (Takeuchi & Hulse, 1993). AP musicians can identify musically important tones (e.g., tones in C-major mode) faster and more accurately (Miyazaki, 1988). And it has been reported that AP possessors are significantly faster in identifying white key notes compared to black key notes (Miyazaki, 1988), which could be due to two reasons: (i) children learn white key tones usu-

ally before they learn the black-key pitches (early learning theory) or (ii) because the white-keys are more common and are used more often (Takeuchi & Hulse, 1993). AP musicians often make semitone mistakes and octave errors (Takeuchi & Hulse, 1993). Because pitch class identification and octave identification are different processes (Takeuchi & Hulse, 1993), it is suggested to disregard semitone mistakes and octave errors when testing AP.

5.3 Prevalence: The Nature – Nurture Controversy of AP

Genetic and environmental contributions to AP are very difficult to disentangle. Profita and Bidder (1988) observed a significant family incidence and claimed that genetic mechanisms play a role in the acquisition of AP. They proposed that a ‘Mendelian mechanism’ could explain the high family incidence found in their study. Ten years later, Baharloo, Johnston, Service, Gitschier, and Freimer (1998) sent surveys to music schools and concluded, based on the results, that early musical training seems to be necessary but not sufficient. Gregersen, Kowalsky, Kohn, and Marvin (1999) reported a large variability in AP prevalence among different student populations, e.g., they showed a larger prevalence among Asian students of music. More AP possessors in this study had parents with AP (6.5%) compared to musicians without AP (1.6%). But the authors emphasised that these results are based on self reports and should therefore be treated as preliminary findings. Drayna et al. (2001) realised a twin study using the Distorted Tunes Test, in which 284 pairs of twins had to recognise deviant notes in well-known melodies. The authors suggested a high heritability for the performance of pitch recognition abilities. But a high family incidence supports both the early learning (environmental) view as well as the genetic view. There are numerous facts which emphasise that early learning plays a role in AP:

- There is a negative correlation between the age of musical commencement and AP ability (Baharloo et al., 1998; Gregersen et al., 1999; Miyazaki, 1988; Takeuchi & Hulse, 1993; Vitouch, 2003),
- the probability is higher that young children develop the ability of AP, compared to older children (Russo, Windell, & Cuddy, 2003; Takeuchi & Hulse, 1993),
- a shift takes place in children from using absolute to relative pitch cues, because relative pitch cues are more important for the acquisition of language and music (Saffran & Griepentrog, 2001; Takeuchi & Hulse, 1993),
- the learning environments between AP musicians and RP musicians differ: The probability of an environment that facilitates the development of AP is higher in

AP musicians (e.g., the access to fixed pitch instruments), compared to RP musicians (Bahr, 1998), and

- the congenitally and early blind show an increased prevalence of AP (Vitouch, 2003).

But why do some people fail to develop AP even though they might start their musical training at a very early age? There are some ideas that it is not only important that musical training is given at a very early age, but also how this musical training is designed. Usually musical training focuses on the relative pitch dimension, which can even inhibit the development of AP (Levitin & Zatorre, 2003). However, it might be crucial to learn to associate musical note names with certain pitches in order to develop AP (Levitin & Zatorre, 2003; Takeuchi & Hulse, 1993; Vitouch, 2003). There are some attempts by adults to learn AP, with the result of improving their pitch identification ability. But there is no study known in which an adult acquired AP through training and reached the same proficiency, in terms of accuracy, speed, and effortlessness, as AP possessors (for an overview see Takeuchi & Hulse, 1993).

5.4 Heterogeneity of AP

Profita and Bidder (1988) suggested that AP is an ‘one-or-nothing quality’ – a view that is controversial. There are many studies that questioned this hypothesis. For example, Halpern (1989) asked participants to hum or sing the first pitch of well-known tunes, after participants had imagined these tunes. She found that nonmusicians are able to store absolute pitch cues to a greater extent than previously believed. A study by Levitin (1994) replicated these results. Deutsch, Henthorn, and Dolson (2004) reported that native speakers of a tonal language (in this case Vietnamese) had a surprisingly high pitch consistency when producing certain words. Therefore, the authors assumed that they must possess a stable and precise internal pitch template. Taken together, these studies indicate that even nonmusicians show a kind of latent AP, particularly speakers of a tonal language.

But also studies within the group of AP possessors reported differences in the performance or strategies of the participants. Many researchers assigned AP musicians to different groups according to their AP performance (e.g., Baharloo et al., 1998; Itoh, Suwazono, Arao, Miyazaki, & Nakada, 2005; Miyazaki, 1988). That these behavioural performance differences *within* the group of AP possessors might be based on strategy differences was shown by Renninger, Granot, and Donchin (2003). They investigated AP musicians with an auditory WM task and observed different strategies: Some AP musicians used more relative pitch cues, whereas others used only absolute pitch information. Vitouch (2003) even claimed that

AP is a gradual ability and does not have an ‘all-or-nothing’ quality. These findings support the notion that the group of AP musicians is not homogeneous.

5.5 Underlying Mechanisms of AP

In order to describe the perceptual and/or cognitive mechanisms and neural correlates of AP, researchers developed different hypotheses or emphasised different aspects: categorical perception/processing of pitch information (Rakowski, 1993; Siegel, 1974), the association of tones/pitches with verbal labels (Siegel, 1974), the use of multiple coding strategies (Zatorre & Beckett, 1989), and the assumption of internal templates of tones, which is associated with differences in neural processes during WM tasks for tonal material (Hantz et al., 1992; Klein et al., 1984; Zatorre, Perry, Beckett, Westbury, & Evans, 1998). These different hypotheses do not exclude each other.

5.5.1 Categorical Perception and Verbal Labelling

The ability of nonmusicians to make absolute judgements concerning one single sensory dimension is pretty much restricted. It is quite difficult for RP possessors to identify tones. Conversely, this is not the case with verbal stimuli. For example, the differentiation between the English consonants /d/ and /t/ is very simple for an English native speaker, although there is variation in only a single sensory continuous dimension: the voice onset time. This implies that individuals perceive and process speech information in a categorical manner. However, this is not the case for pitch or tonal stimuli. One theory is that AP musicians perceive and/or process tones in a similar categorical manner, comparable to our perception and processing of phonemes (Rakowski, 1993; Siegel, 1974; Siegel & Siegel, 1977).

Studies by Siegel (Siegel, 1974; Siegel & Siegel, 1977) and Rakowski (1993) indicated that AP musicians do not have a superior memory for tones. Siegel (1974) compared AP musicians and musicians without AP during a pitch memory task (participants had to judge two tones, separated by 5 seconds filled with tonal stimuli). Two conditions were realised: The tones which participants had to compare were either separated by $\frac{1}{10}$ (same name, different frequency) or $\frac{3}{4}$ semitone steps (different name, different frequency). The six AP musicians showed a superior performance, compared to the six RP musicians, but only when the tones were separated by $\frac{3}{4}$ semitones. There was no behavioural difference between musicians with and without AP in the $\frac{1}{10}$ semitone condition. The author concluded that AP musicians have two distinct modes for remembering tones: one verbal-categorical mode (they encode the tones verbally) and a sensory trace mode (they maintain the sensory event – pitch – for a very limited time). In the $\frac{3}{4}$ semitone condition (different name, different

frequency), they could use the verbal-categorical mode (which requires less effort). During the $\frac{1}{10}$ semitone condition this strategy did not work, therefore participants had to switch to the sensory trace mode. This indicates that AP musicians might not have a superior memory for tones (in the sensory trace mode) than musicians without AP. In a subsequent study, Siegel and Siegel (1977) compared RP musicians and AP musicians during a pitch and interval identification task. They observed that AP possessors could categorise variations in pitch on an absolute basis. Rakowski (1993) asked AP musicians ($N = 3$) to indicate the name of sine wave tones (A# or B) with varying frequency levels (each tone was separated by $\frac{1}{8}$ from the adjacent tones). Two of the three AP musicians showed categorical perception, one did not. These studies suggested that AP musicians might perceive and process tones more categorically than subjects without AP, who perceive tones on a physical continuum, but not as part of categories (Rakowski, 1993; Siegel, 1974; Siegel & Siegel, 1977).

Nevertheless, results gained by Zatorre and Beckett (1989) indicated that verbal labelling is not the key mechanism behind the AP ability. One conclusion of their experiment is that verbal and tonal information are processed by two, more or less independent, systems (Deutsch, 1970). Participants showed, while conducting tonal (with verbal interference) and verbal (with tonal interference) memory tasks, little or no effect of verbal or tonal interference during the tonal memory task. But the same participants showed strong effects of verbal interference during a verbal memory task. This result indicates that AP musicians do not necessarily rely on their labelling ability during pitch memory tasks. The authors suggested that AP musicians have a number of encoding strategies, and the verbal labelling strategy is just one of them.

But this experiment was criticised by Takeuchi and Hulse (1993), who stated that there are several points that might have been overlooked: Zatorre and Beckett (1989) did not test musicians without AP, and the experiment did not involve absolute encoding of pitch, but was rather a pitch memory task, which could have been performed by participants without AP as well (Takeuchi & Hulse, 1993). In addition, Zatorre and Beckett (1989) used piano tones, instead of sine wave tones. AP musicians can use more information when asked to name piano tones (overtones, timbre), therefore this task might have been easier, providing them with more information than just a 'sensory trace', which made the tonal memory task relatively unaffected by verbal and tonal interference.

Zatorre (2003) subdivided the ability of AP into two components. Primarily, AP possessors have very narrow fixed pitch categories and secondly, they need to associate the pitches within these categories with verbal labels. Therefore, he proposed that this skill is composed

of a perceptual component and an associative memory aspect (Zatorre, 2003). Others described AP as the ability to possess an internal template and to map the pitch to a verbal label (Levitin, 1994; Levitin & Rogers, 2005). This is very similar to the view of Zatorre (2003). Levitin and Rogers (2005) claimed furthermore that the perception categories of AP possessors for pitches are fixed, but that this does *not* affect the perception of AP musicians.

5.5.2 Working Memory and Absolute Pitch

The P300 has also been used as an electrophysiological index of WM processes (Donchin, 1981). In an EEG experiment, Klein et al. (1984) compared AP musicians and RP musicians in an auditory and visual oddball task. They observed no differences in the electrophysiological responses between both groups in the visual task, but during the auditory oddball task the P300 was smaller in AP musicians, compared to RP musicians. Furthermore, they reported a negative correlation between the performance in an AP test and the P300 amplitude: The better the subjects performed in this test the smaller was the P300. The authors proposed that AP possessors are able to compare each tone with an internal template enabling them to identify and name tones, therefore they may not need to update their WM in a tonal WM experiment, which explains the lack of the P300. This result, that AP musicians show no or a smaller P300, was replicated in different studies (Crummer et al., 1994; Hantz et al., 1992; Wayman et al., 1992), sometimes accompanied by a significantly better performance of AP musicians (Hantz et al., 1992)⁵. Though, some studies questioned the lack of WM involvement in AP musicians during a pitch memory task (Hantz, Kreilick, Braveman, & Swartz, 1995; Hantz, Kreilick, Kananen, & Swartz, 1997; Hirose et al., 2002). Renninger et al. (2003) showed that AP musicians might use two different ‘strategies’ to perform an auditory oddball task. They can rely on absolute pitch cues or they use a relative approach. Renninger et al. (2003) observed a significant correlation between the P300 amplitude in the pitch WM task and the reaction time in a RP test, indicating that the P300 might serve as a marker for the ‘strategy’ AP musicians use. The more AP musicians used relative cues during the auditory oddball task, the larger the P300. This study showed individual differences within the AP group regarding the P300, which could explain the contradictory EEG results in previous studies regarding the P300.

⁵ In most studies AP musicians and RP musicians almost performed 100% correctly, so that no difference between both groups could be evaluated (e.g., Wayman et al., 1992).

Itoh et al. (2005) conducted an experiment including two conditions: a naming task (participants were naming pitches) and a listening task (participants were vocalising “ah” when they heard a stimulus). According to their AP ability, participants were assigned to three groups: high-AP, mid-AP and low-AP. The authors observed differences between the naming and listening task in participants with a lower level of AP ability. The high-AP group did not show any substantial differences between the naming and listening task, which might be due to the automatic naming of pitches. AP musicians with a lower level of AP ability showed two parietal positivities, a P3b like component (peaking over centro-parietally electrodes between 300-450 ms) and a parietally distributed positive ‘slow wave’ (peaking after ~ 450 ms) and one frontal negativity (frontal negative slow wave), compared to the high-AP. These ERP components were interpreted to reflect processes related to RP, such as verbal labelling and WM involvement. In contrast, the high-AP group showed an unique left posterior temporal negativity (AP Negativity, peaking at 150 ms). These results indicate that RP musicians might rely more on association areas (WM), whereas AP musicians seem to rely more on primary and secondary auditory cortices. However, the localisation of the involved structures with adequate methods (e.g., fMRI) is necessary to identify the involved areas, which was one aim of this dissertation.

Using neuroimaging methods (PET) Zatorre et al. (1998) showed that the right IFG was more active in RP musicians during an interval-judgement task compared to AP musicians. The authors suggested, that this region might be responsible for tonal WM and that AP musicians therefore may not, or to a lesser extent, need to update their WM during this task compared to RP musicians. However, Ohnishi et al. (2001) conducted an fMRI experiment and observed, during a passive music listening task, a positive correlation between AP ability and an activation of the left DLPFC, an area known to be involved in WM processes.

Therefore, these results show that the degree of involvement of WM during tonal WM tasks in AP musicians is still controversially discussed.

5.6 Neural Correlates of AP

Researchers have investigated the neural correlates of AP in order to understand the perceptual and/or cognitive mechanism underlying this ability. Several neuroimaging studies have described presumed anatomical and functional brain differences by comparing AP with RP possessors.

Schlaug, Jancke, Huang, and Steinmetz (1995) revealed a greater leftward asymmetry of the planum temporale (PT) in AP musicians, which was found to be due to a significantly smaller

right PT in a replication study (Keenan et al., 2001). Using VBM, Luders, Gaser, Jancke, and Schlaug (2004) showed a grey matter asymmetry difference in the anterior region of the PT in male AP musicians compared to RP musicians. Zatorre et al. (1998) reported a larger volume of the left PT in musicians with AP, compared to a large group of right-handed RP possessors unselected for musical skills. This enlargement of the PT in AP musicians was correlated with the performance in a pitch-naming task. There are some indications that this structural marker of AP is associated with differences in the functional activation pattern when AP and RP are compared with each other. Ohnishi et al. (2001) observed a positive correlation of the AP ability and activation of the left PT during a passive music listening task. Furthermore, Zatorre et al. (1998) observed more activation in the left posterior dorsolateral frontal cortex in AP musicians than in RP musicians while they were listening passively to tones. Because this area has been reported to be related to associative learning of sensory stimuli (Bermudez & Zatorre, 2005), they concluded that the activation could reflect the association of the pitch with a verbal label. This area was only activated in RP musicians when they had to make relative judgements.

5.7 Summary

The underlying perceptual and/or cognitive mechanisms and the neural correlates of the AP ability are not fully understood (Levitin & Rogers, 2005; Schlaug, Jancke, Huang, & Steinmetz, 1995; Takeuchi & Hulse, 1993; Zatorre, 2003; Zatorre & Beckett, 1989; Zatorre et al., 1998). For example, one question that is still discussed controversially is whether AP musicians need to update their WM during a tonal WM task comparable to RP musicians (Crummer et al., 1994; Hantz et al., 1992; Hantz et al., 1995; Hantz et al., 1997; Hirose et al., 2002; Klein et al., 1984; Wayman et al., 1992). Therefore, further research is necessary to understand the rare ability of AP.

Chapter 6

fMRI Methods

This chapter aims to describe the Magnetic Resonance Imaging (MRI) method by giving a short overview of the Nuclear Magnetic Resonance (NMR) principles and the characteristics of the Blood Oxygen Level Dependency (BOLD) signal. Subsequently, the methods concerning the analysis of the MR signal are introduced. Finally, the sparse temporal sampling technique is presented that was designed to circumvent some shortcomings of the fMRI method in auditory stimulation experiments.

6.1 NMR Principles

The MRI technique takes advantage of an inherent physical property of protons and neutrons. The particles, which make up a nucleus, possess a spin (see Fig. 6.1)⁶. This spin is associated with a magnetic dipole moment, which behaves like a small magnet. Nuclei with an odd number of protons and neutrons have a net spin, whereas nuclei with an even number do not. Only nuclei with a net spin are of interest, because only they could create a detectable NMR signal. MRI mainly uses hydrogen (H) for two reasons: (i) H has only a single proton, thus it has a net spin, and (ii) there exist an extraordinary amount of these H nuclei in the human body. The magnetic dipoles of the H protons are randomly aligned in different directions (see Fig. 6.2). However, when these small magnets are placed in an external magnetic field (static), they align in parallel (lower energy state) or anti-parallel (higher energy state) fashion to the magnetic field. More spins will align to the parallel direction. The spins precess around the field axis (z). The frequency of this precession is called the Larmor frequency (ν_0), which can be expressed by the following equation: $\nu_0 = \gamma B_0$. B_0 is the main magnetic field strength and γ is the gyromagnetic ratio (this value is constant and differs in accordance to different types of nuclei).

The local equilibrium magnetisation M_0 is the difference between both types (parallel and anti-parallel) of aligned dipoles. By placing the magnetic dipoles of the H nuclei in the external magnetic field (B_0), a macroscopic magnetisation is created (M_0), which is aligned with B_0 (see Fig. 6.3).

⁶ Figures 6.1 – 6.3 were provided by Dipl.-Ing. Torsten Wüstenberg (torsten.wuestenberg@med.uni-goettingen.de).

If a radio frequency (RF) pulse is sent, it creates an oscillating magnetic field B_1 , which is orthogonal (xy plane) to the B_0 and oscillates with the Lamor frequency of the spins. As a consequence, the net field is tipped slightly away, so that M_0 starts to precess around the new net magnetic field, creating a transverse magnetisation M_{xy} (see Fig. 6.3). When the RF pulse is switched off,



Fig. 6.1: Spin of a Nucleus

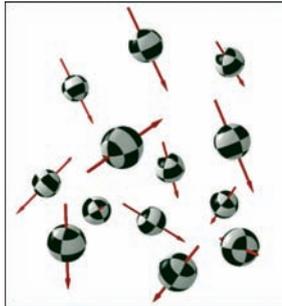


Fig. 6.2: Magnetic Dipoles of H Protons are randomly aligned

M_0 is precessing again around B_0 . The aim of the RF pulse is to tip the magnetisation over, which causes a measurable signal by inducing a current in a coil. This NMR signal is called the free induction decay (FID). After the RF pulse is turned off, the longitudinal magnetisation (M_0) recovers, while the transversal magnetisation (M_{xy}) disintegrates. These processes are called relaxation. There are two different relaxation times that play an important role for MRI measurements: T1 and T2.

T1 relaxation is the recovery process of the longitudinal magnetisation and is defined by a return of high state energy protons to low state energy protons. Over the time period T1 this ‘extra energy’ is exchanged between protons, and finally transformed into heat and thermal energy. The different density of different tissues influences the T1 relaxation time. E.g., the water in the cerebro-spinal fluid precesses at a higher rate than the Lamor frequency, therefore the T1 relaxation is slow, compared to water in the white matter that has a much faster T1 relaxation.

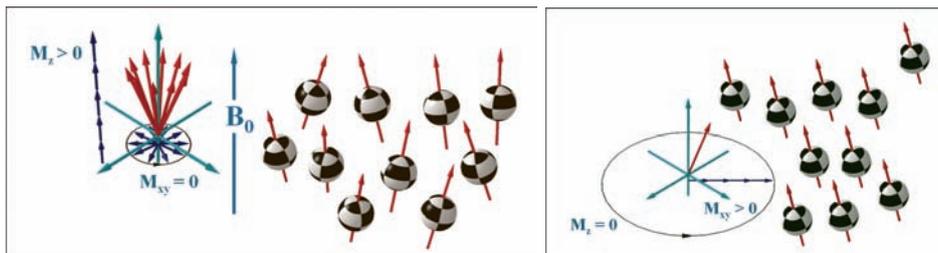


Fig. 6.3: Magnetisation (M_0) is aligned with B_0 (left), Transverse Magnetisation (right)

T2 relaxation describes the decay of the transverse magnetisation. After the RF pulse, the magnetisation that was aligned along the z-axis (longitudinal magnetisation) is tipped into the xy plane (transverse magnetisation). The T2 decay is defined as a result of random molecular fluctuations in the Lamor frequency, which finally leads to the loss of the transverse

magnetisation, whereas the $T2^*$ decay is caused by larger scale variations in the applied magnetic field⁷.

6.2 The BOLD Effect

The local sensitivity of the MR signal to local changes in perfusion and metabolism makes it possible to investigate the working human brain without invasive methods. When neural activity increases in one part of the brain, this causes, among other things, a change in blood oxygenation. Deoxyhemoglobin is paramagnetic and has therefore a different magnetic susceptibility than oxyhemoglobin, which is diamagnetic. Therefore, the susceptibility of the blood is linearly dependent on the level of oxygenation. If there is an increase of activation in one cerebral region, the relation between deoxyhemoglobin and oxyhemoglobin changes in such a way that there is a higher ratio of oxyhemoglobin (diamagnetic). This local reduction of deoxyhemoglobin (paramagnetic) causes $T2^*$ to become longer and therefore leads to a local increase in the MR signal. This BOLD effect is the basis for fMRI (Ogawa, Lee, Kay, & Tank, 1990). Although this BOLD effect is very frequently used to map the healthy human brain, it should be noted that it is not a direct measure of neural activity and that the underlying mechanisms are still not fully understood (Logothetis, 2003).

6.3 Pre-processing and Statistical Analysis

The result of the fMRI scanning procedure is a time course of 3D images of BOLD signal intensity. After the image acquisition, the data has to be prepared for the statistical analysis by improving the signal-to-noise ratio (SNR). One experiment (see Chapter 7) was analysed using the software package SPM99 (<http://www.fil.ion.ucl.ac.uk/spm>), whereas the subsequent experiments (see Experiments 3A-C, Chapters 9 – 12) were analysed using the software program LIPSIA (Lohmann et al., 2001). Both programs have the same or very similar underlying approaches (except the coregistration). In the following section, the essential pre-processing implementations and the statistical analysis of these programs are introduced.

Motion correction – Even very slight movements of the participants can cause motion artefacts. This occurs even more so, when the duration of the experiment is quite long, as is the case when a sparse temporal sampling design is used (see Chapter 6.4). Therefore, it is important to correct for motion artefacts by applying a motion correction. The movement

⁷ For more detailed information please see Buxton (2002) and Jezzard, Matthews, and Smith (2001).

correction involves an estimation of the movement (translatory and rotatory parameters) relative to a reference scan (usually the first scan). Then the later scans are realigned, based on those estimates.

Slice timing – The functional slices are acquired in a sequential order, which results in slightly different acquisition times for each slice. This can cause problems in the statistical evaluation of the data and is corrected by shifting each voxel of each slice backwards in time to simulate a simultaneous acquisition of all slices.

High-pass and low-pass filtering – To increase the signal-to-noise ratio (SNR) it is necessary to remove low frequency drifts as well as high frequencies, which might be due to noise, from the fMRI signal. This is done by the application of a Fast Fourier Transformation (FFT), which cuts out frequencies that are too high (low pass filter) or too low (high pass) to be associated with the BOLD signal.

Spatial smoothing – By smoothing, the MR images are convolved with an isotropic Gaussian kernel. There are several reasons for smoothing fMRI data. Firstly, it increases the SNR, because the noise has a higher spatial frequency compared to the neurophysiological effects of interest (because noise is, in contrast to the signal, independent for each voxel). A second objective is that after the smoothing the data conform more closely to a Gaussian field model. This is important for analysing statistical interferences by using the theory of Gaussian fields. The third reason for smoothing concerns the intersubject averaging. Smoothing decreases the spatial resolution, however, in a meaningful sense: A mapping of a function onto anatomy is only reasonable at a resolution where individual differences still play a role.

Coregistration – The coregistration is used to map the functional images onto an anatomical reference. In LIPSIA the registration is performed in two steps: (i) a transformation matrix is computed that registers the anatomical slices with the 3D data set (by finding the six parameters that realise an optimal match between the 3D reference and the 2D structural slices). This matching metric is realised by a voxel-wise linear correlation coefficient. The matrix describes a rigid, affine linear transformation (three translational and three rotational parameters) and (ii) this computed transformation matrix is subsequently applied to the functional data.

In SPM99 the between modality coregistration is done in three steps: (i) determining the affine registration allows the mapping of images onto the template⁸ (by minimisation of the sum of squares differences, rigid body transformation), (ii) then the images are segmented or partitioned, using the probability images and the modified mixture model algorithm and

⁸ The template used in SPM is the individual anatomical image of the participant.

(iii) finally the image partitions are coregistered using the rigid body transformations. The accuracy of the registration can be visually controlled in both programs.

Normalisation – Because of the anatomical variability of the brain between subjects, the fMRI data is then transformed to a standard anatomical space (e.g., Talairach and Tournoux, 1988). There are two types of normalisations: linear and non-linear normalisation. During linear normalisation, the data set is linearly scaled to a standard size by a rigid body transformation (six parameters: three translations and three rotations). In non-linear (spatial) normalisation an anatomical 3D data is matched onto another 3D reference template or into a standard anatomical space (Talairach & Tournoux, 1988) by calculating a deformation field (which contains the vectors necessary to warp one image into the other).

Statistical analysis or the General Linear Model (GLM) – The statistical analysis in LIPSIA and SPM99 is based on the GLM (Friston et al., 1998; Friston, Holmes, Poline et al., 1995; Friston, Holmes, Worsley et al., 1995). The GLM is an equation that relates the observed signal change to the expected signal change, by expressing the observed variable as a linear combination of explanatory components and a residual error term. Importantly, this model predicts that the error term is not systematic, but independent and therefore normally distributed.

6.4 Sparse Temporal Sampling

Auditory experiments in the fMRI environment are challenging due to the scanning noise. This noise is a result of the interaction of the gradients in the main magnetic field (Belin, Zatorre, Hoge, Evans, & Pike, 1999; Cho et al., 1997; Counter, Olofsson, Grahn, & Borg, 1997; Shellock, Ziarati, Atkinson, & Chen, 1998). This loud MRI acquisition may interfere with the experiment on different levels. First of all, the noise can reach a loudness of more than 100 dB (Cho et al., 1997), therefore the noise itself can cause activation in the brain (Hall et al., 1999; Shah, Jancke, Grosse-Ruyken, & Muller-Gartner, 1999). Passive protection (head phones, ear plugs) can only reduce this noise by approximately 25-40 dB (Ravicz & Melcher, 2001), but cannot eliminate the indirect acoustic transmission by body structures (Cho et al., 1997). Therefore, it is complicated to differentiate the cerebral activation caused by the scanner noise from the activation, which is due to the experimental auditory stimulation (Bandettini, Jesmanowicz, Van Kylen, Birn, & Hyde, 1998; Belin et al., 1999; Hall et al., 1999; Robson, Dorosz, & Gore, 1998). Second, due to the acoustic structure of the NMR signal (Hall et al., 1999), it can mask stimuli with different acoustic structures, e.g., music and speech (Bandettini et al., 1998; Belin et al., 1999; Hall et al., 1999; Shah et al.,

1999). Third, the noisy MR environment is problematic in so far that the participants have to intensively focus on the auditory task to perform it, because they have to separate the auditory stimuli from the background scanner noise. This might increase activation in attention related brain areas, even though under silent circumstances these areas would not be necessary to solve the task (Belin et al., 1999). Fourth, the increased activity induced by the scanner noise makes it more difficult to detect stimulus induced activity statistically (Hall et al., 1999). In addition, Novitski et al. (2003) showed in an ERP experiment, in which they used tape-recorded fMRI noise, that although the fMRI noise did not affect RT and the error rate during an auditory WM experiment, it influenced the ERP components.

To avoid these problems a variation of a 'sparse temporal sampling' technique (Belin et al., 1999; Hall et al., 1999) was used in this dissertation. Two aspects are important for this design. Firstly, there are less images acquired, which is associated with less scanning noise. Secondly, the images are acquired very rapidly, i.e. one scan can be acquired in less than 2 s. This technique, which is termed 'bunched acquisition' or 'clustered volume acquisition', was introduced by Edmister, Talavage, Ledden, and Weisskoff (1999). All in all, this resulted in short periods of scanning noise and long periods of silence, therefore auditory stimulation could be presented in the absence of scanning noise⁹. Hall et al. (1999) and Belin et al. (1999) were the first who conducted experiments with the sparse temporal sampling design by using increased repetition time (TR) (Belin et al. (1999) = 10 s; Hall et al. (1999) = 14 s). Hall et al. (1999) compared sparse temporal sampling and a continuous scanning technique. They reported that the sparse temporal sampling technique is equally effective in investigating the auditory cortex and that the magnitude of the T2* signal is increased due to a greater recovery between the scans (longer TR). Nebel et al. (2005) observed that sparse fMRI was effective in detecting the main primary auditory activation. Furthermore, they observed comparable signal changes with both methods.

The obvious main advantage of this technique is that the auditory stimuli can be presented in the absence of scanning noise (Belin et al., 1999; Hall et al., 1999). In this way, most of the above mentioned problems can be avoided and the participants should experience less stress due to the reduced background noise. In addition, this technique allowed a more sophisticated comparison of WM processes between musicians and nonmusicians, because a continuous scanning design might have been an advantage for musicians, who learned during their musical training to separate musical stimuli from background noise.

⁹ For the specific scanning paradigms for the different experiments please see chapter 7 and 9.

However, there are disadvantages associated with this method as well:

- The duration for the experiment was lengthened, which might result in less motivated participants and increased motion artefacts,
- less images were acquired, which decreased the statistical power and also reduced the temporal resolution, and
- it is still possible that there was an interaction between acquisition noise and auditory stimulation (Belin et al., 1999).

A modified version of a sparse temporal sampling technique was used in this dissertation. In addition, the stimulation of the auditory presentation was shifted in time (relatively to the TR) to (i) investigate the time course of the hemodynamic response (Gaab, Gaser et al., 2003), (ii) to avoid habituation effects (Belin et al., 1999) and (iii) to allow an optimal investigation of the BOLD response.

Chapter 7

Experiment 1 – Neural Correlates of Absolute Pitch

7.1 Introduction

Although AP has fascinated researchers over several decades, the underlying perceptual and cognitive mechanisms as well as the neural correlates of this unique ability are still not fully understood (Levitin & Zatorre, 2003; Saffran & Griepentrog, 2001; Schlaug, Jancke, Huang, & Steinmetz, 1995; Zatorre, 2003; Zatorre et al., 1998; see Chapter 5). Several studies suggested that AP musicians perceive tones more categorically than subjects without AP, who seem to perceive tones on a physical, but category independent, continuum (Rakowski, 1993; Siegel, 1974; Siegel & Siegel, 1977). Anatomical and functional studies suggested the left PT (Keenan et al., 2001; Luders et al., 2004; Ohnishi et al., 2001; Schlaug, Jancke, Huang, & Steinmetz, 1995; Zatorre et al., 1998) and the left posterior dorsolateral frontal region (Zatorre et al., 1998; see Chapter 5.6) as the underlying correlate of AP. As already mentioned, there are contradictory results regarding the degree of WM involvement in AP musicians during a pitch memory task (Crummer et al., 1994; Hantz et al., 1992; Hantz et al., 1995; Hirose et al., 2002; Klein et al., 1984; Wayman et al., 1992; see Chapter 5.5.2).

Thus, there is still some uncertainty, at least from functional brain studies, whether the AP ability can be attributed to a difference in cognitive strategies (e.g., the comparison of the tone with an internal template or learning to associate tones with verbal labels) or to differences in the perceptual and early encoding phase of pitch information (which, eventually, could be followed by a second step, in which labels are associated to pitches).

Using a pitch memory task, an fMRI experiment¹⁰ was designed in order to investigate the neural network differences between AP and non-AP¹¹ musicians, contrasting an early perceptual and a WM phase. By investigating the perceptual and cognitive phase differently, it was intended to investigate at which level (on an earlier perceptual level or on a later cognitive processing level) AP musicians show differences to RP musicians.

¹⁰ The data for this experiment was acquired at the BIDMC/Harvard Medical School (Boston, USA) under the supervision of Prof. Dr. G. Schlaug.

¹¹ The term non-AP musician and RP musicians is used synonymously in this dissertation.

7.2 Hypotheses

It was hypothesised that:

1. AP musicians show a superior performance in this tonal WM task (Hantz et al., 1992; Siegel, 1974),
2. AP musicians, compared to non-AP musicians, show stronger activation of the PT (Luders et al., 2004; Ohnishi et al., 2001; Schlaug, Jancke, Huang, & Steinmetz, 1995; Zatorre et al., 1998) and the posterior DLPFC (Ohnishi et al., 2001; Zatorre et al., 1998), and
3. Non-AP musicians display an enhanced involvement of classical WM areas, like the ventrolateral prefrontal cortex (VLPFC) and parietal areas (Itoh et al., 2005; Klein et al., 1984; Zatorre et al., 1998).

7.3 Methods

7.3.1 Participants and AP Testing

10 AP musicians and 10 non-AP musicians (mean (M) age = 25.33 years, standard error of mean (SEM) = 0.947, age range: 18-40 years) participated in this study, that was approved by the institutional review board of the Beth Israel Deaconess Medical Center (Boston/USA). None of the participants reported any neurological or psychiatric disorder. AP and non-AP musicians were matched for handedness using a standard handedness questionnaire (Annett, 1970) and a tapping test to assess hand dexterity (Jancke, 1996). 18 participants were right-handed and one in each group was ambidextrous. Since Gaab, Keenan, and Schlaug (2003) observed gender effects in a pitch memory task and Luders et al. (2004) showed slight anatomical differences between male and female AP musicians, it was decided to recruit only male musicians for this study in order to reduce inter-subject variability. In addition participants were asked to fill out a Musical Experience/AP questionnaire (see Appendix: Musical Experience and AP questionnaire) to gather information about their musical experience and their AP ability.

AP testing – AP was confirmed using an established test (Keenan et al., 2001; Ward & Burns, 1982; Zatorre & Beckett, 1989) in which individuals had to name 52 sine wave tones. Each sine wave tone had an overall duration of 500 ms with an attack and decay rate of 50 ms. The AP test consisted of 13 tones (F#4 to F#5). Each tone was presented four times, resulting in 52 sine wave tones. In accordance with previous studies (Keenan et al., 2001; Takeuchi & Hulse, 1993; Ward & Burns, 1982) answers within one semitone of the presented pitch were

regarded as correct answers. Participants had an accuracy of more than 90% on this AP test. Participants, who reported to have no AP, did not perform the AP test.

7.3.2 Experimental Paradigm

AP and non-AP musicians listened to either a 6 or 7 tone sequence (total duration of 4.6 seconds for each sequence) and were asked to make a decision whether or not the last or second-to-last tone (as indicated by a visual cue) was “same” or “different” from the first tone. Participants indicated their answers by pressing a button (see Fig. 7.1). All tones were taken from a frequency range of 330 (E4) to 622 (D#5) Hz. The difference in frequency between the target and the probe tone was between 41.2 to 64.2 Hz and the frequency range from the lowest to the highest tone in all sequences was not more than 108 Hz. Target tones corresponded to the frequencies of tones of the Western musical scale (based on A = 440 Hz) and ranged in frequency from 330 (D#4) to 622 (D#5). The distractor tones between a target and a probe did not correspond to fundamental frequencies of the tones from the Western musical scale. It was chosen to vary the total number of tones (6 or

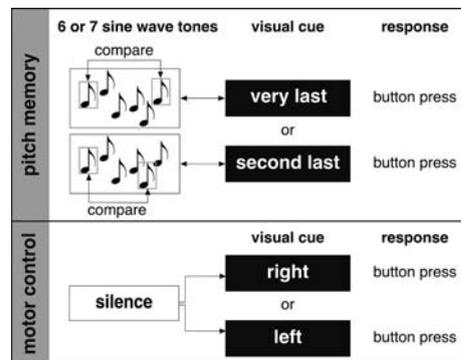


Fig. 7.1: Pitch Memory Task

7 per sequence) and the comparison to be made (second-to-last tone or last tone with first tone) across sequences to reduce the possibility that participants could ignore the interfering tones. The sequence length was kept constant for the 6 and 7 tone sequences by inserting a short silence period prior to the first tone for the 6 tone sequence. The pitch memory task was contrasted with a motor control condition in which no auditory stimulation took place and participants only pressed the right or left button as indicated by a visual cue (for more details see Gaab, Gaser et al., 2003). All subjects were familiarised with the pitch memory task for approximately 10 min prior to the actual fMRI session using samples of the stimulation material. The behavioural performance during the fMRI session was calculated as a percentage of correct responses/all responses.

7.3.3 fMRI Image Acquisition and Analysis

Functional magnetic resonance imaging (fMRI) was performed on a Siemens Vision 1.5 Tesla whole-body MRI scanner (Siemens, Erlangen, Germany). Using a gradient-echo EPI-sequence (effective repetition time (TR): 17 s, echo time (TE): 50 ms, matrix size: 64x64) a total of 24 axial slices (4x4x6 mm voxel size) – parallel to the bi-commissural plane – were acquired over 2.75 s each 17 s. In addition, a high-resolution T1-weighted scan (1 mm³ voxel size) was acquired for coregistration with the functional images.

A spatial Gaussian filter with a FWHM (full width at half maximum) of 8 mm was used to improve the

SNR of the data. A variation of a sparse temporal sampling technique (Hall et al., 1999) with clustered volume acquisition was used to circumvent interference between auditory brain regions and scanner noise (see Chapter 6.4). Furthermore, the stimulus-to-imaging delay time was varied between 0 to 6 seconds in a jitter-like fashion to explore the time course of brain activation in response to the perceptual and cognitive demands (Gaab, Gaser et al., 2003) of this pitch memory task (see Fig. 7.2). A box-car function was applied to the fMRI time series and the pitch memory task was contrasted with the motor control task. The cut-off frequency of the temporal high-pass filter, which was used for signal baseline correction, was 1/200 Hz. Two analyses were performed. In the first analysis, all imaging time points (ITPs; MR acquisitions obtained 0-6 s after the end of the auditory stimulation) were averaged, a contrast pitch memory – motor control was calculated for each participant, and then both groups were compared with each other. In the second analysis, the ITPs were divided into two clusters (0-3 s and 4-6 s after the end of the auditory stimulation), making the assumption that the early ITPs (0-3) are more reflective of perceptual and early encoding processes, while the later ITPs (4-6) are more reflective of WM or other multimodal encoding processes (for more details see Gaab, Gaser et al., 2003). fMRI data were analysed using the SPM99 software package (<http://www.fil.ion.ucl.ac.uk/spm/>; Institute of Neurology, London, UK). For more details on the analysis of sparse temporal sampling fMRI data see Gaab, Gaser et al. (2003) and Gaab, Keenan et al. (2003).

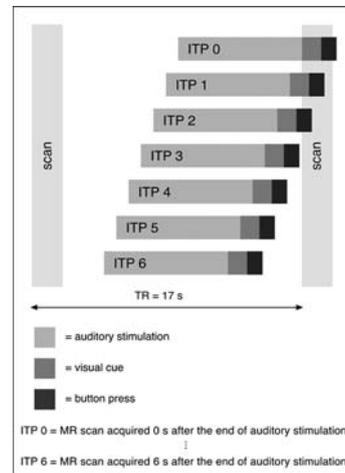


Fig. 7.2: Scanning Paradigm - (ITP = imaging time point)

7.4 Results

7.4.1 Behavioural Data

The AP musicians had a 96.92% accuracy rate ($SEM = 1.00\%$) in the AP test. Applying an independent-samples t -test, no significant difference ($t(18) = 0.693$, $p = .497$) in the age of commencement of instrumental training between the AP ($M = 7.80$ years, $SEM = 0.90$ years) and non-AP musician group ($M = 7.00$ years, $SEM = 0.72$ years) was observed.

The AP musicians ($M = 84.53\%$, $SEM = 5.59\%$) did not differ significantly from the non-AP musicians ($M = 76.32\%$, $SEM = 2.54\%$) in their performance (percent of correct answers) for the fMRI pitch memory task ($t(18) = 1.337$, $p = .198$) as revealed by an independent-samples t -test. However, one of the confirmed AP musicians showed only an accuracy of 38.30% in the fMRI task, despite the fact that this participant had an accuracy of 90% in the AP test, which employed some of the same sine wave tones. Because this participant performed as accurate as an AP musician in the AP test, it was decided to include him in the fMRI group analysis. But when he was excluded from the behavioural analysis, the performance of AP and RP musicians in this tonal WM task differed significantly ($t(17) = 3.757$, $p = .002$), with a superior performance of 89.67% ($SEM = 2.45\%$) for the AP musicians. Within the AP group no significant correlation was observed between the performance in the AP test and the number of correct answers in the experimental pitch memory fMRI task ($r = .060$, $p = .861$).

7.4.2 fMRI Data

Pitch memory vs. motor control – Contrasting the pitch memory task with the motor control task, a threshold of $p < 0.001$ (uncorr., voxel extend (k) = 10) was applied (see Fig. 7.3). Only clusters (cluster level) which showed significant activation ($p < 0.05$, corrected) are reported (see Tab. 7.1), therefore please note that not all activations displayed in Fig. 7.3 are mentioned here, because they did not reach significance on a cluster level. During the early ITPs (0-3) AP musicians showed bilateral activation of the STG, the left pre-SMA, in the IPL bilaterally, and in the cerebellum bilaterally. During the later ITPs (4-6) AP musicians activated the anterior part of the left STG, the IFG bilaterally, the right IPL, and the cerebellum bilaterally (see Tab. 7.1).

The non-AP musicians showed a similar pattern: bilateral activation of the STG, the right pre-SMA, the right pars opercularis, the right IPL, the left cerebellum, as well as the left thalamus during the early ITPs (0-3). During the later ITPs (4-6) significant activation was seen in the right IPL and in the left cerebellum.

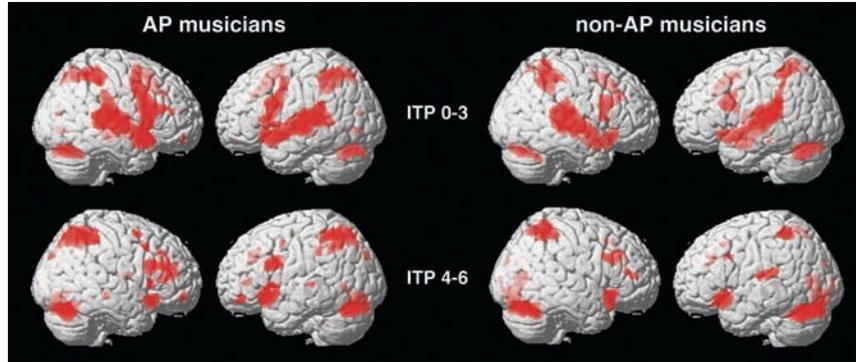


Fig. 7.3: AP and non-AP mus. – early (0-3) and late (4-6) ITPs ($p < 0.001$, uncorr., $k = 10$)

Tab. 7.1: Brain Areas activated in non-AP and AP musicians during the Pitch Memory Task, activated Clusters (cluster level $p < 0.05$, FDR) are reported for a Contrast ($p < 0.001$, uncorr.)

area	left hemisphere					right hemisphere				
	BA	x	y	z	t-value	BA	x	y	z	t-value
AP musicians, ITPs 0-3 (cluster level $p < 0.05$, $k = 10$, FDR corr.)										
pre-SMA	6	0	8	53	6.60					
IPL	40	-50	-38	50	6.32	40	53	-34	50	6.91
STG	42	-63	-23	7	14.03	42	65	-19	8	13.21
cerebellum		-24	-71	-17	5.19	30	-69	-17		7.24
						8	-31	-3		6.23
AP musicians, ITPs 4-6 (cluster level $p < 0.05$, $k = 10$, FDR corr.)										
pars opercularis/IFG	44	-51	15	21	6.52	45	51	20	21	5.43
IPL						40	48	-48	54	7.79
anterior STG	38	-51	17	-11	7.92					
cerebellum		-38	-65	-17	6.65	32	-71	-18		7.67
non-AP musicians, ITPs 0-3 (cluster level $p < 0.05$, $k = 10$, FDR corr.)										
pars opercularis/IFG						44	53	17	25	6.11
pre-SMA						6	0	14	45	6.21
IPL						40	46	-40	57	8.71
STG	42	-65	-25	12	13.77	22	63	-6	-1	12.85
thalamus		0	-11	8	6.71					
cerebellum		-32	-63	-20	6.93					
non-AP musicians, ITPs 4-6 (cluster level $p < 0.05$, $k = 10$, FDR corr.)										
IPL						40	46	-44	56	7.43
cerebellum		-36	-63	-19	8.96					

AP musicians vs. non-AP musicians – The pitch memory task was compared between AP and non-AP musicians ($p < 0.05$, voxel extent (k) = 10, uncorrected) to see the entire network that differed between both groups in this task (see Tab. 7.2 and Fig. 7.4). However, after FDR (false discovery rate) correction ($p < 0.05$, $k = 10$) the AP musicians showed significantly more activation of a region centred in the dorsal part of the left superior temporal sulcus (Talairach coordinates: -61 -18 -4, cluster = 25 voxel, black arrows in Fig. 7.4, also see Appendix Fig. A.1) compared to the non-AP musicians for the early ITPs (0-3). On the contrary, the non-AP musicians showed significantly more activation after FDR correction ($p < 0.05$, $k = 10$) of the right superior parietal lobe/intraparietal sulcus (SPL/IPS) than the

AP musicians (Talairach coordinates: 40 -42 63, cluster = 17 voxel, black arrows in Fig. 7.4, also see Appendix Fig. A.2) for all ITPs (0-6).

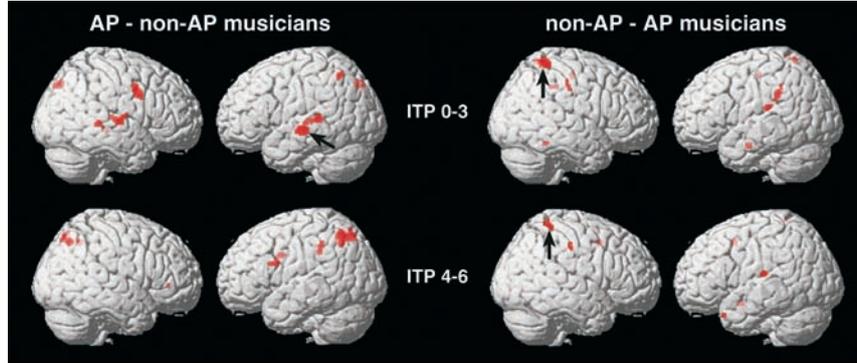


Fig. 7.4: Between-Group Contrasts ($p < 0.001$, uncorr., $k = 10$), black Arrows indicate Regions that survive FDR Corrections ($p < 0.05$).

Tab. 7.2: Comparison between non-AP and AP musicians during the Pitch Memory Task

area	left hemisphere					right hemisphere				
	BA	x	y	z	t-value	BA	x	y	z	t-value
non-AP musicians – AP musicians, ITPs 0-3 ($p < 0.001$, $k = 10$, uncorr.)										
SMA	6	0	-15	49	3.43					
postcentral gyrus						2	59	-19	40	4.16
postcentral sulcus						7	22	-45	69	3.13
SPL	7	-14	-51	65	3.59	7	30	-45	67	3.80
IPS						7/40	40	-42	63	4.57
IPL	40	-61	-39	39	3.21	40	36	-33	39	3.30
SMG	40	-63	-35	31	3.98					
STG	22	-59	-24	18	3.58					
inferior temporal gyrus	20	-42	-9	-18	3.52					
fusiform gyrus						37	44	-45	-13	3.57
thalamus		0	-8	4	4.22					
non-AP musicians – AP musicians, ITPs 4-6 ($p < 0.001$, $k = 10$, uncorr.)										
cingulate gyrus	32	-2	10	44	3.39					
postcentral gyrus						2	59	-19	40	4.10
SPL						7	36	-43	65	4.09
IPS						7/40	42	-40	61	3.75
STG	42	-63	-23	14	3.78					
	34	-24	1	-15	3.32					
anterior STG	38	-38	18	-24	3.48					
AP musicians – non-AP musicians, ITPs 0-3 ($p < 0.001$, $k = 10$, uncorr.)										
premotor cortex						6	55	7	31	4.78
						6	53	2	39	3.69
IPS	7/40	-42	-54	51	3.66					
anterior STG						22	61	-7	11	3.19
						22	65	-15	4	4.45
STS	21/22	-61	-18	-4	5.34	21/22	67	-35	4	3.67
	21/22	-65	-33	7	4.54					
	21/22	-63	-23	5	3.56					
precuneus						7	2	-76	42	3.43
brainstem						10	-31	-3		3.55
AP musicians – non-AP musicians, ITPs 4-6 ($p < 0.001$, $k = 10$, uncorr.)										
IFG	44	-50	13	21	3.54	47	28	37	-2	3.26
inferior precentral gyrus	6/44	-34	5	29	3.41					
SPL	7	-18	-66	49	4.15	7	16	-69	51	4.00
	7	-18	-56	43	3.54					
IPL	40	-40	-58	51	4.13	40	38	-64	47	3.68
	40	-46	-33	35	3.67					
precuneus						7	4	-54	47	3.54

A region of interest (ROI) analysis was performed in order to investigate these between-group differences. The clusters of voxels that showed a significant difference (after FDR correction for multiple comparisons) between groups were used to define two ROIs: a ROI in the left STS and a ROI in the right SPL/IPS. The mean regional t -values for both ROIs for each imaging time point (0 through 6) were plotted (see Fig. 7.5). The AP musicians had higher mean regional t -values in the left STS region compared to the non-AP musicians, especially during initial imaging time points (ITPs 0-3; see Fig. 7.5). The non-AP musicians had higher mean regional t -values than the AP musicians in the right SPL/IPS region during all ITPs (0-6; see Fig. 7.5).

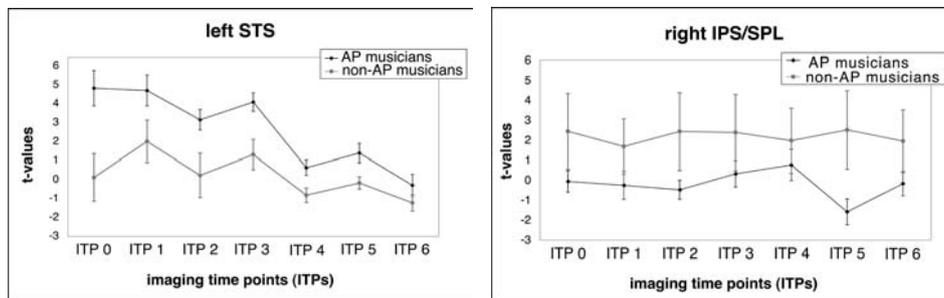


Fig. 7.5: ROI Analyses for the left STS and the right SPL/IPS

7.5 Discussion

7.5.1 Behavioural data

Commencement of musical training – No correlation was observed between the age of musical commencement and AP ability. Therefore, the result obtained by this experiment could not support the hypothesis that an early commencement of musical training increases the probability of developing AP (e.g., Baharloo et al., 1998; Miyazaki, 1988; Russo et al., 2003). On the other hand, Levitin and Zatorre (2003) pointed out that early musical training is not necessary for the acquisition of AP, because musical training enhances the ability of relative pitch, whereas only the training to relate a particular auditory stimulus consistently to a certain category would train the AP ability. Therefore, early musical commencement and AP ability might not be correlated in all cases, which is supported by the results of this dissertation.

Performance in the pitch memory task – In Hypothesis 1, a superior performance for AP musicians in this tonal WM task was postulated, but no behavioural difference was observed between RP and AP musicians. However, when an outlier was excluded from the behavioural analysis, the AP musicians showed a significantly superior performance for the

tonal WM task. This not very pronounced difference between both groups could be a consequence of the stimulus material: The distractor tones did not correspond to the frequencies of the Western musical scale (this is discussed in more detail in Chapter 12.5).

7.5.2 Pitch Memory vs. Baseline – Correlates of Tonal WM

Overall, when comparing the pitch memory task to a motor control condition, AP and non-AP musicians showed similar activation patterns that included the STG (primary and secondary auditory areas), the SPL and IPL, the posterior IFG, the pre-SMA, and superior lateral cerebellar regions. Both AP and non-AP musicians showed strong activations of primary and secondary auditory areas during the early ITPs (0-3), but hardly any activation of primary and early secondary auditory regions during the second cluster of ITPs (4-6). This supports the assumption that the early ITPs (0-3) were more representative of the perceptual and early auditory encoding phase, while the later ITPs (4-6) corresponded to higher cognitive processes such as WM or multimodal encoding. Though, considering the different hemodynamic lags for the different regions of the brain (Hall et al., 1999), it does not mean that only the observed areas are involved in the perception during this pitch memory task, but it is also possible that other areas with a longer hemodynamic lag contributed as well.

The overall activation pattern of this pitch memory task was similar to what other groups have described before (Gaab, Gaser et al., 2003; Gaab, Keenan et al., 2003; Griffiths, Johnsrude, Dean, & Green, 1999; Zatorre et al., 1994). Previous work with nonmusicians (Gaab, Gaser et al., 2003) revealed a similar brain network including the STG bilaterally, the posterior inferior frontal region bilaterally, the SPL and IPL bilaterally, the pre-SMA as well as cerebellar areas bilaterally.

AP musicians and non-AP musicians showed activation in the *IPL* during the ITPs 0-3 as well as during the ITPs 4-6. The *IPL* was shown to play an important role in short-term storage of pitch information in nonmusicians (Gaab, Gaser et al., 2003), similar to the role that this region might play in short-term storage of verbal auditory information (Baddeley, 2003; Gruber & von Cramon, 2003; Ravizza et al., 2004). The *pre-SMA* may be engaged in this process as well, since several studies reported activation of the *pre-SMA* during verbal WM tasks (Gruber, 2001; Gruber & von Cramon, 2003; Smith & Jonides, 1998).

The right *IFG* (*BA 44*) was activated in non-AP musicians and AP musicians during this tonal WM task. The posterior *IFG* (in the left hemisphere commonly referred to as Broca's region) might be involved in auditory sequence analysis and predictions of auditory events or their violations, since it has been found to be active in a variety of tasks from pitch discrimination to rhythm discrimination, musical syntax violation, pitch memory, and auditory-motor

integration (Bangert et al., 2006; Gaab, Gaser et al., 2003; Griffiths, 2001; Griffiths et al., 1999; Koelsch, Fritz et al., 2005; Koelsch, Gunter et al., 2002; Zatorre et al., 1994). Inferior frontal regions have also been shown to be involved in verbal WM tasks (Awh et al., 1996; Chen & Desmond, 2005; Fiez et al., 1996; Gruber, 2001; Gruber & von Cramon, 2003; Ravizza et al., 2004; see Chapter 3), particularly during the active rehearsal process.

The *cerebellum* was activated in both groups during both ITPs 0-3 and ITPs 4-6. The role of cerebellar areas in musical tasks is still under active investigation. It is thought that the cerebellum plays a role in the ongoing auditory discrimination tasks as tested in a pitch memory experiment (Gaab, Gaser et al., 2003; Parsons, 2001). Regional activation of the cerebellum cannot be explained by motor activity because the pitch memory task was contrasted against a motor control task. Recent research has indicated that the cerebellum subserves perceptual and cognitive functions (Paquier & Marien, 2005; Schmahmann & Sherman, 1998), such as attention (Akshoomoff, Courchesne, & Townsend, 1997), timing (Ivry, 1997), musical tempo, duration discrimination (Parsons, 2001; Petacchi, Laird, Fox, & Bower, 2005), verbal WM (Chen & Desmond, 2005; Kirschen et al., 2005), as well as tonal WM (Gaab, Gaser et al., 2003; Zatorre et al., 1994).

In summary, the results of Experiment 1 support the hypothesis that the extratemporal neural network underlying tonal WM includes mainly inferior frontal, (pre-)SMA, bilateral inferior and superior parietal and cerebellar areas (Gaab, Gaser et al., 2003; Zatorre et al., 1994).

7.5.3 AP Musicians vs. Non-AP Musicians

AP musicians differed from non-AP musicians by showing significantly more activation within a left dorsal STS region during the initial ITPs (0-3). Although it was stated in Hypothesis 2 that AP musicians should show a stronger activation of the PT, the observed result is in agreement with several electrophysiological studies. Itoh et al. (2005) reported a difference in ERPs between musicians with RP and AP in a tone listening task. They observed an early left posterior temporal negativity in AP musicians compared to RP musicians, which they termed ‘AP Negativity’ (latency 150 ms). Hirata, Kuriki, and Pantev (1999) also found support for an electrophysiological difference (N1m) in the auditory cortex between AP and non-AP musicians in a passive pitch listening task using MEG. This electrophysiological characteristic was mapped to the posterior superior temporal plane (PT), which has been found to be significantly leftward asymmetric in AP compared to non-AP musicians (Keenan et al., 2001; Luders et al., 2004; Schlaug, Jancke, Huang, & Steinmetz, 1995). Ohnishi et al. (2001) found significantly more activation of this region in a passive music listening task and related the activity in this region to performance in an AP test. How

is the left PT, the area that has been hypothesised to be stronger activated in AP musicians, related to the left STS region? First, there is a wealth of data supporting a reciprocal functional connection between both areas (Barnes & Pandya, 1992; Kaas & Hackett, 2000; Kaas et al., 1999; Morosan, Schleicher, Amunts, & Zilles, 2005; Sweet, Dorph-Petersen, & Lewis, 2005). It is possible that the PT serves as an early auditory processing region that influences the processing of auditory information in higher order auditory or multimodal sensory areas in a bottom-up process. The strong leftward structural asymmetry of the PT in AP musicians is assumed to create a functional asymmetry or hemispheric bias that facilitates the left hemispheric or left temporal processing of particular auditory information. Thus, the PT could serve as a ‘hub region’ that directs the further processing of auditory information (Griffiths & Warren, 2002). The PT as an auditory association region presumably processes elementary properties of sounds such as pitch height and spectral information (Warren et al., 2003), while the STS might be involved in the categorisation of sounds and recognition of sounds based on their elementary properties (Belin, Zatorre, Lafaille, Ahad, & Pike, 2000). Several studies described a role for the STS in the identification or categorisation of a variety of sounds (Belin et al., 2000; Binder et al., 2000; Liebenthal et al., 2005; Mottonen et al., 2006), which has immediate relevance for the pitch identification/categorisation done by AP possessors. Belin et al. (2000) found increased activation within the STS during the perception of vocal compared to non-vocal environmental sounds. Similarly, Liebenthal et al. (2005) found more activation in the left STS comparing phonemic with non-phonemic sounds. This suggests that the left STS is involved in categorical perception. This is supported by Mottonen et al. (2006). The authors investigated speech perception with ‘sine wave speech’, which can be perceived as either non-speech (before the training) or speech (after the training). They scanned the participants twice: before and after a training. During the training, the participants learned to categorise the ‘sine wave speech’ stimuli and perceive them as speech. Therefore, in both scanning sessions participants were presented with the same auditory stimuli, however, during the first scan they perceived it as non-speech and during the second scan (after the training) participants perceived it as speech. The authors reported a stronger activation of the left posterior STS when ‘sine wave speech’ was perceived as speech after the training compared to the scan prior to the training, when participants perceived the auditory stimuli as non-speech.

The proposed function of this STS region and the differential activation of this region comparing AP with non-AP musicians fits nicely with the hypothesis that AP represents a form of categorical perception (Rakowski, 1993; Siegel, 1974; Siegel & Siegel, 1977). An

alternative explanation could be, that the stronger STS activation does not reflect categorical/phonemic perception per se, but (also) verbal labelling. Although this might be possible, the finding that this difference between AP and non-AP musicians was observed during the early phase (ITPs 0-3) of the pitch memory task suggests that it is more related to perception.

Non-AP musicians showed significantly more activation of the right SPL/IPS compared to the AP musicians, as formulated in Hypothesis 3. Two alternative explanations could account for this. The first explanation is related to the potential use of WM in non-AP musicians in order to succeed in this task. Studies have shown activation of the SPL/IPS during verbal (Awh et al., 1996; Crottaz-Herbette et al., 2004; Gruber, 2001; Gruber & von Cramon, 2003) and tonal WM tasks in nonmusicians (Gaab, Gaser et al., 2003; Zatorre et al., 1994), indicating an important role of this area during WM processes. Activity in the SPL has also been shown to increase as a result of training in a WM task (Olesen et al., 2004). In addition, Itoh et al. (2005) reported, that non-AP musicians, while performing a pitch naming task, showed three ERP components, two of them over parietal electrodes with latencies of 300-450 ms (P3b) and 450-500 ms (parietal positive slow wave), and over frontal electrodes with latencies of 400 ms (frontal negative slow wave). These responses were not observed in AP musicians, who showed a prominent earlier response over temporal leads. The authors suggested that the parietal components seen in RP subjects presumably reflect relative pitch strategies related to the use of a WM strategy. As described above, several studies showed a smaller or absent P300 during tonal WM tasks in AP musicians (Crummer et al., 1994; Hantz et al., 1992; Klein et al., 1984; Wayman et al., 1992). This WM related P300 component was localised in the SPL/IPS (Moore et al., 2003). Considering these findings, the increased SPL/IPS activation in non-AP musicians may indicate a difference of WM processes between AP and non-AP musicians.

An alternative interpretation is related to the role that the SPL plays in multimodal sensory integration. Multimodal sensory integration combined with motor planning, preparation and output is of great importance for an instrumental musician (Sergent, Zuck, Terriah, & MacDonald, 1992; Stewart et al., 2003). Additionally, it has been shown that the SPL is involved in musicians during the imagination of playing an instrument (Langheim, Callicott, Mattay, Duyn, & Weinberger, 2002; Meister et al., 2004). Therefore, the enhanced activation of right SPL in non-AP musicians, compared to AP musicians, might reflect a different strategy, which either involves enhanced WM processes, e.g., the storage (Awh et al., 1996; Crottaz-Herbette et al., 2004; Gaab, Gaser et al., 2003; Gruber, 2001; Gruber & von Cramon,

2003) or the multimodal encoding (Sergent et al., 1992; Stewart et al., 2003) of this auditory information (e.g., associating the tones with visual and/or motor representations).

The differences between both groups were only marginal. This could be due to the heterogeneity in the AP group. Miyazaki (1988) divided, based on the results in a pitch identification task, participants in three different groups (precise, imprecise and non-AP), regarding their different AP ability. Renninger et al. (2003) showed that there are individual differences in the AP group, not only in their performance, but also in their strategy, which was significantly correlated to the neural responses, the P300. This indicates, that AP is not an ‘all-or-nothing’ ability, as has been already suggested in Chapter 5, but rather a gradual ability (Vitouch, 2003). This would explain interindividual differences between the AP possessors (Renninger et al., 2003), which might account for the minimal functional differences between AP musicians and non-AP musicians.

7.6 Summary

The aim of this study was to compare the neural networks for tonal perception and WM related processes between AP and non-AP musicians. Both groups showed a common activation pattern that included the STG, parietal areas, the IFG as well as the pre-SMA and cerebellar regions, when the pitch memory task was compared to a motor control condition. Interestingly, AP musicians showed more activation than the non-AP musicians in a region located in the left STS. Because this activation was most pronounced in the early perceptual phase (ITPs 0-3) of the tonal WM task, this indicates a difference in the perception of tonal information (Itoh et al., 2005; Rakowski, 1993; Siegel, 1974) between both groups. As hypothesised, the non-AP musicians differed from the AP musicians by demonstrating more activation of the right SPL/IPS for all ITPs (0-6), indicating the use of WM strategy (Awh et al., 1996; Crottaz-Herbette et al., 2004; Gruber, 2001; Gruber & von Cramon, 2003), such as visual-spatial mapping of the relevant tones (Sergent et al., 1992; Stewart et al., 2003). Therefore, this experiment indicates an important basic difference between both groups: AP musicians differ from non-AP musicians already on an early perceptual level. That is, they presumably perceive tones differently (e.g., categorical, comparable to verbal material), whereas non-AP musicians seem to engage a different WM strategy for tones.

Chapter 8

Experiment 2 – Tonal WM in AP and RP Musicians – A Behavioural Study

8.1 Introduction

When comparing the functional activation pattern of AP and non-AP musicians during a tonal WM task, the AP musicians showed stronger activation of the left STS during the perceptual period. Because this area is thought to be involved in categorical perception of verbal material (Liebenthal et al., 2005; Mottonen et al., 2006), it was hypothesised that AP musicians might perceive tonal stimuli in a more categorical way. This hypothesis has been investigated by studies supporting the notion that AP musicians perceive and process tones categorically compared to individuals without AP, who perceive tones on a physical continuum (Rakowski, 1993; Siegel, 1974; see Chapter 5.5.1). However, these experiments only investigated small numbers of participants. Siegel (1974) included six AP musicians and six non-AP musicians in her experiment, whereas Rakowski (1993) investigated three AP musicians.

The behavioural Experiment 2 was designed to further investigate whether AP musicians perceive tonal stimuli categorically. AP musicians and RP musicians listened to and remembered sequences, which consisted of ‘microtones’ (four microtones corresponded to one semitone of the Western musical scale = $\frac{1}{4}$ semitone steps). The experiment consisted of two conditions: the two microtones in a sequence, which should be compared, had a different frequency, but belonged to the same tone category (same name condition), whereas in the second condition the two tones to compare had a different frequency and a different name, i.e. belonged to a different tone category (different name condition).

8.2 Hypotheses

It was hypothesised that the AP musicians would show a superior performance (percentage of correct responses and a faster reaction time) during the different name condition compared to the same name condition (Rakowski, 1993; Siegel, 1974). By contrast, it was hypothesised that musicians without AP would not show this difference between the conditions.

8.3 Methods

8.3.1 Participants and AP Testing

20 AP musicians and 28 non AP musicians¹² were tested for their AP abilities. AP was confirmed using an established test, in which AP musicians were asked to name sine wave tones (Keenan et al., 2001; Zatorre & Beckett, 1989). Each sine wave tone had a duration of 500 ms with an attack and decay rate of 50 ms. The frequencies of all sine wave tones corresponded to the frequency of the tones of the Western musical scale. Participants were presented with these tones via headphones. The AP test 1 consisted of 13 tones (F#3 to F#4). Each tone was played four times, resulting in 52 sine wave tones to name. The AP test 2 consisted of sine wave tones taken out of a larger range of tones, from 4 ½ octaves (F2 to G5). 12 tones were taken from this range, which were separated by a musical fourth (F2, Bb2, Eb3, etc.), to avoid duplication of chroma across octaves, with large differences in frequency. The twelve tones were presented four times pseudorandomly, resulting in 48 tones to name. According to the literature, no reference tone or feedback was provided during the test (Takeuchi & Hulse, 1993). In addition, answers within a deviance of a semitone to the correct tone were regarded as correct answers (Keenan et al., 2001; Takeuchi & Hulse, 1993; Ward & Burns, 1982). Only participants who performed more than 90% correctly in the AP test 1 were classified as AP musicians. 20 AP musicians were tested: Four of them had to be excluded because they performed less than 90% correctly in AP test 1. RP musicians, which underwent the AP test ($N = 21$), gave up very quickly. 16 AP musicians (8 male, mean age 23.69 years, $SEM = 0.72$ years and age range 21-32) and 28 non-AP musicians (11 male, mean age 23.79 years, $SEM = 0.78$ years and age range 18-38) took part in this experiment. In addition, AP and RP musicians were asked to fill out a Musical Experience/AP questionnaire to gather information about their musical training and their AP ability (see Appendix: Musical Experience and AP questionnaire).

8.3.2 Stimuli and Experimental Task

Sine wave tones with a frequency range of 258.75 to 539 Hz were used in this experiment. Each sine wave tone had a duration of 400 ms, six were presented in a sequence, separated by a 300 ms period of silence, resulting in a duration of 3900 ms for each auditory sequence. The sine wave tones were generated in the following way: Each tone is defined by a certain frequency, e.g., the tone D has a frequency of 294 Hz and the tone D# has a frequency of 311 Hz. Between these two 'centre frequencies' the frequency was calculated (in this case

¹² This study was partly conducted at the BIDMC/Harvard Medical School in (Boston/USA).

303 Hz) and defined as the upper frequency border of D and the lower frequency border of D#. So each tone had an upper and lower frequency (e.g., for D the lower and upper frequency was 286 and 303 Hz). Between these frequencies four equidistant¹³ frequencies were calculated (see Fig. 8.1). Therefore, four microtones related to each semitone were designed, all of them belonged to this name

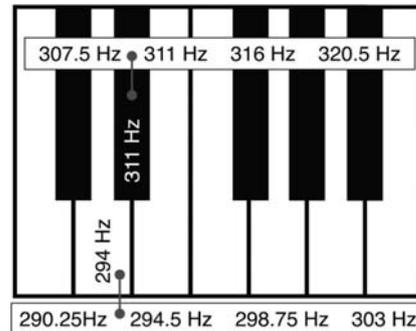


Fig. 8.1: Structure of the Microtones

category (see Appendix Tab. A.1). This procedure resulted in microtones with a distance of $\frac{1}{4}$ semitone difference between the tones. Participants listened to 104 sequences. After each sequence participants were presented with a visual cue, indicating whether they had to compare the last tone to the first tone or the second-to-last tone with the first tone in terms of pitch (Is the last/second-to-last tone higher or lower than the first tone?). Participants pressed a button (higher/lower) and after 5 s the next trial started.

This experiment consisted of two conditions:

- In 50% of the trials the first tone and the very last or the second-to-last tone had a different frequency but the same name (*same name condition*), and
- In 50% of the trials the first tone and the very last or the second-to-last tone had a different frequency and a different name (*different name condition*).

8.4 Results

Musical Experience/AP questionnaire – As revealed by the questionnaire, the AP musicians ($N = 16$) started their musical training at a mean age of 6.94 years ($SEM = 0.59$ years). The mean age when AP was discovered was 9.45 years ($SEM = 1.33$ years). The RP musicians ($N = 28$) started their musical training at the mean age of 6.18 years ($SEM = 0.38$ years). An independent-samples t -test did not reveal a significant difference in the age of musical commencement between both groups ($t(42) = 1.130, p = .265$).

AP test 1 and 2 – The AP musicians performed 96.03% ($SEM = 0.81\%$) correctly in AP test 1, and 87.11% ($SEM = 3.88\%$) in AP test 2. The RP musicians (who conducted the AP tests; $N = 21$) performed 23.35% ($SEM = 2.84\%$) correctly in AP test 1 and 23.41% ($SEM = 2.55\%$) correct in AP test 2. Therefore, RP musicians performed below the chance level of 25% in AP test 1 and 2.

¹³ Importantly, the distance between a tone and the next tone within a category or the next tone out of a category was the same (but adapted to the increasing frequency distances between semitones at higher frequencies).

Performance during Experiment 2 – The overall performance of AP musicians for the experiment was 79.99% ($SEM = 2.14\%$) correct, with 81% ($SEM = 2.21\%$) correct for the same name condition and 79% ($SEM = 2.57\%$) correct for the different name condition (see Fig. 8.2). For the same name condition AP musicians showed a mean RT^{14} of 2101 ms ($SEM = 158$ ms) and 2076 ms ($SEM = 211$ ms) for the different name condition (see Fig. 8.2). The RP musicians ($N = 28$) performed 76.10% ($SEM = 1.40\%$) correctly, with 75.80% ($SEM = 1.64\%$) correct for the same name condition and 76.44% ($SEM = 1.52\%$) correct for the different name condition (see Fig. 8.2). For the same name condition RP musicians showed an average RT of 2067 ms ($SEM = 106$ ms) and 1963 ms ($SEM = 104$ ms) for the different name condition (see Fig. 8.2).

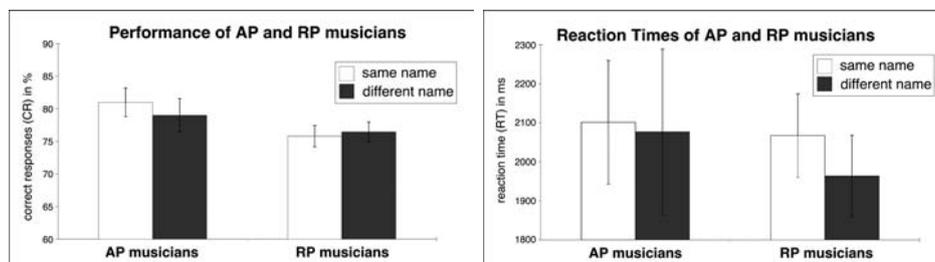


Fig. 8.2: Performance (in percentage of correct responses) and Reaction Time (in ms) of AP and RP musicians

8.4.1 Within Group Comparison

AP musicians – A paired-samples t -test revealed neither a significant difference between the percentage of correct responses (CR) in the same name and different name condition ($t(15) = 0.926$, $p = .369$), nor for the RT of the same and different name condition ($t(15) = 0.313$, $p = .759$).

RP musicians – The RP musicians did not show a difference between the same name condition and the different name condition in the percentage of CR ($t(27) = -0.433$, $p = .668$), but they showed a significant difference between the RT in the same name and different name condition ($t(27) = 2.896$, $p = .007$), with faster RT in the different name condition.

8.4.2 Between Groups Comparison

To examine whether AP musicians performed better in general in the tonal WM task an independent-samples t -test was conducted. No significant difference between AP and RP musicians for the overall percentage of CR in the experiment was observed ($t(42) = 1.584$,

¹⁴ The reaction time (RT) is defined by the time between the begin of the visual cue (that indicated which tones have to be compared) and the button press response.

$p = .121$). No significant difference was observed between both groups concerning the percentage of CR of the same name condition ($t(42) = 1.902, p = .064$) and the different name condition ($t(42) = 0.919, p = .363$) as revealed by an independent-samples t -test.

In addition, no statistical significant difference was found for the RT in the same name ($t(42) = 0.183, p = .856$) and in the different name ($t(42) = 0.538, p = .593$) condition for both groups.

8.4.3 Correlations

The following variables out of the Musical Experience/AP questionnaire for the AP musicians were analysed using a Pearson correlation: the starting age of musical training, the age when AP was detected, the percentage of CR, the percentage of CR in the same name condition, the percentage of CR in the different name condition, RT in the same name condition, RT in the different name condition, as well as the percentage of CR in AP test 1 and 2. The following correlations were observed in AP musicians (correlations between conditions of the experiment or the AP tests are not reported):

- The starting age of musical training correlated positively with the detection age of AP ($r = .703, p = .016, N = 11$)¹⁵.
- The detection age of AP ($r = -.744, p = .009, N = 11$) and the age of musical commencement ($r = -.521, p = .039, N = 11$) correlated negatively with the percentage of CR in the same name condition, but not with the percentage of CR in the different name condition.
- The RT in the same name condition correlated negatively with the percentage of CR in AP test 2 ($r = -.501, p = .048, N = 16$) and the RT in the different name condition correlated negatively with the percentage of CR in AP test 2 ($r = -.559, p = .024, N = 16$).

For the RP musicians none of these correlations reached significance.

8.5 Discussion

The hypothesis were not borne out by the results of Experiment 2, which did not reveal differences between AP and RP musicians for the same name and the different name condition. Although a larger sample of participants was tested in this study ($N = 44$), the findings by Siegel (1974; $N = 12$) and Rakowski (1993; $N = 3$) were not replicated.

¹⁵ Not all AP musicians completed the Musical Experience/AP questionnaire. Therefore, it is indicated how many musicians were included in the correlation analysis.

Likewise, the correlations do not suggest a difference between both conditions: The correlations in AP musicians indicate that, the better they performed in AP test 2, the faster they answered in both experimental conditions.

Differences between the experiments – How do the present results relate to the ability of AP and the previous results reported in the literature? There are differences in the experimental design between the present study and the study conducted by Siegel (1974). Firstly, Siegel (1974) used two conditions: One condition in which the tones were separated by $\frac{1}{10}$ and one condition in which the tones were separated by $\frac{3}{4}$ semitone steps. She reported, that in the $\frac{1}{10}$ condition AP musicians used a sensory trace mode, which allowed them to maintain the sensory auditory information over a temporally quite limited time. In this condition they show no performance difference compared to the RP musicians. Conversely, they performed significantly better, compared to the RP musicians, in the $\frac{3}{4}$ condition, when they could use a verbal labelling mode. Secondly, the participants in Siegel's (1974) study always had to remember the first tone, ignore the distractor tones, and compare the first to the last tone. Therefore they only had to remember one tone. Thirdly, the distractor tones also were taken from a wider frequency range, making it easier to ignore them.

In contrast, the present study firstly used tones, which were separated by $\frac{1}{4}$ semitone steps (which is between $\frac{1}{10}$ and $\frac{3}{4}$ semitone steps). Secondly, participants were asked to remember the whole sequence, but had at least to remember three tones, because they did not know in advance, which tones they should compare (first tone with the very last tone or the first tone with the second-to-last tone). Thirdly, the distractor tones were taken from within and outside (one adjacent) category, and therefore had a very narrow frequency range. Because AP musicians were asked to remember more than one tone, which in addition came from a very narrow frequency range, they presumably used as a memory strategy ONLY a sensory trace mode, instead of switching between a verbal labelling mode and the sensory trace mode (which might have been ineffective). Rakowski (1993) used $\frac{1}{8}$ semitone steps when investigating the categorical perception, but the employed task did not involve memory. These differences in the experimental design might explain the difference in the results between this experiment and the results reported in the literature (Rakowski, 1993; Siegel, 1974).

Perception and Memory – Another major point is that Experiment 2 involved perception AND memory components. It could be the case, that AP musicians perceived tones categorically, but still used a sensory trace mode in order to remember them, because this is the most effective strategy to remember the whole sequence (or at least three tones), which also included some tones with the same note name.

However, it is important to note that in Experiment 1 the AP musicians showed a significant superior performance during the tonal WM task, when an outlier (one AP musician) was excluded. In Experiment 1 the target tones corresponded to the frequency of the Western musical scale and the distractor tones did not. Nevertheless, the frequency range within one auditory sequence was wider, making the use of verbal labelling in AP musicians more probable. Additionally, by using fMRI in Experiment 1 it was possible to distinguish between perception and WM processes, and the AP musicians showed a stronger involvement of the left STS during the perceptual phase, indicating a difference between both groups already during the perception. It is important to note that Experiment 2 did not show behavioural differences in the tonal WM performance between AP and RP musicians, presumably because the tones did not correspond to the frequencies of the tones of the Western musical scale.

Therefore, Experiment 1 indicates a difference in AP musicians that already influence the perception, in a more categorical/phonemic way, and Experiment 1 and 2 together suggest, that there are different memory modes for tones in AP musicians, i.e. when AP musicians can use a verbal labelling mode, they show a superior performance during a tonal WM task. To investigate this issue further, in Experiment 3C AP musicians were compared with RP musicians, using exclusively tones which frequencies corresponded to the frequency of the Western musical scale (see Chapter 12).

8.6 Summary

Based on the result gained in Experiment 1, this behavioural study was designed to test whether AP musicians perceive tonal stimuli categorically. Therefore, ‘microtones’ were designed (sine wave tones, $\frac{1}{4}$ semitone steps). AP musicians and RP musicians listened to 6 tone sequences. Afterwards, they indicated whether the last or the second-to-last tone was higher or lower than the first tone. The experiment consisted of two conditions: The two microtones which should be compared had a different frequency, but belonged to the same tone category (same name condition), whereas in the second condition the two tones to be compared had a different frequency and a different name (different name condition). It was hypothesised that AP musicians have an advantage, compared to RP musicians, if they can label the tones verbally (in the different name condition, but not in the same name condition). Surprisingly, contrary to the hypothesis, there was no difference between AP and RP musicians for the tonal WM performance in the same name as well as in the different name condition, concerning the percentage of CR and the RT (Rakowski, 1993; Siegel, 1974; Siegel & Siegel, 1977).

This is in so far interesting, that AP musicians in the present experiment, which used microtones, seemed to use a sensory trace mode (Siegel, 1974), and did not label the tones verbally (which might have been even disadvantageous). This is important, because together with Experiment 1, it was concluded that the ability of AP influences already the tonal perception, so that AP musicians might perceive tones in a more categorical way (Experiment 1), comparable to verbal stimuli. Furthermore, the results gained by Experiment 2 suggest that AP musicians have not a superior WM for tones, if they are not able to assign them to a certain (e.g., verbal) category.

Chapter 9

Experiment 3 – Neural Correlates of WM Components for Verbal and Tonal Stimuli

9.1 Introduction

Experiment 3 is composed of the Experiments 3A – C. These fMRI experiments were designed to investigate auditory perception and auditory WM (with the focus on auditory WM) under different aspects.

Experiment 3A: Verbal vs. Tonal – As already described in Chapter 2, there are still many open questions concerning the link between language and music. So far neuroscience research has mainly emphasised the investigation of language and the exploration of the neural correlates of music perception and processing started only recently. Because there are differences and similarities in the perception (e.g., Binder et al., 2000; Liebenthal et al., 2005; Mottonen et al., 2006; Zatorre et al., 1992) and processing of language and music (e.g., Koelsch et al., 2004; Maess et al., 2001), Experiment 3A investigated the perception and WM processes for tonal and verbal stimuli in nonmusicians (because the investigation of nonmusicians allows a broad generalisation).

Experiment 3B: Nonmusicians vs. RP musicians – This experiment analysed the role and the influence of musical expertise on the neural correlates underlying tonal perception and tonal WM by comparing RP musicians and nonmusicians. Many musicians start their musical training at a very early age. The long-term musical practise results in increased auditory and somatosensory input, as well as in an intensive training of motor functions (see Chapter 4.2). Therefore musicians are excellent participants to investigate to what extent the environment can shape the brain (anatomical and functional changes) (Munte et al., 2002; Schlaug, 2001), or in other words to investigate neural plasticity.

Experiment 3C: Musicians with and without AP – This experiment examined the influence of AP on tonal perceptual and WM processes. As described in Chapter 5, musicians with AP can name every tone of the Western musical scale without a reference tone (Takeuchi & Hulse, 1993). Nonetheless, not only are the underlying cognitive and neural mechanisms of AP still not fully understood, but there are also contradictory results concerning the degree of WM involvement in pitch memory tasks in AP musicians (Crummer et al., 1994; Hirose et al., 2002; Klein et al., 1984; Wayman et al., 1992). By comparing AP musicians to RP musicians while perceiving tones and holding them in WM, Experiment 3C explored if the ability of AP

has an influence on the cognitive processes (degree of involvement) and the neural organisation of WM.

In this chapter the experimental design, the stimuli and the scanning paradigm are introduced, which have been used in Experiments 3A – 3C. In addition, a first overall analysis of the data is presented, including all participants (nonmusicians, RP musicians and AP musicians).

9.2 Hypotheses

1. Based on the behavioural experiments (see Appendix: Pretest 1-4) a superior performance, in terms of reaction time and correct answers, was hypothesised to occur for the verbal information.
2. During the perception of the verbal material stronger activation was hypothesised in the left STS (Binder et al., 2000; Dehaene-Lambertz et al., 2005; Jancke et al., 2002; Mottonen et al., 2006) and in the left IFG (Friederici, 2002), when compared to the tonal perception.
3. For the WM related processes a similar network was hypothesised to show activation during the tonal and verbal rehearsal, including following brain areas: the premotor cortex (ventrolateral (PMv) and dorsolateral (PMd) premotor cortex), the (pre-)SMA, the mid-DLPFC, the VLPFC, the IPL, as well as cerebellar areas (Awh et al., 1996; Baddeley, 2003; Chen & Desmond, 2005; Gaab, Gaser et al., 2003; Gruber, 2001; Gruber & von Cramon, 2003; Henson et al., 2000; Kirschen et al., 2005; Petrides, 2000a, 2005; Ravizza et al., 2004).

9.3 Methods

9.3.1 Participants

41 participants (17 nonmusicians, 16 RP musicians and 8 AP musicians) took part in these experiments (for a more detailed description see Chapters 10 - 12). The mean age was 24.68 years ($SEM = 0.48$ years), with a range between 20 and 33 years. Participants were asked to fill out a Musical Experience/AP questionnaire (see Appendix: Musical Experience and AP questionnaire) to gather information about their musical experience and AP ability. Handedness of participants was assessed using the Edinburgh inventory (Oldfield, 1971).

9.3.2 Stimuli and Experimental Task

The experimental stimuli were developed based on the results of the pretests (see Appendix: Pretest 1-4). Participants were presented with auditory sequences, which consisted of five auditory stimuli. Each stimulus comprised a spoken syllable and a simultaneously presented

sine wave tone. The frequency of the sine wave tones corresponded to the frequency of the tones of the Western musical scale (based on A = 440 Hz), and ranged from 261 Hz to 523 Hz (one octave). The syllables were spoken by a professional male speaker and were the names of the tones of the Western musical scale in German (e.g. “GIS” (G#), “C” etc.). Each stimulus had a duration of 400 ms, with periods of 150 ms of silence between them. One sequence contained five auditory stimuli and had a duration of 2600 ms. The volume between syllables and sine wave tones had been subjectively controlled by different listeners, i.e. both stimuli sounded alike in terms of intensity.

Participants listened to sequences of five auditory stimuli. Subsequently, they had to rehearse, depending on the condition, either the syllables (verbal rehearsal condition) or the sine wave tones (tonal rehearsal condition) subvocally. Afterwards, a probe stimulus was presented and participants had to indicate by a button press, whether the syllable (verbal rehearsal condition) or the sine wave tone (tonal rehearsal condition) had already been presented during the sequence (see Fig. 9.1). The rehearsal period had a duration of 4200 to 6200 ms (see Fig. 9.4). There was no predictable connection between syllables and sine wave tones, i.e. it was not possible to solve the tonal task by paying attention to the syllables. Two control conditions, pink noise and silence, were designed. The pink noise (2600 ms) controlled for the perceptual input and for the motor response (participants pressed the button after the end of the pink noise ‘probe’), but participants did not rehearse information during the rehearsal period (pink noise nonrehearsal). During the silence condition participants were not presented with auditory stimuli and they did not rehearse.

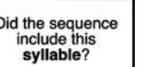
condition	visual cue	aud. sequence (syllables & tones)	silence	control stimulus	response (button press)
verbal rehearsal	B		rehearsal syllables		Did the sequence include this syllable?
tonal rehearsal	T		rehearsal tones		Did the sequence include that tone?

Fig. 9.1: Experimental task¹⁶

Key and non-key sequences – To further investigate the effect of musical training on a tonal WM task the tonal sequences could be divided into two types (see Fig. 9.2): key sequences (all five tones were in key, and three of them belonged to one triad; 50% of the tonal trials) and non-key sequences (consisted of neither triad nor key; 50% of the tonal trials). Key sequences might trigger the use of a strategy in RP musicians in order to rehearse/store the

¹⁶ visual cue: B = Buchstaben (German for letters), T = Töne (German for tones)

tones. Furthermore, it has been shown that also nonmusicians have an implicit musical knowledge (Koelsch et al., 2000; Tillmann et al., 2003) and therefore might show a better performance for these key sequences as well.

Congruent and incongruent sequences – In order to gather new knowledge about the AP ability an additional condition for the AP musicians was implemented (see Fig. 9.3): a congruent (the frequency of the sine wave tones did not correspond to the simultaneously presented syllables, 50% of the tonal trials) and an incongruent condition (the frequency of the sine wave tone did not correspond to the syllables, 50% of the tonal trials). Congruent and incongruent conditions were only compared during the tonal condition (tonal congruent and tonal incongruent condition). AP musicians were hypothesised to show a superior performance during tonal WM for the congruent compared to the incongruent stimuli, because the incongruent sequences might distract them in a ‘Stroop-like’ way (Itoh et al., 2005; Miyazaki, 1999; Siegel, 1974).

The sequences were counterbalanced between the conditions for several issues (see Appendix: Sequences of Experiment 3A – C). 40 sequences were created, which were afterwards flipped, i.e. the spoken syllables became tones (e.g., a spoken “C” became a sine wave tone with the frequency C) and vice versa. Each sequence was presented twice, once for the verbal condition and once for the tonal condition. Thus, participants were presented with the same auditory stimuli, but had to pay attention/rehearse either the tonal or the verbal stimuli. This resulted in 160 highly comparable sequences (see Appendix: Sequences of Experiment 3A – C). 30 sequences of pink noise and 20 sequences of silence were presented during the experiment. Therefore the experiment consisted of 210 sequences overall, which were presented in 10 runs (21 trials per run). The whole experiment had a duration of 47.3 min. The sequences were presented pseudorandomly in a blocked design. At the beginning of each block a visual cue (see Fig. 9.1) indicated the condition (verbal or tonal). 50% of the participants started with the tonal and 50% with the verbal condition (verbal and tonal blocks alternated). In addition, during a trainings session (approx. 20 min) participants were repeatedly instructed not to sing or hum aloud during the scanning session.

It is important to note that all groups of participants (nonmusicians, RP musicians and AP musicians) in Experiment 3A-C were presented with the same stimuli. Therefore, all hypotheses could be investigated with one set of stimuli in three experiments.

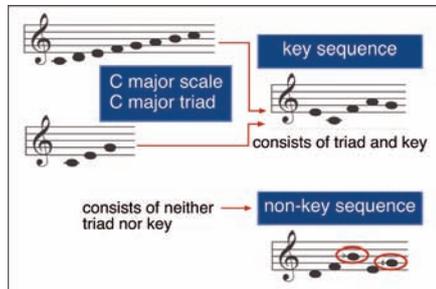


Fig. 9.2: Key and non-key Sequences

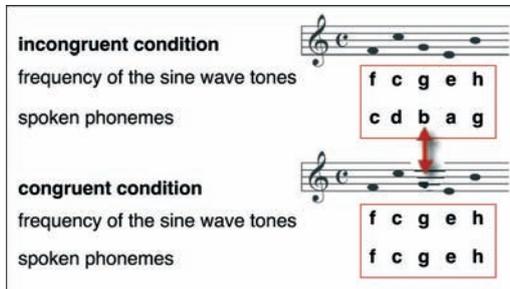


Fig. 9.3: Incongruent and congruent Sequences

9.3.3 Scanning Design

The scanning paradigm was a modified version of the sparse temporal sampling technique (Hall et al., 1999), i.e. auditory stimulation was presented in the absence of the scanner noise (see Chapter 6.4). It was intended to scan the hemodynamic response correlated with the processes active during (a) the perception (first scan) and (b) the rehearsal period of the stimuli (second scan). During one trial it was scanned twice, the first time after the end of the sequence, the second time after the rehearsal period (see Fig. 9.4). The onset of the sequence presentation was shifted, resulting in five different time points for the first scan (first time point = immediately after the sequence, the fifth time point = 2 s after the sequence). The rehearsal time differed in length (4.2 – 6.2 s), according to the five different time points (see Fig. 9.4).

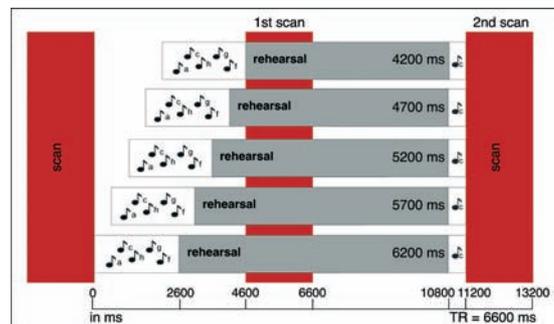


Fig. 9.4: Scanning Paradigm

9.3.4 Image Acquisition and Processing

The experiment was carried out on a 3T (Tesla) scanner (Siemens TRIO, Erlangen). Before each functional session, an anatomical reference data set was acquired for each participant, which was standardised to the talairach stereotactic space (Talairach & Tournoux, 1988).

Functional imaging – A bunched gradient-echo EPI (echo planar imaging) sequence was used with a TE of 30 ms, a flip angle of 90° and a TR of 6600 ms and an acquisition bandwidth of

100 kHz. 24 axial slices were acquired rapidly within approximately 1600 ms, so that no scanning occurred during the rest of the TR. The matrix dimensions were 64 x 64 with a field of view (FOV) of 192 mm, resulting in a voxel size of 3 x 3 x 4 mm with an interslice gap of 1 mm. The data pre-processing, the statistical analysis and the visualisation of the data was performed using the software package LIPSIA (Lohmann et al., 2001).

Pre-processing of the images – An off-line motion correction was performed on the functional images, using a Siemens motion correction protocol (Siemens, Erlangen, Germany) and a matching metric based on linear correlation. It took ca. 1600 ms to acquire one scan, therefore there is a temporal offset between the first and the last slice. To correct for the different acquisition time between the slices, a cubic spline-interpolation was used (Lohmann et al., 2001). The cut-off frequency of the temporal high-pass filter, which was used for signal baseline correction, was 1/300 Hz. A spatial gaussian filter with a FWHM of 5.65 mm was used to improve the SNR of the data.

To align the functional data with a 3D stereotactic coordinate reference system, a rigid linear registration with six degrees (three translations (x, y, x) and three rotations (pitch, yaw, roll)) was performed. The translational and rotational parameters were acquired using the anatomical reference brain. In the following, the calculated translational and rotational parameters were used to transform the functional data set to the stereotactic coordinate system, by using a trilinear interpolation. Then the functional data was linearly normalised. Because musicians have been shown to differ anatomically from nonmusicians (Amunts et al., 1997; Munte et al., 2002; Schlaug, 2001; Schlaug, Jancke, Huang, Staiger et al., 1995; Schneider et al., 2002), the functional images were only linearly normalised, because a non-linear normalisation would have removed the differences between the groups.

Statistical evaluation – The statistical evaluation used the general linear model (GLM; see Chapter 6.3) and was based on a least-square estimation for serially autocorrelated observations (Friston, 1994; Friston, Holmes, Poline et al., 1995; Friston, Holmes, Worsley et al., 1995; Worsley & Friston, 1995). The design matrix was generated using one synthetic hemodynamic response function (Friston et al., 1998; Josephs, Turner, & Friston, 1997). In order to deal with the temporal autocorrelation, the design matrix, the acquired data and the error term, was convolved with a Gaussian kernel of 4 s. Subsequently, for each participant contrast-images were calculated, which is a raw-score difference between specified conditions. Afterwards, the contrast-images for each participant and each contrast were entered into a second-level random effect analysis. During the group analysis a one-sample *t*-test was performed to evaluate whether observed differences were significantly different

from zero. The t -values were transformed into z -values. To define significant activation, a double threshold was applied to protect against false positive activations (Forman et al., 1995), i.e. only activations which z -values were greater than 3.09 (according to a p -value of .001) and a voxel extent (k) of 10 voxels or more were considered as significant activations. The search radius (SR), which is used to identify local maxima, is indicated in mm. For some analyses a different threshold was applied (e.g., for the AP musicians, because only eight AP musicians were investigated which resulted in an inferior statistical power), which is described for each individual contrasts in the following chapters (see Chapters 10-12). Only activations within the grey matter are reported.

Following contrasts were of interest: verbal or tonal perception vs. silence, verbal vs. tonal perception, verbal or tonal rehearsal contrasted against pink noise nonrehearsal, and verbal compared to tonal rehearsal. Following contrasts were compared between the groups: tonal perception vs. pink noise perception and tonal rehearsal vs. pink noise nonrehearsal for nonmusicians vs. RP musicians and RP musicians vs. AP musicians.

9.4 Results

First, the different contrasts for all participants are visualised and discussed. The following chapters (see Chapters 10 – 12, Experiments 3A – 3C) address and discuss the more specific contrasts, i.e. the results for each group individually and the comparison between the groups.

9.4.1 Behavioural Data

An overview over the results can be found in the Appendix (see Appendix Tab. A.2 and A.3). Paired-samples t -tests were conducted to investigate potential differences between the conditions. All participants ($N = 41$) showed a mean performance of 66.30% ($SEM = 2.08\%$) for the tonal condition (in percentage of correct responses (CR)), and 87.32% ($SEM = 1.25\%$) CR for the verbal condition, the difference between conditions being significant ($t(40) = -11.323, p = .000$). The reaction times (RT)¹⁷ varied between the tonal ($M = 1503$ ms, $SEM = 57$ ms) and verbal ($M = 1369$ ms, $SEM = 49$ ms) condition significantly as well ($t(40) = 4.774, p = .000$). The participants of all groups showed a mean performance of 68.20% ($SEM = 1.94\%$) CR for the key sequences, and 64.38% ($SEM = 2.49\%$) CR for the non-key sequences. The performance between both conditions differed significantly ($t(40) = 2.358, p = .023$). The difference in the RT between the key condition ($M = 1495$ ms, $SEM = 54$ ms) and the non-key condition ($M = 1512$ ms, $SEM = 62$ ms) did not reach

¹⁷ The RT defined as the time between the beginning of the auditory probe and the button press.

significance ($t(40) = -0.927, p = .360$). No difference was observed between the CR in the tonal incongruent condition ($M = 66.05\%$, $SEM = 2.313\%$) and the tonal congruent condition ($M = 66.54\%$, $SEM = 2.143\%$) ($t(40) = -0.307, p = .761$). Also the RT did not differ between the tonal incongruent ($M = 1505$ ms, $SEM = 58$ ms) and the tonal congruent condition ($M = 1502$ ms, $SEM = 58$ ms) ($t(40) = 0.228, p = .821$).

9.4.2 fMRI Data

Verbal and tonal perception vs. silence in all groups – During the verbal as well as during the tonal perception (both compared to the silence baseline) the participants ($N = 41$) showed significant activation of the STG bilaterally¹⁸ as hypothesised (see Appendix Fig. A.3 and Tab. A.6).

Verbal vs. tonal perception in all groups – Contrasting the verbal against the tonal perception, the verbal perception condition showed significant more activation of the STG and the STS bilaterally, whereas only a few areas were observed to be more strongly activated during the tonal perception (see Fig. 9.5 and Tab. 9.1).

Tab. 9.1: Comparison of verbal and tonal Perception in all Groups

area	left hemisphere					right hemisphere				
	BA	x	y	z	z-value	BA	x	y	z	z-value
<i>all groups: verbal – tonal perception ($z > 3.09, k = 10, SR = 10$)</i>										
frontopolar area	10	-20	57	21	4.41	10	13	60	18	3.93
	10	-11	51	18	4.68					
	10	-5	51	9	4.60					
	10	-8	51	-3	4.20					
SFG						9	1	57	24	4.13
cingulate gyrus	24	-14	33	12	3.71					
	24	-8	36	-3	5.33					
	31	-2	-39	36	5.19					
postcentral gyrus	3	-47	-12	33	4.02					
STG	39	-50	-60	27	3.82					
	22	-38	-24	6	3.70	22	52	-12	-3	4.72
STS	21/22	-56	-18	-9	4.63	21/22	52	-30	3	4.08
MTG						21	43	-12	-18	4.05
						21	43	0	-27	3.95
ITG						20	55	-18	-18	3.91
precuneus	7/31	-14	-51	33	4.83					
	31	-17	-60	21	4.32					
cuneus	17/18	-2	-87	3	3.96	18	1	-87	24	3.54
						18	16	-90	21	4.31
middle occipital gyrus	19	-47	-72	0	3.60	19/39	43	-63	9	4.39
	18/19	-35	-81	15	3.92					
inferior occipital gyrus	18	-26	-90	6	4.42					
cerebellum		-5	-57	3	3.64					
		-29	-75	-24	4.19					
<i>all groups: tonal – verbal perception ($z > 3.09, k = 10, SR = 10$)</i>										
insular cortex		-32	18	3	4.55					
pre-SMA	6	-5	18	45	4.17					
PMv						6	40	6	30	3.85

¹⁸ Relevant activations are mentioned in the text. All activations can be found in the corresponding table.

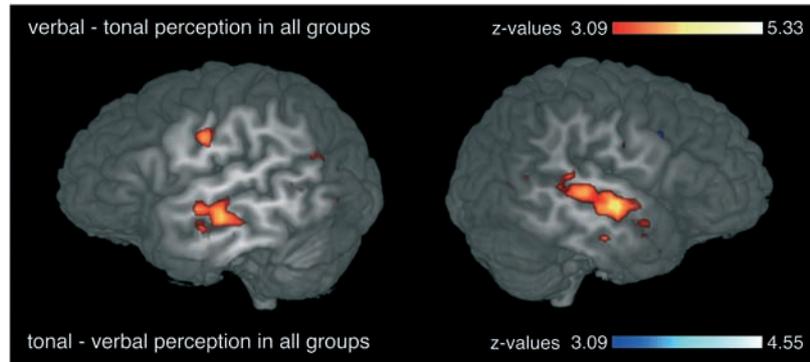


Fig. 9.5: Verbal – tonal Perception in all Groups ($z > 3.09$, $k = 10$, $SR = 10$)

Verbal rehearsal vs. pink noise nonrehearsal in all groups – During the verbal rehearsal (contrasted against the pink noise nonrehearsal condition; $z > 3.09$, $k = 10$, $SR = 10$), the participants showed activation of the mid-DLPFC bilaterally, the left pars opercularis, the insular cortex bilaterally, the left pre-SMA, the PMv and PMd bilaterally, the SPL and IPS bilaterally (activations also spread in the IPL bilaterally), and the cerebellum bilaterally (see Fig. 9.6 and Appendix Tab. A.7).

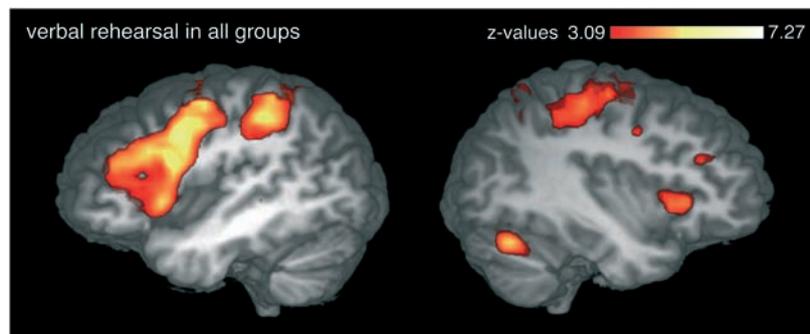


Fig. 9.6: Verbal Rehearsal – pink noise Nonrehearsal in all Groups ($z > 3.09$, $k = 10$, $SR = 10$)

Tonal rehearsal vs. pink noise nonrehearsal in all groups – During the tonal rehearsal contrasted against the pink noise nonrehearsal ($z > 3.09$, $k = 10$, $SR = 10$) following activations were observed: left mid-DLPFC, left pars opercularis, insular cortex bilaterally, left pre-SMA, premotor cortex bilaterally, SPL bilaterally, left IPL, as well as the cerebellum bilaterally (see Fig. 9.7 and Appendix Tab. A.7).

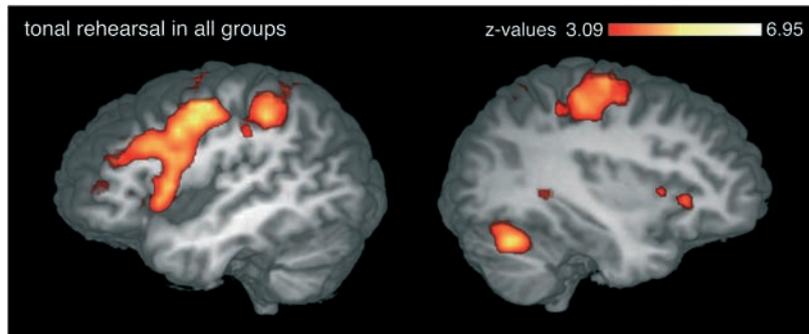


Fig. 9.7: Tonal Rehearsal – pink noise Nonrehearsal in all Groups ($z > 3.09$, $k = 10$, $SR = 10$)

Verbal vs. tonal rehearsal in all groups – When comparing the verbal vs. the tonal rehearsal condition ($z > 3.09$, $k = 10$, $SR = 10$), the verbal condition showed mainly enhanced activation of the left pars opercularis, the insular cortex bilaterally, the left pre-SMA, the premotor cortex bilaterally, the SPL bilaterally and the left IPL (see Fig. 9.8 and Tab. 9.2). In contrast, during the tonal rehearsal ($z > 3.09$, $k = 10$, $SR = 10$) significant differences were primarily observed in the following areas: the left frontopolar area, the superior (bilateral) and middle (left) frontal cortex, the cingulate gyrus bilaterally, the right SMG, the angular gyrus bilaterally, as well as in the STG bilaterally, and in related visual areas like the cuneus bilaterally (see Fig. 9.8 and Tab. 9.2).

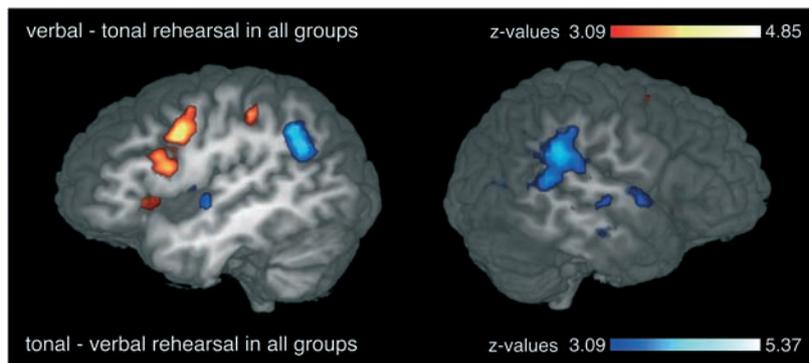


Fig. 9.8: Verbal – tonal Rehearsal in all Groups ($z > 3.09$, $k = 10$, $SR = 10$)

Tab. 9.2: Activated Brain Areas during the Comparison between verbal and tonal Rehearsal in all Groups

area	left hemisphere					right hemisphere				
	BA	x	y	z	z-value	BA	x	y	z	z-value
<i>all groups: verbal – tonal rehearsal (z > 3.09, k = 10, SR = 10)</i>										
pars opercularis/IFG	44	-50	12	18	4.33					
	44	-56	12	9	4.02					
insular cortex		-35	18	3	4.71	28	15	0		3.96
pre-SMA	6	-2	21	42	4.70					
PMd						6	25	3	51	3.86
PMv	6	-41	0	36	4.86					
SPL	7	-26	-63	45	3.59	7	25	-57	42	3.75
IPL	40	-44	-33	45	4.17					
<i>all groups: tonal – verbal rehearsal (z > 3.09, k = 10, SR = 10)</i>										
frontopolar area	10	-8	54	3	4.80					
	10	-17	57	21	4.68					
SFG	8	-14	42	42	4.13	9	7	57	30	3.77
middle frontal gyrus	8	-29	24	42	3.87					
insular cortex						37	-15	-3		3.74
cingulate gyrus	31	-8	-30	39	4.68	31	13	-42	42	4.07
	24	-2	21	-6	5.01					
	31	-5	-45	30	5.37					
gyrus rectus						11	1	42	-12	3.59
medial frontal gyrus	9	-5	48	18	4.01					
SMG						40	55	-39	24	4.49
angular gyrus	39	-50	-54	36	4.47	39	43	-60	36	4.01
	39	-50	-60	27	4.37	39	37	-57	27	3.90
STG	22	-41	-18	0	3.83	22	49	3	0	4.01
						22	58	-15	6	3.79
posterior STS						21/22	55	-45	9	4.28
MTG						20/21	49	-21	-12	3.82
cuneus	19	-23	-87	24	4.52	19	7	-81	33	4.32
fusiform gyrus	19/37	-26	-57	-3	4.06	19	25	-69	-3	4.72
						19/37	22	-51	-9	4.14
orbital gyrus	19	-38	-75	27	3.42					
middle occipital gyrus	19	-35	-81	15	3.79					
inferior occipital gyrus						19/37	40	-72	6	4.19
cerebellum		-17	-69	-6	4.08					
		-32	-57	-15	3.71					
		-38	-75	-30	3.31					
		-20	-78	-27	3.89					
		-8	-54	-33	3.86					

9.5 Discussion

9.5.1 Behavioural Data

As postulated in Hypothesis 1, participants displayed a significantly better and faster performance for the verbal stimuli compared to the tonal stimuli, indicating a more automatic and superior WM performance for verbal compared to tonal information. All participants showed a better performance for the key sequences, compared to the non-key sequences, whereas no difference was observed in the RT between both types of stimuli. This difference in the key and non-key stimuli is presumably due to a more strategy based processing during the key sequences of the RP musicians, which may be based on musical regularities (see Chapter 11.5.2.3).

No difference was observed for all participants during tonal WM performance for the incongruent and congruent sequences. This was hypothesised, because the potential difference was only formulated for the AP musicians (see Chapter 12.2).

9.5.2 fMRI Data

9.5.2.1 Comparison between verbal and tonal Perception in all Groups

When comparing the verbal and the tonal perception, the most pronounced result was a stronger activation of the STG and the STS bilaterally during the verbal perception. In Hypothesis 2 a stronger activation in the left STS and the left IFG it was postulated for the comparison between verbal and tonal perception. Thus, the results support partially Hypothesis 2, because the STS was more strongly activated during the verbal perception, but the left IFG did not show stronger activation.

The enhanced activation of the STS is a typical finding, which was observed in numerous auditory perception studies (e.g., Binder et al., 2000; Dehaene-Lambertz et al., 2005; Jancke et al., 2002; Liebenthal et al., 2005; Mottonen et al., 2006). Binder et al. (2000) published a review in which they described studies comparing tonal and verbal stimulation. These studies revealed a stronger bilateral activation of the STS (see Fig. 9.9) for the verbal compared to the tonal perception. Dehaene-Lambertz et al. (2005) presented participants auditorily with sine wave tones, which were in complexity analogous to speech, and investigated the neural correlates when participants switched into a ‘speech mode’ and perceived them as syllables. During the speech mode, participants displayed stronger activation of the left STS and the posterior STG.

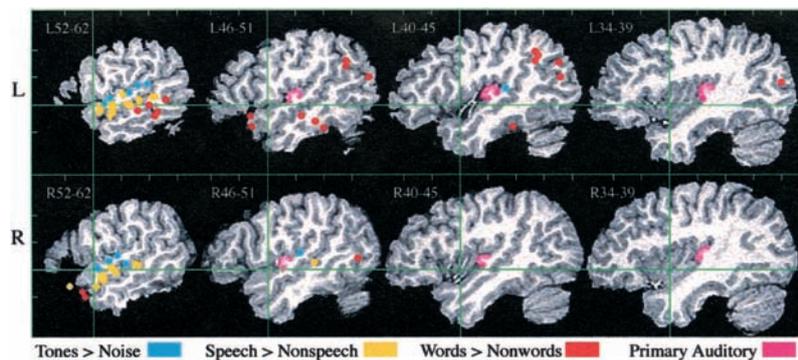


Fig. 9.9: Comparison of verbal and tonal Perception (Binder et al., 2000)

Liebenthal et al. (2005) compared the perception of familiar consonant-vowel syllables to comparably complex auditory pattern, which cannot be associated with learned phonemic

categories. The authors showed that the familiar consonant-vowel syllables activated the left STS more strongly, and therefore argued that the STS is involved in the process of phonemic, possibly categorical perception. This is supported by Mottonen et al. (2006). The authors investigated speech perception with ‘sine wave speech’, which can be perceived as speech or non-speech. They scanned the participants twice: before and after a training. During the training, the participants learned to categorise the ‘sine wave speech’ stimuli and perceive them as speech. Therefore, in both scanning sessions participants were presented with the same auditory ‘sine wave speech’ stimuli, however, during the first scan they perceived it as non-speech and during the second scan (after the training) participants perceived it as speech. The authors reported a stronger activation of the left posterior STS when ‘sine wave speech’ was perceived as speech after the training compared to the scan prior to the training, when participants perceived the auditory stimuli as non-speech.

Additionally, studies showed that tones usually do not show significantly more activation, when compared to verbal activation (Binder et al., 2000). This assumption is supported by the results gained in this dissertation, where also only a few areas have been observed to show additional activation during the tonal perception, when compared to the verbal perception.

All in all, the results of the present study concerning the comparison of verbal and tonal perception showed a stronger activation of the STS for the verbal perception, which is in accordance with the literature. However, it is important to keep in mind that in the present study participants always listen to both stimuli, and only focus on either the verbal or tonal information. Therefore, the observed differences may be due to different top-down processes, which modulate the perception and processing of syllables and tones.

9.5.2.2 Verbal and tonal Rehearsal in all Groups

The verbal and tonal rehearsal (contrasted against the pink noise nonrehearsal condition) activated the left IFG, the mid-DLPFC, the premotor areas bilaterally, the insular cortex bilaterally, parietal areas bilaterally (SPL, IPS and IPL), as well as the cerebellum bilaterally. These areas have been observed in numerous WM Experiments and have been furthermore hypothesised to show activation during the rehearsal (Hypothesis 3). Broca’s area, the premotor cortex, and the cerebellum are known to support the internal rehearsal component of verbal WM (Awh et al., 1996; Baddeley, 2003; Chen & Desmond, 2005; Kirschen et al., 2005; Paulesu et al., 1993; Smith & Jonides, 1998). These structures have also been reported to be involved during tonal WM (Gaab, Gaser et al., 2003) and during listening to music (Janata et al., 2002).

Activation of the IPL has been reported during verbal WM, indicating a role for this area for the phonological store (Awh et al., 1996; Baddeley, 2003; Crottaz-Herbette et al., 2004; Gruber, 2001; Gruber & von Cramon, 2003; Henson et al., 2000; Jonides et al., 1998; see Chapter 3). Also the SPL and the IPS have been reported to be involved during WM tasks (Awh et al., 1996; Crottaz-Herbette et al., 2004; Gruber, 2001; Gruber & von Cramon, 2003). The insular cortex has been found to subservise verbal rehearsal (Bamiou et al., 2003; Paulesu et al., 1993), whereas the mid-DLPFC (area 9/46, Petrides, 2000a) has been described as being important for monitoring the performance and manipulating information during WM tasks (Petrides, 2000a; Petrides, Alivisatos, Meyer et al., 1993). Therefore, the experimental task that was used successfully engaged a known WM network, both during the verbal and tonal rehearsal condition.

When comparing the verbal vs. the tonal rehearsal condition, the verbal condition showed significantly stronger activation of Broca's area, the premotor cortex bilaterally, the insular cortex bilaterally, the left pre-SMA, the SPL bilaterally, and the left IPL.

As already mentioned, *Broca's area* has been observed to be involved in verbal WM tasks (Awh et al., 1996; Chen & Desmond, 2005; Fiez et al., 1996; Gruber, 2001; Gruber & von Cramon, 2003; Paulesu et al., 1993; Ravizza et al., 2004; see Chapter 3.3). Besides this, Broca's area is known to be strongly engaged in language processing, i.e. during processing syntactic and semantic information (for an overview see Friederici, 2002). Fiebach et al. (2005) showed that Broca's area plays an important role during syntactic WM processes. The importance of this area in this contrast (verbal vs. tonal rehearsal) is further analysed and discussed in Experiment 3A and 3B (see Chapters 10 and 11).

The *premotor areas* (including PMv, PMd and pre-SMA) have been suggested to underlie the active phonological rehearsal component of the verbal WM (Baddeley, 2003; Gruber & von Cramon, 2003; Henson et al., 2000; Paulesu et al., 1993; Smith & Jonides, 1998). Considering that the phonological rehearsal is comparable with subvocal speech (for an overview see Baddeley, 1992, 2003) the premotor areas might be involved in the translation of auditory sensory information into a motor representation that can be used for the internal rehearsal or to articulate the verbal items (Baddeley, 2003). The stronger activation of premotor areas in the present study indicates that this is presumably more effective for verbal material (see Chapters 10 and 11).

While the *insula* has been shown to be important for verbal WM (Bamiou et al., 2003; Paulesu et al., 1993), the *IPL* has been suggested to serve as the underlying neural correlate of the phonological store (Baddeley, 2003; Chen & Desmond, 2005; Crottaz-Herbette et al.,

2004; Gruber, 2001; Gruber & von Cramon, 2003; Henson et al., 2000; Jonides et al., 1998; Kirschen et al., 2005; Ravizza et al., 2004). Also the *IPS/SPL* has been reported to be involved during verbal WM tasks (Awh et al., 1996; Crottaz-Herbette et al., 2004; Gruber, 2001; Gruber & von Cramon, 2003).

The tonal rehearsal, when compared to the verbal rehearsal, showed stronger activation of superior and middle frontal areas, the cingulate cortex, the angular gyrus bilaterally and the right SMG, the STG bilaterally, as well as visual areas (e.g., cuneus bilateral). Some of these activations might be due to a compensation strategy. The supramarginal gyrus has been shown to be involved in tonal WM tasks (Gaab, Gaser et al., 2003), additionally, this area was more involved in musicians, when compared to nonmusicians during tonal WM (Gaab & Schlaug, 2003). Because during the tonal rehearsal the participants presumably did not use strategies as effectively as during the verbal rehearsal, e.g., the translation of the sensory information into a motor program to rehearse the information subvocally, it might have been necessary to use another mechanism, which included the activation of the sensory areas, the STG, in order to remember/rehearse the information. It is known that activation of the STG can be modulated by attention (Grady et al., 1997; Jancke, Mirzazade, & Shah, 1999; Mitchell, Morey, Inan, & Belger, 2005; Petkov et al., 2004; Pugh et al., 1996). However, it is unlikely that this activation is due to attentional compensation caused by a more demanding tonal task, because the opposite pattern is observed during the perception period (that is, a stronger activation of the STG during verbal compared to tonal perception). The cingulate gyrus is known to be involved in WM processes, e.g., during the use of a strategy (H. Kondo et al., 2004; Y. Kondo et al., 2005). Whereas the involvement of visual areas in the tonal rehearsal might be due to visual imagery (Kosslyn, Ganis, & Thompson, 2001) of the tonal information (e.g. the imagination of the keys of the piano), probably in RP musicians (see Chapter 11).

9.6 Summary

Experiment 3, which is composed of Experiments 3A–3C, was designed to compare the functional pattern for verbal and tonal perception and rehearsal, and to investigate whether there are differences between nonmusicians and musicians with and without AP during the perception and WM rehearsal of tonal stimuli (with the focus on WM processes). In the present chapter, the overall results concerning the verbal and tonal rehearsal for all groups are presented.

Participants (nonmusicians, RP musicians and AP musicians) listened to sequences of five auditory stimuli. Each stimulus consisted of a spoken syllable and a simultaneously presented sine wave tone. Subsequently, participants had to rehearse either the syllables (verbal condition) or the sine wave tones (tonal condition) subvocally, and then to indicate whether a presented syllable or sine wave tone had already been presented during the sequence. The frequency of the sine wave tones corresponded to the frequency of the tones of the Western musical scale, whereas the syllables were the names of the tones.

The analysis of all groups in Experiment 3 showed two substantial results:

1. *Stronger activation of the STS during the verbal, compared to the tonal condition* – In accordance with the literature (e.g., Binder et al., 2000; Dehaene-Lambertz et al., 2005; Liebenthal et al., 2005; Mottonen et al., 2006) and as hypothesised, stronger activation of the STS and the STG bilaterally were observed during the verbal perception. Strikingly, this difference was observed although participants were always presented with *both* stimuli simultaneously. Therefore, the stronger activation of the STG/STS indicates a top-down influenced correlate of phonemic and categorical perception. This fits nicely with the results in Experiment 1, which indicated a stronger involvement of the STS in AP musicians when compared to RP musicians. Together these results support the notion that AP musicians perceive tones categorically, comparable to verbal perception.
2. *Activation of a known WM network* – Because the cognitive and neural relationships between language and music are still not fully understood, the potential differences or similarities between the neural networks underlying WM for tonal and verbal stimuli have remained elusive. Consequently, this dissertation investigated the similarities and differences between the organisation and the underlying neural networks of WM for verbal and tonal material using fMRI. Importantly, the verbal, as well as the tonal, rehearsal task successfully activated a WM network, comprising the mid-DLPFC, Broca's area, the premotor cortex, the insular cortex, the SPL, IPS and IPL, and the cerebellum (e.g., Baddeley, 2003; Crottaz-Herbette et al., 2004; Gruber & von Cramon, 2003; Kirschen et al., 2005; Paulesu et al., 1993; Petrides, 2000a; Ravizza et al., 2004). The underlying WM related networks for verbal and tonal stimuli showed a considerable overlap. However, there seem to be areas which are more strongly involved during verbal (e.g., Broca's area, premotor areas) and during tonal (e.g., SMG, angular gyrus) WM. These differences and similarities were further analysed during the Experiments 3A – 3C, to analyse and disentangle the influence of musical training and absolute pitch on tonal WM related neural networks.

Chapter 10

Experiment 3A – Neural Correlates of WM for Tonal and Verbal Stimuli in Nonmusicians

10.1 Introduction

Considering the differences and similarities in the perception (e.g., Binder et al., 2000; Liebenthal et al., 2005; Mottonen et al., 2006; Zatorre et al., 1992) and processing of language and music (e.g., Koelsch, Gunter et al., 2002; Koelsch et al., 2004; Maess et al., 2001; Tillmann et al., 2003; see Chapter 2) and the fact that WM processes have been mainly investigated under the aspect of language (e.g., Baddeley et al., 1998; see Chapter 3), this fMRI experiment was designed to compare organisation and underlying neural networks of WM for verbal (syllables) and tonal (sine wave tones) stimuli. Experiment 3A was conducted with nonmusicians, because this allows a broad generalisation of the results.

10.2 Hypotheses

1. Based on the pretest data nonmusicians were hypothesised to show a better behavioural performance for the verbal stimuli, compared to the tonal stimuli (see Appendix: Pretest 1–3).
2. It was assumed that the WM process of verbal rehearsal activates a more left-lateralised network of frontal areas (Broca's area, premotor cortex), as well as parietal and cerebellar areas (e.g., Baddeley, 2003; Friederici, 2002; Gruber & von Cramon, 2003; Kirschen et al., 2005; Paulesu et al., 1993; Ravizza et al., 2004), when compared to tonal rehearsal.
3. It was hypothesised that, although the brain activation pattern during WM processes for tonal and verbal stimuli are basically similar, differences in brain activations exist. A pitch memory task (Gaab, Gaser et al., 2003) showed the involvement of the SMG, posterior dorsolateral frontal regions, SPL and dorsolateral cerebellar regions. These areas were hypothesised to be activated during the rehearsal of the tonal stimuli.

10.3 Methods

10.3.1 Participants

17 right-handed nonmusicians (9 male) participated in this study. The age of the participants ranged from 21 to 29, with a mean of 25.47 years ($SEM = 0.61$ years). Nonmusicians did not have formal music lessons and/or practised to play an instrument regularly over years.

10.3.2 Stimuli, Experimental Design, Image Acquisition and Processing

The stimuli, experimental design, the fMRI paradigm, as well as image acquisition and processing are described in Chapter 9.3.

10.4 Results

10.4.1 Behavioural Data

Verbal vs. tonal – Participants performed on average 84.49% ($SEM = 2.09\%$) correctly in the verbal and 56.28% ($SEM = 1.76\%$) in the tonal condition, with a reaction time (RT) of 1227 ms ($SEM = 61$ ms) for the verbal and 1318 ms ($SEM = 69$ ms) for the tonal sequences. A paired-samples t -test revealed a significant difference between the tonal and verbal condition in terms of the percentage of CR ($t(16) = -17.322, p = .000$) and RT ($t(16) = 2.237, p = .040$). The performance during the tonal condition was significantly above chance level ($t(16) = 3.563, p = .003$), which was shown by a one-sample t -test (see Appendix Tab. A.2 and A.3).

Key vs. non-key – Participants exhibited a mean of 57.87% ($SEM = 1.65\%$) CR and a mean RT of 1327 ms ($SEM = 69$ ms) for the key sequences and a mean CR of 54.70% ($SEM = 2.60\%$) and a mean RT of 1308 ms ($SEM = 69$ ms) for the non-key sequences. By applying a paired-samples t -test no significant differences were observed between the key and non-key sequences in terms of the percentage of CR ($t(16) = 1.241, p = .232$) or RT ($t(16) = 1.080, p = .296$) (see Appendix Tab. A.2 and A.3).

Incongruent vs. congruent – As revealed by a paired-samples t -test no difference between tonal incongruent (CR: $M = 55.92\%$, $SEM = 2.47\%$; RT: $M = 1316$ ms, $SEM = 72$ ms) and tonal congruent (CR: $M = 56.65\%$, $SEM = 1.63\%$; RT: $M = 1319$ ms, $SEM = 67$ ms) condition was observed for the CR ($t(16) = -0.326, p = .749$) or RT ($t(16) = -0.119, p = .907$) in the nonmusicians (see Appendix Tab. A.2 and A.3).

10.4.2 fMRI Data

Verbal and tonal perception vs. silence in nonmusicians – During the verbal as well as during the tonal perception ($z > 3.09, k = 10, SR = 20$), both compared to the silence baseline, nonmusicians ($N = 17$) showed significant activation of the STG bilaterally (see Appendix Fig. A.4 and Tab. A.8).

Verbal vs. tonal perception in nonmusicians – In this contrast ($z > 3.09, k = 10, SR = 10$) the verbal perception activated significantly stronger the left superior frontal gyrus and the left

middle occipital gyrus (see Appendix Tab. A.9). At a lower threshold ($z > 2.58$, $k = 10$, $SR = 10$) the right STS was activated as well (Talairach coordinates: 43 -39 3). No additional significant activation was observed when contrasting the tonal against the verbal perceptual condition.

Verbal rehearsal vs. pink noise nonrehearsal in nonmusicians – Nonmusicians displayed during the verbal rehearsal ($z > 3.09$, $k = 10$, $SR = 10$) activation of the left mid-DLPFC, the pars opercularis/the premotor cortex bilaterally, the left insular cortex, the left pre-SMA, the IPS bilaterally, the left IPL, as well as the cerebellum bilaterally (see Fig. 10.1 and Appendix Tab. A.10). Because the activation of the premotor cortex and the pars opercularis were located quite closely, the search radius (SR) was decreased. When applying the same threshold ($z > 3.09$, $k = 10$) but changing the SR to 5, the left pars opercularis (BA 44) was significantly activated (Talairach coordinates: -50 15 12).

Tonal rehearsal vs. pink noise nonrehearsal in nonmusicians – The tonal rehearsal, contrasted against the pink noise nonrehearsal ($z > 3.09$, $k = 10$, $SR = 10$), showed mainly activation of the left pars orbitalis, the left pre-SMA, the left PMv, the left IPL, the left STS and the left MTG, and the right cerebellum (see Fig. 10.2 and Appendix Tab. A.10). The left pars opercularis (Talairach coordinates: -50 15 12) showed only activation, when the threshold was lowered ($z > 2.58$) and the search radius (SR) was decreased ($SR = 5$).

Verbal vs. tonal rehearsal in nonmusicians – By contrasting the verbal vs. the tonal rehearsal condition directly ($z > 3.09$, $k = 10$, $SR = 10$), the verbal rehearsal showed stronger activation of the left insular cortex, the left pre-SMA and the left PMv, the SPL and IPS bilaterally, as well as the left IPL (see Fig. 10.3 and Tab. 10.1). However, the left pars opercularis showed significant stronger activation during the verbal rehearsal condition with only 9 (instead of 10) voxels per cluster of activation. The opposite contrast, tonal – verbal rehearsal ($z > 3.09$, $k = 10$, $SR = 10$), revealed more activation of the left cingulate gyrus and the left angular gyrus (see Fig. 10.3 and Tab. 10.1).

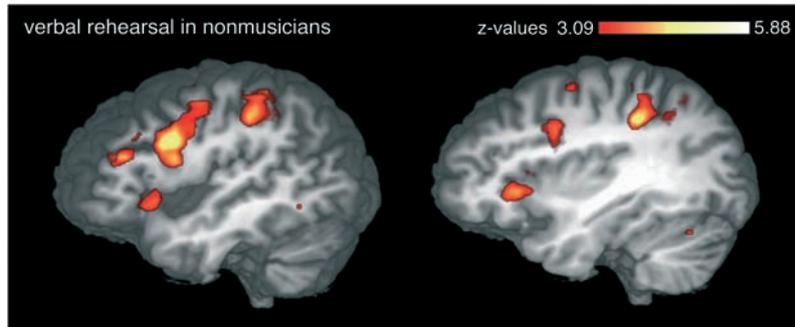


Fig. 10.1: Verbal Rehearsal vs. pink noise Nonrehearsal in Nonmusicians ($z > 3.09$, $k = 10$, $SR = 10$)

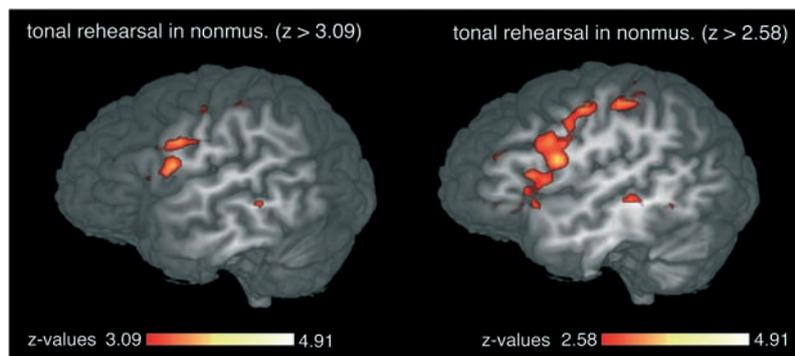


Fig. 10.2: Tonal Rehearsal vs. pink noise Nonrehearsal in Nonmusicians ($z > 3.09$, $k = 10$, $SR = 10$)

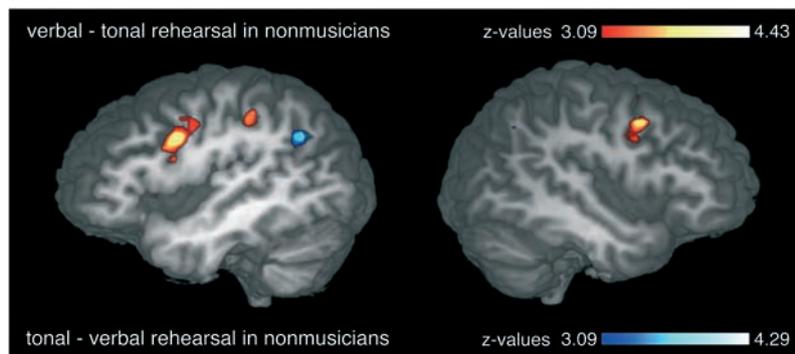


Fig. 10.3: Verbal vs. tonal Rehearsal in Nonmusicians ($z > 3.09$, $k = 10$, $SR = 10$)

Tab. 10.1: Activated Brain Areas during the Comparison between verbal and tonal Rehearsal in Nonmusicians

area	left hemisphere					right hemisphere				
	BA	x	y	z	z-value	BA	x	y	z	z-value
nonmusicians: verbal – tonal rehearsal ($z > 3.09, k = 10, SR = 10$)										
pars opercularis ¹⁹	44	-56	12	6	3.79					
insular cortex		-32	24	3	3.96					
pre-SMA	6	-2	24	42	3.84					
PMv	6	-44	0	33	4.44	6	43	6	39	4.35
SPL	7	-26	-66	51	3.50	7	28	-63	48	3.58
IPS	7/40	-29	-51	39	4.01	7/40	28	-54	42	3.57
IPL	40	-38	-39	42	4.29					
nonmusicians: tonal – verbal rehearsal ($z > 3.09, k = 10, SR = 10$)										
cingulate gyrus	31	-8	-45	30	3.45					
angular gyrus	39	-47	-60	33	4.29					

Key and non-key in nonmusicians – In accordance with the behavioural data, the nonmusicians did not show a functional difference ($z > 3.09, k = 10, SR = 10$), neither in the perception nor in the rehearsal, between key and non-key sequences.

10.5 Discussion

10.5.1 Behavioural Data

As stated in Hypothesis 1, nonmusicians showed a better performance, in terms of RT and CR, for verbal stimuli, compared to tonal stimuli. Because nonmusicians have to actively use their verbal WM in everyday life, but not their tonal WM, this difference is thought to be due to the unequal amount of training between verbal and tonal material. It is important to note that nonmusicians performed in the tonal condition significantly above chance, which demonstrates that nonmusicians were able to perform the tonal WM task.

Although no significant performance difference was observed between key and non-key sequences, a tendency towards a better performance for the key sequences was displayed by the nonmusicians. This tendency shows that also nonmusicians may have an implicit sense for tonality, which is according to the literature (Koelsch et al., 2000; Tillmann et al., 2003), and which they could use, to a certain degree, to rehearse these abstract tonal sequences. However, Maess et al. (2001) and Tillmann et al. (2003) used musical stimuli that built up strong musical expectations about the harmonic progressions, which were subsequently violated. In the present study the auditory stimuli did not have the potential to build up such a context (e.g., the non-key sequences are unstructured in terms of musical regularities), and therefore no expectations were built up or violated. Secondly, in the above mentioned studies (Maess et al., 2001; Tillmann et al., 2003) chords were used, whereas in Experiment 3 sequences which consisted of sine wave tones were presented.

¹⁹ This cluster of activation consists of 9 voxels.

Taken together, in this study no significant differences between the tonal (key) and atonal (non-key) sequences were observed in nonmusicians. The used musical stimuli presumably were too abstract (sine wave tones) and the tonal context too subtle to be clearly recognised by nonmusicians.

10.5.2 fMRI Data

10.5.2.1 Verbal and tonal Perception in Nonmusicians

The stronger activation of the left middle occipital gyrus during the verbal perception compared to the tonal perception could reflect the access of visual images or visualisation (Kosslyn et al., 2001), with which the nonmusicians tried to memorise the verbal material, which was not possible for the tones for this group of participants.

When lowering the threshold ($z > 2.58$), the verbal perception activated stronger the right STS, which is in accordance with the literature (e.g., Binder et al., 2000; Dehaene-Lambertz et al., 2005; Jancke et al., 2002; Mottonen et al., 2006) and the results of the comparison of verbal and tonal perception in all groups, which was interpreted in Experiment 3 (see Chapter 9.5). The tonal perception did not activate additional areas when compared to the verbal condition. This has been also described in the literature (e.g., Binder et al., 2000).

10.5.2.2 Verbal and tonal rehearsal in Nonmusicians

During the verbal rehearsal, compared to the pink noise nonrehearsal, nonmusicians activated a WM network, including the left mid-DLPFC, the pars opercularis/the premotor cortex bilaterally, the left pre-SMA, the IPS bilaterally, the left IPL, as well as the cerebellum bilaterally. These areas have been reported to be involved in verbal WM tasks (e.g., Baddeley, 2003; Petrides, 2000a; see Chapter 9.5.2) and were formulated to be involved during verbal WM (Hypothesis 2).

The overall activation pattern elicited by the tonal rehearsal was not as strong as the activation during the verbal rehearsal. Nevertheless, a WM network was activated including the left pars orbitalis, the left pre-SMA, the left PMv, as well as the left IPL, and the right cerebellum. The left pars opercularis showed activation, but only when the threshold ($z > 2.58$) and the search radius (SR = 5) were lowered. All areas, except the SMG, showed activation as stated in Hypothesis 3. However, activation of the left angular gyrus/SMG were observed when comparing the tonal against the verbal rehearsal at a lower threshold ($z > 2.58$).

These observed areas have been reported in tonal (and verbal) WM tasks (e.g., Baddeley, 2003; Gaab, Gaser et al., 2003; Gaab, Keenan et al., 2003; Gruber & von Cramon, 2003;

Petrides, 2000a; see Chapter 9.5.2). The involvement of the left pars opercularis is involved during verbal and tonal WM, but to a lesser degree in tonal WM. Evaluating the verbal and the tonal rehearsal, both contrasted against pink noise nonrehearsal, it appeared that both conditions activated similar WM associated areas, as postulated in Hypothesis 3.

Nevertheless, when contrasting the verbal vs. the tonal rehearsal, the left pars opercularis, the left insular cortex, the left pre-SMA, the PMv bilaterally, the SPL and IPS bilaterally, as well as the left IPL showed stronger activation during the verbal rehearsal. Because it was hypothesised that verbal rehearsal, when compared to tonal rehearsal, would activate a more left-lateralised network, which includes Broca's area, the premotor cortex, as well as parietal and cerebellar areas, the obtained results support Hypothesis 2.

Broca's area – The stronger involvement of the left pars opercularis during the verbal, compared to the tonal rehearsal, is in accordance with the literature. Broca's area (BA 44) has been shown to be heavily involved in the processing of language, or more specifically in the processing of syntactic and semantic language information (for an overview see Friederici, 2002 and Chapter 2). Because with higher syntactical complexity in a sentence, and thus increasing WM demands, Fiebach et al. (2001) suggested that the observed activation in Broca's area during syntactic processing might reflect WM related processes which are necessary to process 'long-distance syntactic dependencies' rather than only reflecting the processing of syntactical language information per se. In a subsequent fMRI study, Fiebach et al. (2005) supported this assumption. They showed increased activation of Broca's area when processing syntactically and WM demanding sentences compared to sentences with a low WM load but a complex syntax. However, the present study did not contain syntactic language information. Therefore, it is suggested that Broca's area is strongly involved when verbal information has to be maintained in WM, compared to tonal information, independent of syntactical information processing. Another interpretation is that this difference in activation is due to the significant behavioural performance difference between both types of stimuli and cannot solely be ascribed to the difference in stimulus modality. If this argument holds true, then the activation should decrease in this area when the behavioural difference between both conditions decrease, which might be the case in RP musicians. Therefore, this activation is analysed and discussed in detail in the RP musicians (see Chapter 11.5.2).

The premotor areas play an important role during the verbal rehearsal in WM tasks (Baddeley, 2003; Crottaz-Herbette et al., 2004; Gruber, 2001; Gruber & von Cramon, 2003; Kirschen et al., 2005; Paulesu et al., 1993; Smith & Jonides, 1998). Haller, Radue, Erb, Grodd, and Kircher (2005) demonstrated bilateral premotor activation during an overt

sentence production, and Braver et al. (1997) showed that the activation in the premotor cortex increased with the number of verbal items to be rehearsed. Additionally, Gruber and von Cramon (2003) reported that the left premotor cortex was involved during verbal rehearsal, but not during the rehearsal of visual material. This could be due to the fact that visual material is most often not rehearsed using a phonological (motor) code, which is comparable to subvocal speech (Baddeley, 2003). In addition, in Chapter 3 it was described that the verbal rehearsal is comparable to subvocal speech (Baddeley, 1992, 1998, 2003). A lesion study (Vallar et al., 1997) showed, that the patient T.O. was impaired to maintain verbal items in the articulatory rehearsal process, which was thought to be due to the lesion in the premotor and rolandic regions. Further evidence for the motor coding of information in WM comes from sign language. It has been shown that there is a length effect (comparable with the word length effect) in signers for long compared to short signs (for an overview see Wilson, 2001). Additionally it has been shown that children, who misarticulate certain phonemes (e.g., /w/ for /r/) do not have problems to understand words that contain that phonemes and can point to the corresponding pictures, but if asked to perform a WM task with these words, they substitute the phonemes again and point to the wrong pictures (e.g. wing instead of ring) (for an overview see Wilson, 2001). Therefore, the stronger premotor activation during the verbal subvocal rehearsal implicates that the verbal material, which has to be rehearsed, is translated from a sensory input code into an internally rehearseable motor code, which is usually used for verbalising this verbal material. The activation of the premotor cortex was observed in both conditions, in the verbal as well as in the tonal rehearsal condition. But, during the verbal rehearsal the PMv was bilaterally significantly more strongly activated compared to the tonal rehearsal. Because nonmusicians are experts for language (they are trained daily to verbalise), but not for music, they might not have such a strong association between the sensory tonal input and a corresponding motor representation.

IPL – Another important functional difference between the rehearsal of verbal and tonal information is the activation of the left IPL. The IPL has been suggested to be involved in verbal WM as the underlying neural correlate of the phonological store (e.g., Awh et al., 1996; Braver et al., 1997; Chen & Desmond, 2005; Crottaz-Herbette et al., 2004; Gruber, 2001; Henson et al., 2000; Jonides et al., 1998; Kirschen et al., 2005; Paulesu et al., 1993; Ravizza et al., 2004; Vallar et al., 1997). In Fig. 10.4 Talairach coordinates of activation foci in the parietal lobe during verbal WM tasks in several studies were exemplarily visualised (Braver et al., 1997; Crottaz-Herbette et al., 2004; Henson et al., 2000; Ravizza et al., 2004)

in comparison to the parietal activation observed in Experiment 3A. In other studies WM related activation in the parietal lobe were located slightly more inferior than in this study (Baddeley, 2003), however activation of the SPL and IPS have been repeatedly reported during verbal WM, indicating that also these parts of the brain is involved in the phonological storage (Awh et al., 1996; Crottaz-Herbette et al., 2004; Gruber, 2001; Gruber & von Cramon, 2003). In the WM model by Baddeley and Hitch (1974) this store refers to a temporary storage of “acoustic or speech based information” (Baddeley, 1992; p. 558). Because of the superior behavioural performance of the verbal rehearsal and the significantly stronger activated left IPL, it is speculated that the IPL activation in the present experiment reflects the underlying correlate of the phonological store, which presumably can be better used for verbal material. Because nonmusicians are less experienced to maintain tonal information in WM, they might be able to use this phonological store in a more effective way for verbal information, i.e. this store is only partly accessible for tonal information. However, the present experiment was not designed to disentangle the rehearsal component and the phonological store.

Therefore, this interpretation might be ventured for several reasons. First, studies identified different locations of the phonological store. Second, not only the location of the

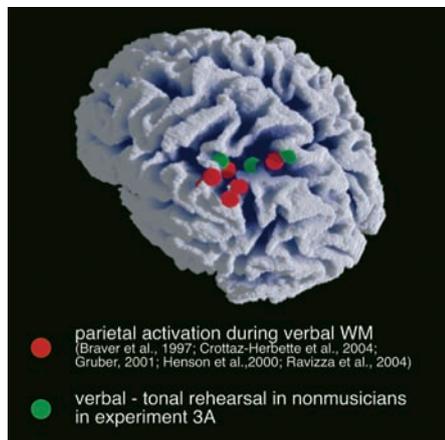


Fig. 10.4: Left parietal Activation during verbal WM Tasks

phonological store, but even its existence have been discussed rather controversially in the literature (e.g., Chein & Fiez, 2001; Hickok et al., 2003; Jones et al., 2004; Ravizza et al., 2004). Ravizza et al. (2004) observed two separate storage systems in the IPL, but they showed only partly the properties predicted by the WM model (Baddeley & Hitch, 1974). The dorsal inferior parietal cortex (DIPIC) showed load effects, but no specificity for verbal (phonological encodable) material. Nevertheless, the described location of this DIPIC activation is quite near the IPL activation in the present study²⁰. The ventral inferior parietal cortex (VIPIC) was suggested to be more associated with attention.

²⁰ One exemplary Talairach coordinate in the Ravizza et al. (2004) study of DIPIC activation: -37 -42 37, Talairach coordinates for stronger IPL activation during the verbal rehearsal, compared with tonal rehearsal, in the present study: -38 -39 42.

These diverse results (e.g., Chein & Fiez, 2001; Hickok, Buchsbaum, Humphries, & Muftuler, 2003; Jones, Macken, & Nicholls, 2004; Ravizza, Delgado, Chein, Becker, & Fiez, 2004) are likely to be due to the fact that the IPL is an association area, known to subserve many functions, e.g., attention (Corbetta & Shulman, 2002), compatibility in a Stroop task, orientation, division of attention, spatial localisation, reaching and grasping, processing of shape, spatial and non-spatial WM, mental imagery, tasks switching, mental rotation, alertness, calculation, pain processing, and meditation (for an overview see Cabeza & Nyberg, 2000; Culham & Kanwisher, 2001). Especially the involvement of the IPL in attention makes it difficult to interpret the observed activation in the present experiment. Further studies are needed to investigate this issue.

Nevertheless, in the last years it became obvious that a very important function of the IPL had been previously neglected. The IPL plays also an important role during motor related tasks and motor control (Fogassi et al., 2005; Petrides & Pandya, 1984; Rizzolatti, Fogassi, & Gallese, 1997; Rizzolatti & Luppino, 2001; Rizzolatti, Luppino, & Matelli, 1998), i.e. it connects sensory information with information necessary for a motor response (Fogassi et al., 2005; Sakata, Taira, Kusunoki, Murata, & Tanaka, 1997) and forms internal representations of action (Rizzolatti & Luppino, 2001). As it was described in primates, the posterior parietal cortex in the monkey is arranged in a mosaic order, each of these areas receives specific sensory input and converts it into appropriate information that can be used for an action response (Fogassi et al., 2005; Fogassi & Luppino, 2005). The posterior parietal cortex in the monkey is, as anatomical studies showed, reciprocally connected with the motor cortex (Fogassi & Luppino, 2005). In addition, lesion studies in primates and humans show motor related impairments after a lesion in the posterior part of the parietal lobule (e.g., misreaching, apraxia, motor neglect, for an overview see Fogassi & Luppino, 2005). Fogassi et al. (2005) observed in an experiment with monkeys that neurons in the posterior parietal lobule were activated when the monkey performed a motor action, and observed the experimenter performing a similar motor response. Therefore, the authors termed these neurons parietal mirror neurons. Furthermore, neurons in the posterior parietal cortex were involved in the performance of goal-directed hand and mouth movements (Fogassi et al., 2005). These neurons are even speculated to have similar functions to those in the ventral premotor area, which is connected with the IPL (Fogassi & Luppino, 2005). This motor interpretation fits nicely with the stronger activation of the premotor areas during the verbal rehearsal, compared to the tonal rehearsal. It could be assumed that the premotor areas and the IPL are involved in coding motor representations (see also Chapter 11.5.2.5). However,

the connection to motor related responses and transformation of the IPL does not contradict the potential existence of a phonological store, but it might indicate, how this information (motor coded) is stored in the IPL.

IPS/SPL – The IPS and SPL bilaterally showed stronger activation during the verbal, compared to the tonal rehearsal. This is in accordance with the literature, where the SPL and the IPS have been reported to be involved during WM tasks (Awh et al., 1996; Baddeley, 2003; Chen & Desmond, 2005; Crottaz-Herbette et al., 2004; Gruber, 2001; Gruber & von Cramon, 2003; Henson et al., 2000; Jonides et al., 1998; Kirschen et al., 2005; Paulesu et al., 1993). In nonmusicians it seems to play an important role during verbal WM, compared to tonal WM processes. As a part of the parietal cortex, and therefore of the association cortex, the above discussed problem concerning the manifold functions is also relevant for these structures.

Left insular cortex – In the present study, the left insula showed stronger activation during the verbal rehearsal, compared to the tonal rehearsal. The insula has been described to be engaged during the processing of auditory language and music information (Bamiou et al., 2003; Friederici, Ruschemeyer, Hahne, & Fiebach, 2003; Platel, Baron, Desgranges, Bernard, & Eustache, 2003; Rumsey et al., 1997), as well as during verbal WM (for an overview see Bamiou et al., 2003). It is suggested that this activation is due to verbal WM processes rather than to semantic language processing, because the names of the tones of the Western musical scale do not have a semantic meaning for nonmusicians.

The opposite contrast, tonal – verbal rehearsal, revealed more activation of the left posterior cingulate gyrus and the left angular gyrus.

Left posterior cingulate gyrus – It was reported in a recent study that activity in the posterior cingulate cortex is likely to be associated with the switch of a strategy during a visual WM task (Y. Kondo et al., 2005). Therefore, this increased activity in the posterior cingulate cortex is interpreted as the change of a strategy during the tonal WM task in nonmusicians.

Left angular gyrus – This area is usually known to be involved during language, especially during semantic processing (Binder et al., 2003; Binder, Medler, Desai, Conant, & Liebenthal, 2005; Friederici, 2002; Poldrack et al., 2001). Notwithstanding, activation of this area has been observed during various tasks. E.g., the angular gyrus appeared to play a role during calculation/comparing numbers (Gobel, Walsh, & Rushworth, 2001), in learning to process an artificial grammar (Skosnik et al., 2002), in spatial orientation (Blanch, Brennan, Condon, Santosh, & Hadley, 2004; Chambers, Payne, Stokes, & Mattingley, 2004), and in

processing categorical and spatial relations (Baciu et al., 1999). Additionally, the angular gyrus is also engaged during tone-related processes, e.g., during the processing of prosodic information (Hesling, Clement, Bordessoules, & Allard, 2005), during the perception and processing of voices (Stevens, 2004), and during musical priming, where it was involved in the processing of musical structure (Tillmann et al., 2003). Because the angular gyrus appears to subservise manifold tasks, it is challenging to interpret the stronger activation of the angular gyrus during the tonal rehearsal, when compared to the verbal rehearsal. One possible explanation could be that nonmusicians use a special strategy to remember the tones, e.g., involving the association of spatial information (Baciu et al., 1999; Blanch et al., 2004; Chambers et al., 2004) to image the ups and downs of the tonal sequences.

10.6 Summary

Potential differences and similarities in the neural pattern underlying language and music processing, especially for WM processes, have still remained elusive. Experiment 3A was designed to pursue this question using verbal and tonal stimuli.

Participants showed a better behavioural performance for the verbal compared to the tonal stimuli. Because nonmusicians have to actively use their verbal WM in everyday life, but to a lesser extent their tonal WM, this difference is presumably a consequence of the unequal amount of training between verbal and tonal material.

During the verbal rehearsal nonmusicians activated a known WM network, including the left mid-DLPFC, the pars opercularis/premotor cortex bilaterally, the left pre-SMA, the IPS bilaterally, the left IPL, as well as the cerebellum bilaterally. These areas have been reported to be involved in verbal WM tasks (e.g., Baddeley, 2003; Gruber & von Cramon, 2003; Petrides, 2000a; see Chapter 9.5.2).

Notably, a known WM network was activated during the rehearsal of sine wave tones as well, including the left pars orbitalis, the left pre-SMA, the left PMv, and the right cerebellum. Although, the neural network underlying tonal rehearsal showed weaker activation. When comparing the verbal directly against the tonal rehearsal, Broca's area, the premotor areas bilaterally, the left IPL, and the SPL bilaterally were more strongly involved during the verbal WM task. Because Broca's area is known to be involved in the processing of language (for an overview see Friederici, 2002) and during verbal WM (Awh et al., 1996; Chen & Desmond, 2005; Fiez et al., 1996; Gruber, 2001; Gruber & von Cramon, 2003; Paulesu et al., 1993; Ravizza et al., 2004), these results propose a special role of Broca's area during verbal WM tasks, when compared to a tonal WM task. Importantly, the more pronounced involve-

ment of the premotor areas appear to reflect a stronger connection between the sensory stimulus and a motor representation in the verbal modality, which can be used to rehearse the verbal information internally.

An interesting finding was the stronger activation of the left IPL during the verbal, compared to the tonal rehearsal, in nonmusicians. One interpretation is that the left IPL indicates a unique role for the phonological store for verbal material (Baddeley, 2003; Braver et al., 1997; Crottaz-Herbette et al., 2004; Gruber & von Cramon, 2003; Paulesu et al., 1993; Ravizza et al., 2004). Alternatively, the IPL might be engaged in motor representations (Fogassi et al., 2005; Fogassi & Luppino, 2005; Rizzolatti & Luppino, 2001), which would fit nicely with the interpretation of the stronger activation of the premotor areas. However, both interpretations are not contradictory, but suggest an idea how the verbal material is decoded in the phonological store.

Importantly, this experiment indicates a considerable overlap between the neural networks underlying WM for verbal and tonal stimuli. However, there are also areas that seem to be engaged specifically, and/or are more involved in verbal (e.g., Broca's area, left IPL, premotor areas) or tonal (e.g., angular gyrus) WM processes in nonmusicians. Therefore, the present experiment suggests that the main neural networks related to WM are similar for both types of stimuli, but each network emphasises and/or involves slightly different (neural) subcomponents. This question is further pursued in Experiment 3B.

Chapter 11

Experiment 3B – The Effect of Musical Expertise on WM Processes

11.1 Introduction

Previous studies demonstrated anatomical and functional differences between professional musicians and nonmusicians (Koelsch et al., 1999; Munte et al., 2002; Schlaug, 2001; Schneider et al., 2002; see Chapter 4.2). Furthermore, Experiments indicated that musical expertise has an influence on the cognitive and functional organisation of WM (Gaab & Schlaug, 2003; Pechmann & Mohr, 1992; see Chapter 3.2). Additionally, fMRI experiments showed that WM training induced changes in WM associated brain areas, mostly related to frontal and parietal regions (Jansma et al., 2001; Olesen et al., 2004; see Chapter 4.3). The Experiment 3B was conducted to investigate whether musical expertise and musical training might have an influence on perception and WM related processes for tonal and verbal stimuli by comparing WM associated neural activation between RP musicians and nonmusicians during a tonal and verbal WM task.

11.2 Hypotheses

1. It was hypothesised that RP musicians show a better performance for tonal stimuli compared to nonmusicians (for an overview see Carterette & Kendall, 1999 and appendix pretest 1-4).
2. Because RP musicians train their verbal and their tonal WM, it was assumed that they show less difference in the activation pattern between both types of stimuli, e.g., in premotor areas or in the IPL, compared to nonmusicians (see Chapter 10).
3. RP musicians were hypothesised to show a superior performance for key compared to non-key sequences (Koelsch, Schroger et al., 2002; Tillmann et al., 2003). Additionally, RP musicians were hypothesised to show an enhanced activation of the IFG bilaterally during the key compared to the non-key sequences (Koelsch, Schroger et al., 2002; Tillmann et al., 2003).
4. Differences in the brain activation between RP musicians and nonmusicians for tonal stimuli were assumed, e.g., the increased involvement of parietal areas (Gaab & Schlaug, 2003; Olesen et al., 2004).

11.3 Methods

11.3.1 Participants

16 right-handed (9 male) professional musicians without AP took part in this experiment. The age ranged within this group from 20 to 27 years, resulting in a mean age of 23.50 years ($SEM = 0.63$ years). Musicians were students at the “University of Music and Theatre Mendelssohn Bartholdy” in Leipzig and studied an instrument (e.g., piano, violin, saxophone, etc.). Singers were not included in this experiment in order to reduce the inter-subject variability. Musicians started their musical training at an average age of 6.10 years ($SEM = 0.19$ years) and practiced several hours each day. Because of their fluent German, two non-German native speakers (one male) were included in the analysis. Although these musicians without AP claimed to have no AP, they were asked to try to perform the AP test. All RP musicians underwent this test.

11.3.2 Stimuli, Experimental Design, Image Acquisition and Processing

The stimuli, the experimental design, the fMRI paradigm, as well as image acquisition and processing are described in Chapter 9.3.

11.4 Results

11.4.1 Behavioural Data

Verbal vs. tonal – RP musicians performed 88.13% ($SEM = 1.98%$) correctly in the verbal condition, whereas they answered in 69.53% ($SEM = 2.64%$) of the trials correctly during the tonal condition. For the verbal sequences RP musicians answered within 1386 ms ($SEM = 66$ ms) and for the tonal sequences within 1614 ms ($SEM = 90$ ms). A paired-samples *t*-test revealed a significantly higher percentage of correct answered trials during the verbal condition ($t(15) = -6.003, p = .000$), and in addition RP musicians showed a faster RT for the syllables compared to the sine wave tones ($t(15) = 5.626, p = .000$) (see Appendix Tab. A.2 and A.3).

Key vs. non-key and incongruent vs. congruent – The RP musicians showed a significantly higher performance for the key sequences with 72.50% ($SEM = 2.28%$) of CR, compared to the non-key sequences with 66.56% ($SEM = 3.32%$) of CR ($t(15) = 2.775, p = .014$) as tested with a paired-samples *t*-test. The RT for the key sequences were 1593 ms ($SEM = 82$ ms), and for the non-key sequences 1640 ms ($SEM = 100$ ms). There was no significant difference between both conditions in terms of the RT ($t(15) = -1.289, p = .217$). By applying a paired-samples *t*-test no difference was observed between the tonal incongruent (CR: $M = 70.94%$,

$SEM = 3.22\%$; RT: $M = 1609$ ms, $SEM = 90$ ms) and tonal congruent (CR: $M = 68\%$, $SEM = 2.56\%$; RT: $M = 1623$ ms, $SEM = 90$ ms) sequences in terms of CR ($t(15) = 1.160$, $p = .264$) and RT ($t(15) = -0.819$, $p = .426$) in RP musicians (see Appendix Tab. A.2 and A.3) as revealed by applying paired-samples t -tests.

AP test – RP musicians performed around chance level (25%) during the AP test 1 and 2 (see Appendix Tab. A.2 and A.3).

Correlations – No significant correlation was observed between the behavioural performance in the tonal WM task and the age of musical commencement²¹.

Comparison between RP musicians and nonmusicians – To investigate potential differences between the groups (nonmusicians, RP musicians and AP musicians) a one-way-ANOVA was applied and subsequently Scheffé post-hoc tests (SPHT) were calculated. The results are summarised in table A.4 of the Appendix.

There was no significant difference during the verbal condition between RP musicians and nonmusicians concerning the percentage of CR ($F(2,38) = 2.548$, $p = .092$; SPHT: $p = .407$) or the RT ($F(2,38) = 5.898$, $p = .006$; SPHT: $p = .277$). This was also true, when testing the nonmusicians against the 14 native German-speaking RP musicians (CR: $M = 88.13\%$, $SEM = 2.23\%$, $F(2,36) = 2.444$, $p = .101$; SPHT: $p = .446$; RT: $M = 1400$ ms, $SEM = 73$ ms $F(2,36) = 4.489$, $p = .018$; SPHT: $p = .051$).

However, RP musicians showed a significantly higher percentage of CR for the tonal sequences compared to nonmusicians ($F(2,38) = 19.404$, $p = .000$; SPHT: $p = .001$), although there was only a marginally significant difference between the RT for this condition between both groups ($F(2,38) = 4.413$, $p = .019$; SPHT: $p = .054$). RP musicians showed a better performance for the key sequences ($F(2,38) = 25.330$, $p = .000$; SPHT: $p = .000$) as well as for the non-key sequences ($F(2,38) = 11.215$, $p = .000$; SPHT: $p = .042$), compared to nonmusicians. There was no difference in the RT between both groups for the key ($F(2,38) = 4.018$, $p = .026$; SPHT: $p = .074$), but for the non-key sequences ($F(2,38) = 4.633$, $p = .016$; SPHT: $p = .043$).

11.4.2 fMRI Data

Verbal and tonal perception vs. silence in RP musicians – During the verbal and tonal perception, both compared to the silence baseline ($z > 3.09$, $k = 20$, $SR = 15$), the

²¹ Correlations for the behavioural performance in the tonal WM task with the age of musical commencement: tonal CR: $r = .315$; $p = .235$; tonal RT: $r = .205$; $p = .447$; key CR: $r = .447$; $p = .083$; key RT: $r = .207$; $p = .442$; non-key CR: $r = .193$; $p = .473$; non-key RT: $r = .194$; $p = .472$

RP musicians ($N = 16$) showed significant activation of the STG bilaterally (see Appendix Fig. A.5 and Tab. A.12).

Verbal vs. tonal perception in RP musicians – By comparing the verbal vs. the tonal perception, during the verbal condition ($z > 3.09$, $k = 10$, $SR = 10$) stronger activation was observed in the right STG/STS (see Fig. 11.1 and Tab. 11.1). No area showed stronger activation in the contrast tonal – verbal perception ($z > 3.09$, $k = 10$, $SR = 10$).

Tab. 11.1: Brain Areas activated during the Comparison between verbal and tonal Perception in RP musicians

area	left hemisphere					right hemisphere				
	BA	x	y	z	z-value	BA	x	y	z	z-value
RP musicians: verbal – tonal perception ($z > 3.09$, $k = 10$, $SR = 10$)										
frontopolar area	10	-20	54	18	4.65					
SFG	8	-8	42	48	4.70					
	9	-8	51	36	3.83					
posterior insular cortex		-32	-18	27	3.51					
cingulate gyrus						24	1	27	-6	4.61
						24	1	-15	39	3.46
orbitofrontal cortex	11	-11	33	-15	3.60					
M1	4	-47	-12	42	4.22					
postcentral gyrus	2	-44	-21	30	3.61					
paracentral lobule	5/7	-2	-39	57	4.35					
STG						42	58	-15	9	3.71
STG/STS						21/22	52	-15	0	3.51
MTG	21	-56	-24	-9	3.86					
	39	-44	-66	21	3.75					
ITG	19/37	-50	-72	0	4.15					
precuneus	7	-5	-57	33	3.91					
	31	-17	-57	21	3.72					
putamen		-23	0	0	3.95					
RP musicians: tonal – verbal perception ($z > 3.09$, $k = 10$, $SR = 10$)										
not significant (n.s.)										

Verbal rehearsal vs. pink noise nonrehearsal in RP musicians – During the verbal rehearsal ($z > 3.09$, $k = 10$, $SR = 10$) a neural network was activated in RP musicians, which consisted of the left pars opercularis, the insular cortex bilaterally, the pre-SMA bilaterally, the premotor cortex bilaterally, the left SPL and IPS (activation spread also in the left IPL), as well as the right cerebellum (see Fig. 11.2 and Appendix Tab. A.13).

Tonal rehearsal vs. pink noise nonrehearsal in RP musicians – During the tonal rehearsal ($z > 3.09$, $k = 10$, $SR = 10$) the RP musicians recruited following brain areas: the left mid-DLPFC, the left pars opercularis, the insular cortex bilaterally, the pre-SMA bilaterally, the PMd and PMv bilaterally, the left SPL, IPS and IPL, and the cerebellum bilaterally (see Fig. 11.3 and Appendix Tab. A.13).

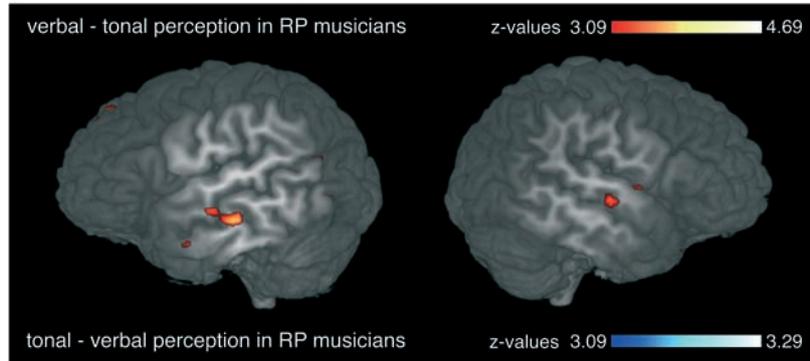


Fig. 11.1: Verbal vs. tonal Perception in RP musicians ($z > 3.09$, $k = 10$, $SR = 10$)

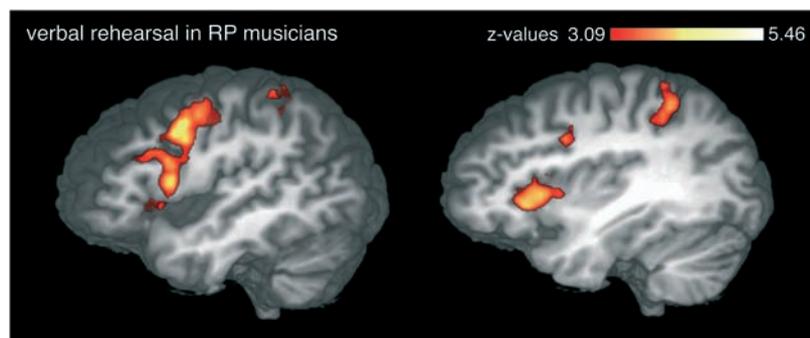


Fig. 11.2: Verbal Rehearsal vs. Pink Noise Nonrehearsal in RP mus. ($z > 3.09$, $k = 10$, $SR = 10$)

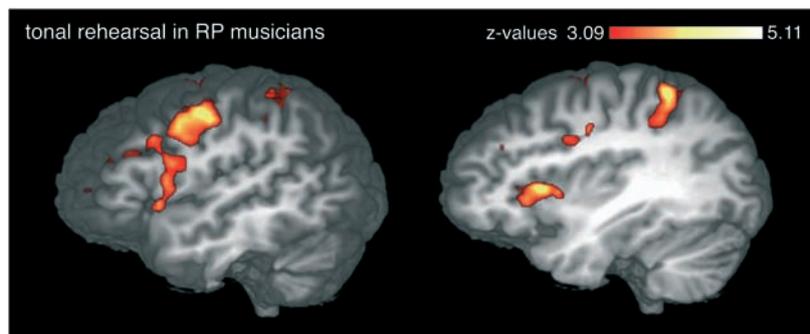


Fig. 11.3: Tonal Rehearsal vs. Pink Noise Nonreh. in RP musicians ($z > 3.09$, $k = 10$, $SR = 10$)

Verbal vs. tonal rehearsal in RP musicians – During the verbal rehearsal ($z > 3.09$, $k = 10$, $SR = 10$) the left pars opercularis and the right pre-SMA showed significantly more activation than during the tonal rehearsal condition (see Fig. 11.4 and Tab. 11.2).

During the tonal rehearsal ($z > 3.09$, $k = 10$, $SR = 10$), compared to the verbal rehearsal, significantly stronger activation was displayed in the left frontopolar area, the superior frontal gyrus bilaterally, the left middle frontal gyrus and the right medial frontal gyrus, the left pars orbitalis, the left insular cortex, the cingulate gyrus bilaterally, the right SMA, the IPL/SMG bilaterally, the right supramarginal and angular gyrus, the right STG/STS, as well as visual areas (e.g., lingual gyrus and cuneus bilaterally)(see Fig. 11.4 and Tab. 11.2).

Tab. 11.2: Brain Areas activated during the Comparison between verbal and tonal Rehearsal in RP musicians

area	left hemisphere					right hemisphere				
	BA	x	y	z	z-value	BA	x	y	z	z-value
RP musicians: verbal – tonal rehearsal ($z > 3.09$, $k = 10$, $SR = 10$)										
pars opercularis/IFG	44	-50	9	12	3.54					
pre-SMA						6	4	21	48	3.78
RP musicians: tonal – verbal rehearsal ($z > 3.09$, $k = 10$, $SR = 10$)										
frontopolar area	10	-17	45	12	3.85					
SFG	8	-17	42	42	3.88	8	16	39	39	3.80
middle frontal gyrus	8	-32	27	48	4.82					
medial frontal gyrus						8	7	33	45	3.50
pars orbitalis/IFG	47	-35	33	-12	4.07					
insular cortex		-32	-36	24	4.02					
cingulate gyrus	23/24	-2	-12	33	4.09	25	1	21	-6	4.42
	31	-14	-24	39	4.44	31	13	-18	39	3.92
	31	-5	-42	42	4.32	31	4	-45	30	4.27
	32	-11	42	0	4.33					
SMA						6	1	-24	54	3.50
PMv/M1						4/6	49	-6	6	3.72
postcentral gyrus	2	-44	-21	24	3.32	3	46	-12	48	3.60
paracentral lobe						5	16	-33	45	4.37
IPL/SMG	40	-53	-57	39	4.58	40	52	-36	27	4.70
SMG						40	34	-48	24	3.69
						40	37	-27	18	4.13
angular gyrus						39	55	-48	24	4.54
STG						22	61	-15	6	3.68
						22	46	3	-6	4.47
STS						21/21	46	-15	-9	4.67
MTG	21	-56	-15	-12	3.93					
	21	-59	-30	0	4.39					
posterior MTG						39	46	-66	12	3.67
precuneus	7	-11	-60	39	4.52	7	19	-69	36	3.98
						18/31	1	-66	27	4.36
cuneus	18	-5	-81	21	4.02	18	16	-87	21	3.98
	18/19	-5	-81	33	4.46	19	10	-81	36	4.53
fusiform gyrus	18	-26	-78	0	3.71					
lingual gyrus	18	-11	-72	-3	3.98	18	7	-72	3	4.47
	19	-29	-60	0	4.83	18/19	22	-72	0	3.90
parahippocampal gyrus						19	19	-48	-3	4.20
putamen		-23	9	3	4.11		22	3	3	4.68
		-29	-3	0	4.42					
cerebellum		-14	-87	-15	3.80					

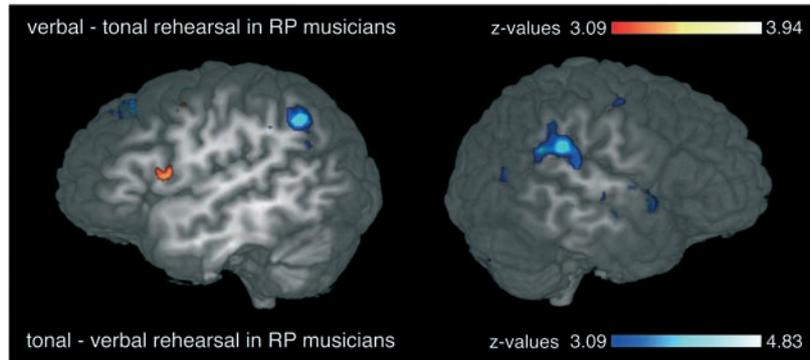


Fig. 11.4: Verbal vs. tonal Rehearsal in RP musicians ($z > 3.09$, $k = 10$, $SR = 10$)

Key and non-key perception and rehearsal in RP musicians – There was no significant difference between the key and non-key perception in RP musicians ($z > 3.09$, $k = 10$, $SR = 10$). However, when comparing the key and non-key rehearsal in RP musicians ($z > 3.09$, $k = 10$, $SR = 10$), the key rehearsal showed stronger activation of the right mid-DLPFC (although this activation only included 8 suprathreshold voxels), the right inferior precentral sulcus (IPCS), and the premotor cortex bilaterally. The non-key rehearsal did not show any additional activation when compared to the key rehearsal (see Fig. 11.5 and Tab. 11.3).

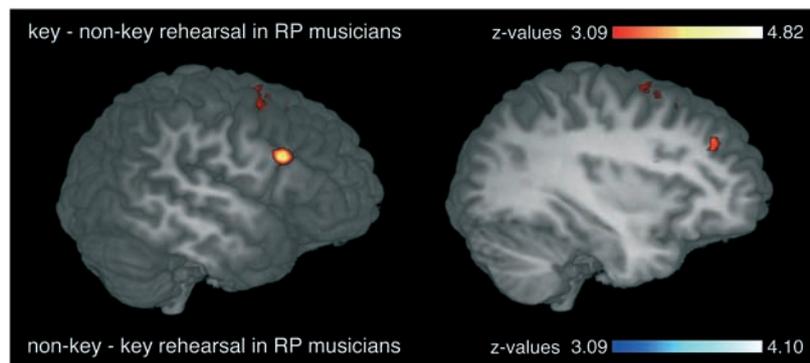


Fig. 11.5: Key rehearsal vs. non-key rehearsal in RP musicians ($z > 3.09$, $k = 10$, $SR = 10$)

Tab. 11.3: Comparison of Brain Activations in RP musicians during key and non-key Rehearsal

area	left hemisphere					right hemisphere				
	BA	x	y	z	z-value	BA	x	y	z	z-value
RP musicians: key – non-key rehearsal ($z > 3.09, k = 10, SR = 10$)										
mid-DLPFC ²²						9/46	31	36	33	3.81
IPCS						6/9/44	49	12	24	4.83
PMd	6	-38	-3	57	4.04	6	28	9	57	3.50
PMv						6	37	6	48	3.99
RP musicians: non-key– key rehearsal ($z > 3.09, k = 10, SR = 10$)										
n.s.										

Tonal perception contrasted against pink noise perception: RP musicians vs. nonmusicians – Comparing the tonal perception between RP musicians and nonmusicians ($z > 3.09, k = 10, SR = 10$), the RP musicians showed a stronger activation in the left supramarginal gyrus/posterior STG (BA 40/42). Conversely, nonmusicians did not show stronger activations compared to RP musicians during the tonal perception (see Fig. 11.6 and Appendix Tab. A.14).

Tonal rehearsal contrasted against pink noise nonrehearsal: RP musicians vs. nonmusicians – The RP musicians, compared to the nonmusicians ($z > 3.09, k = 10, SR = 10$), appeared to display stronger activation of a mostly left pronounced network during the tonal rehearsal, including the insular cortex bilaterally, the left PMd, as well as the left SPL and IPS/IPL (see Fig. 11.7 and Tab. 11.4). Most importantly, when lowering the threshold ($z > 2.58, k = 10, SR = 10$), the RP musicians showed additional stronger activation of the left pre-SMA and the left PMv (with 9 suprathreshold activated voxels) (see Appendix Tab. A.15).

In contrast, during the tonal rehearsal the nonmusicians engaged ($z > 3.09, k = 10, SR = 10$) more the left frontopolar area, the left cingulate gyrus, and the left middle temporal/angular gyrus (see Fig. 11.7 and Tab. 11.4). The right angular gyrus was activated as well when the threshold was lowered ($z > 2.58, k = 10, SR = 10$; see Appendix Tab. A.15).

Tab. 11.4: Comparison of Brain Activations between RP musicians and Nonmusicians during tonal Rehearsal

area	left hemisphere					right hemisphere				
	BA	x	y	z	z-value	BA	x	y	z	z-value
RP musicians – nonmusicians: tonal rehearsal – pink noise nonrehearsal ($z > 3.09, k = 10, SR = 10$)										
insular cortex		-32	21	6	3.90		31	15	6	3.62
PMd	6	-23	-6	51	3.50					
SPL	7	-17	-57	51	3.60					
IPS/IPL	7/40	-35	-48	51	4.24					
nonmusicians – RP musicians: tonal rehearsal – pink noise nonrehearsal ($z > 3.09, k = 10, SR = 10$)										
frontopolar area	10	-2	57	12	4.00					
	10	-8	57	24	3.27					
cingulate gyrus	24	-2	33	3	4.36					
medial frontal lobe	9	-5	48	33	3.22					
MTG/angular gyrus	39	-41	-57	24	4.13					

²² This cluster contained 8 voxels.

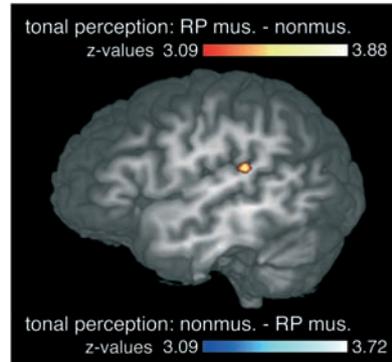


Fig. 11.6: Comparison of tonal Perception between RP musicians and Nonmusicians

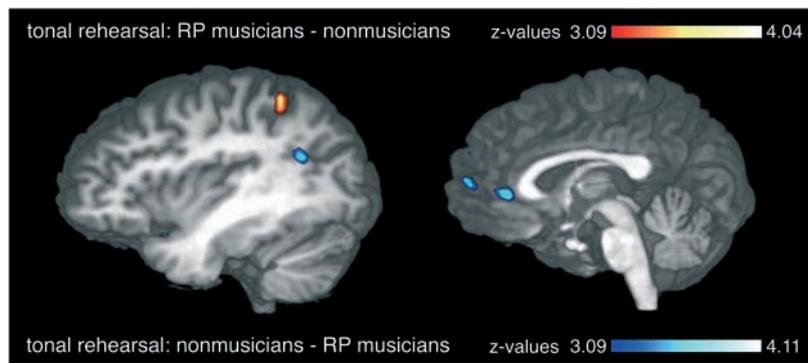


Fig. 11.7: Tonal Rehearsal between RP musicians and Nonmusicians ($z > 3.09$, $k = 10$, $SR = 10$)

11.5 Discussion

11.5.1 Behavioural Data

Only professional musicians were included in the study. Thus, a homogeneous pool of excellent RP musicians was tested.

Verbal and tonal performance in RP musicians – A significant difference between tonal and verbal stimuli was observed in RP musicians, which indicated that even for RP musicians the verbal sequences were easier to perform. Additionally, RP musicians showed, as stated in Hypothesis 1, a significant superior performance for the tones, compared to the nonmusicians. This result is in accordance with the literature (for an overview see Carterette & Kendall, 1999), and indicates the influence of the musical training. Musical training comprises the necessity to remember and maintain tonal stimuli, which has been shown to influence the organisation of tonal WM in musicians (Pechmann & Mohr, 1992; see Chapter 3.2). Therefore, it is assumed that the WM for tonal material in RP musicians is better trained,

compared to nonmusicians. As a consequence RP musicians might be able to maintain tonal information more efficiently, automatically and easily, which could be confirmed in the present study.

Key vs. non-key in RP musicians – As formulated in Hypothesis 3, the RP musicians showed a superior performance for the key, compared to the non-key sequences. This result will be discussed in relation to the functional activation pattern of this comparison in further detail in Chapter 11.5.2.3.

Comparison of verbal and tonal performance between RP musicians and nonmusicians – Because no significant difference for the verbal performance was observed between the groups, it cannot be concluded that transfer effects took place from the music domain to the language domain, as has been reported by Chan et al. (1998; see Chapter 3.2).

Correlations – There was no significant correlation between the behavioural performance and the age of musical commencement. This might be due to the fact, that only highly skilled musicians were recruited (see Chapter 11.3.1), who started musical training on average with 6.10 years ($SEM = 0.19$ years) of age, between the age of 5 and 8. Therefore, the variance concerning the starting age was quite small, which could account for the fact that no correlation between the age of commencement and the performance during the tonal task was observed.

11.5.2 fMRI Data

11.5.2.1 Verbal and tonal perception in RP musicians

When comparing the verbal with the tonal perception, RP musicians showed enhanced activation of the right STG/STS during the verbal perception. Because during both conditions RP musicians listened to the same stimuli and the stimuli had the same loudness, this cannot be due to differences in intensity. Stronger activation of the STS bilaterally for verbal, compared to tonal, information has been also reported in the literature (e.g., Binder et al., 2000; Dehaene-Lambertz et al., 2005; Jancke et al., 2002; Liebenthal et al., 2005; Mottonen et al., 2006) and was also observed for the contrast verbal – tonal perception in all groups (see Chapter 9.5.2.1). Therefore, this suggests a stronger involvement of the STS and STG in the perception of verbal stimuli, compared to tonal stimuli, also in RP musicians. Comparable to nonmusicians and to all groups, no area showed stronger activation in the contrast tonal – verbal perception.

11.5.2.2 Verbal and tonal rehearsal in RP musicians

During the verbal, as well as during the tonal, rehearsal (compared to pink noise nonrehearsal) RP musicians activated a neural network, including the left pars opercularis, the insular cortex bilaterally, the pre-SMA bilaterally, the premotor cortex bilaterally, the left SPL and IPS (including the IPL as well), and the cerebellum. These areas are known to subservise WM tasks (Awh et al., 1996; Baddeley, 2003; Chen & Desmond, 2005; Crottaz-Herbette et al., 2004; Gruber, 2001; Gruber & von Cramon, 2003; Jonides et al., 1998; Kirschen et al., 2005; Paulesu et al., 1993; Ravizza et al., 2004; Smith & Jonides, 1998) and were involved in nonmusicians as well (see Chapter 10.5.2.2).

When comparing the tonal and verbal rehearsal in nonmusicians, a major difference in the strength of activation was observed: a weaker activation during the tonal rehearsal. Remarkably, this difference in strength of activation between the tonal and verbal rehearsal condition was not found in RP musicians, supporting Hypothesis 2. Like in the verbal rehearsal (compared to pink noise nonrehearsal), RP musicians recruited WM related areas, including the left pars opercularis, the insular cortex bilaterally, the pre-SMA bilaterally, the premotor cortex bilaterally, the left SPL, IPS and IPL, as well as the cerebellum bilaterally during the tonal rehearsal (compared to pink noise nonrehearsal). More than in nonmusicians, the tonal rehearsal activated in RP musicians a neural network associated with tonal WM processes (Gaab, Gaser et al., 2003; Gruber & von Cramon, 2003; see Chapter 10.5.2.2), but these areas are also known from verbal WM tasks (e.g., Awh et al., 1996; Baddeley, 2003; Chen & Desmond, 2005; Crottaz-Herbette et al., 2004; Gruber & von Cramon, 2003; Paulesu et al., 1993; Ravizza et al., 2004), indicating a stronger similarity between verbal and tonal WM processes in RP musicians, compared to nonmusicians.

When comparing the verbal and tonal rehearsal in RP musicians directly against each other, the verbal rehearsal showed increased activation of Broca's area and the right pre-SMA.

Broca's area – RP musicians, as nonmusicians, (see Chapter 10.5.2.2) showed a significantly stronger activation of *Broca's area* during the verbal rehearsal, when compared to the tonal rehearsal. During the discussion of Experiment 3A (nonmusicians; see Chapter 10.5.2.2) the question was raised, if the stronger activation of Broca's area during the verbal WM task could also be due to difficulty differences between the tonal and verbal task, rather than to their properties as verbal or tonal stimuli per se. Although, RP musicians showed a smaller performance difference between verbal and tonal material than nonmusicians, the increased activation of Broca's area in RP musicians during the verbal rehearsal appears to be even more pronounced than in the nonmusicians. This supports the assumption that the stronger

activation of Broca's area during the verbal condition is due to the stimulus modality and not to task difficulty, suggesting that Broca's area plays a special role in verbal WM. Following findings support the presumption of a special role for Broca's area during verbal WM:

- Broca's area was more strongly activated during the verbal, compared to the tonal, rehearsal in nonmusicians and RP musicians, although the difference in the behavioural performance is diminished in the group of RP musicians.
- There was no functional difference in this region between RP musicians and nonmusicians during the tonal rehearsal, although this should be the case, if the activation of this area really reflected increasing WM task difficulty (see Chapter 10.5.2.2). To investigate this further, an analysis was conducted, in which only the hit trials (trials in which participants answered correctly) were analysed and the stronger activation of Broca's area during the verbal condition was still observed ($z > 2.58$, $k = 10$, $SR = 5$, Talairach coordinates: -55 11 5).
- Broca's area did not show any difference after a WM training in an fMRI study conducted by Olesen et al. (2004).
- Activation in Broca's area is usually positively correlated with increasing WM load or WM demands (Braver et al., 1997; Chen & Desmond, 2005; Fiebach et al., 2005; Ravizza et al., 2004; Smith & Jonides, 1998; Xue et al., 2004), i.e. the activation in Broca's area increases with increasing task demands. In the present study the opposite pattern was observed: With increasing task demand the activation in Broca's area decreased.

Therefore, the results obtained by the present study suggest a special role for Broca's area during verbal WM.

The tonal rehearsal showed an enhanced activation of a complex network when compared to the verbal rehearsal condition, mainly the cingulate gyrus bilaterally, the SMG bilaterally, the right STG/STS, as well as visual areas (e.g., the cuneus bilaterally).

The *cingulate gyrus* is known to be involved in WM processes as well as during performance monitoring with the aim to optimise the behaviour (H. Kondo et al., 2004; Ullsperger & von Cramon, 2004). This is in accordance with the behavioural data (superior performance for verbal material).

The right *supramarginal gyrus (SMG)* has been reported to show increased engagement during verbal compared to tonal WM (Celsis et al., 1999), which is the opposite pattern of what was found in the present experiment. Conversely, Gaab, Gaser et al. (2003) showed that the SMG bilaterally played also an important role during tonal WM. In addition, the authors observed a positive correlation between the tonal WM performance and the left SMG. The

data in the present experiment support the special role of the SMG during a tonal WM task, and adds the result that in RP musicians the SMG seems to be more strongly involved during the tonal rehearsal compared to verbal rehearsal. It also supports the notion that the activation of the SMG observed by Gaab, Gaser et al. (2003) is not due to verbalisation of the tonal stimuli. In addition, the SMG has been observed for verbal WM task (e.g., Baddeley, 2003; Chen & Desmond, 2005; Gruber & von Cramon, 2003). Therefore, it can be concluded that the SMG plays a role in verbal and tonal WM processes, and that in RP musicians this role is enhanced for tonal WM.

The right *premotor cortex* was more strongly activated during the tonal, compared to the verbal rehearsal. This strong involvement of premotor areas during the tonal rehearsal in RP musicians is discussed in detail below (see Chapter 11.5.2.5).

In nonmusicians the *IPL* was more strongly activated during the verbal rehearsal, when compared to the tonal rehearsal. RP musicians showed additional activation of the *IPL* during the tonal rehearsal, when compared to verbal rehearsal. Therefore, the more similar activation pattern between the verbal and tonal condition concerning the *IPL* in RP musicians might implicate that the ‘phonological store’ is more accessible for tones in RP musicians, compared to nonmusicians. The stronger involvement of the *IPL* during the tonal rehearsal will be discussed in more detail below (see Chapter 11.5.2.5).

Because there was no additional auditory input during the rehearsal period (all participants were repeatedly instructed not to sing or hum aloud during the scanning session), the stronger activation of the right *STS* and *STG* during the tonal rehearsal, compared with the verbal rehearsal, in RP musicians cannot be due to perceptual differences (also because during the perception period participants always hear verbal and tonal material simultaneously). The tones were more difficult to rehearse, which was also reflected in the behavioural performance in RP musicians. Therefore, the RP musicians presumably also involved auditory sensory areas in order to remember and rehearse the tonal stimuli. Studies showed that the activation of the auditory cortex can be modulated by attention (Grady et al., 1997; Jancke et al., 1999; Mitchell et al., 2005; Petkov et al., 2004; Pugh et al., 1996). Furthermore, it has been observed, that there is an auditory coactivation when musicians played or imagined to play an instrument, due to strong motor-auditory associations in musicians (Bangert et al., 2005; Lotze, Scheler, Tan, Braun, & Birbaumer, 2003). Because a strong premotor activation during the tonal rehearsal was observed in RP musicians as well, it appears plausible that the activation of the right *STG/STS* reflects a WM strategy to remember tones in RP musicians, which involves motor imagination, the translation of

sensory input (sine wave tones) into an internally rehearseable motor code and therefore motor-auditory associations.

The *visual areas* are likely to support the tonal rehearsal by visual imagery (Kosslyn et al., 2001), which is not necessary during the verbal condition.

11.5.2.3 Key and non-key perception and rehearsal in RP musicians

As postulated in Hypothesis 3, RP musicians showed a significantly superior performance for the key sequences compared to the non-key sequences. However, this difference between both types of sequences was only observed in RP musicians, neither in nonmusicians nor in AP musicians. For nonmusicians the musicological differences in the tonal sequences might have been too subtle. Musicians have a better implicit and explicit knowledge for musical regularities compared to nonmusicians, which has been also observable in their neurophysiological responses to deviations to these rules (Carterette & Kendall, 1999; Koelsch, Schmidt et al., 2002). This might explain why a behavioural difference was observed in RP musicians, but not in nonmusicians.

When comparing the functional images of the key and the non-key perception, no significant difference was observed. However, there was a significant difference in the functional pattern between both types of sequences during the rehearsal period in RP musicians. During the key rehearsal RP musicians involved significantly more strongly the right mid-DLPFC, the right IPCS, and the premotor cortex bilaterally (PMd bilaterally, right PMv). The mid-DLPFC (area 9/46 according to Petrides, 2000a) is an important structure during WM insofar, as this area plays a special role for online monitoring of the performance and manipulation of the information during WM processes (Curtis & D'Esposito, 2003; D'Esposito, Postle, Ballard, & Lease, 1999; Fletcher & Henson, 2001; Owen et al., 1999; Petrides, 2000a; Petrides, Alivisatos, Evans et al., 1993; Petrides, Alivisatos, Meyer et al., 1993). Because this area was more strongly activated during the strategy-based (key) compared to the non-strategy based (non-key) tonal WM task, it is suggested that RP musicians used their knowledge about musical regularities to cluster the tonal (key) information, which was not possible during the atonal (non-key) information.

In addition, some of the observed areas have been reported to be activated in experiments, which analysed the neural correlates underlying strategic WM. Using fMRI, Bor, Duncan, Wiseman, and Owen (2003) investigated chunking and strategy based WM processes. They asked participants to maintain spatial patterns, which could belong to 'structured sequences' (the spatial patterns looked similar to a known shape, e.g., a letter) or to 'unstructured sequences' (the spatial pattern was random and did not remind on a certain pattern) (see

Fig. 11.8). The performance was better for the structured, compared to the unstructured sequences. The authors reported also stronger activation of the right IPCS (Talairach coordinates: 46 13 20) during the maintenance of structured sequences, which is very close to the activation observed in this experiment

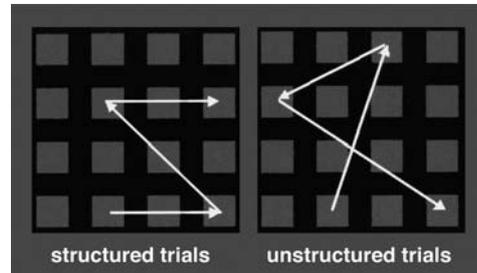


Fig. 11.8: Participants remembered structured and unstructured spatial Patterns (Bor et al., 2003)

(Talairach coordinates: 52 15 26). Therefore, the IPCS seems to play an important role in strategy based WM tasks, which includes chunking, independent of the modality of the stimuli. Furthermore, Savage et al. (2001) used PET and asked participants to learn lists of words, whereas the semantic organisation was manipulated. For the most semantically organised condition, the authors reported enhanced activation of the left DLPFC and the left IFG.

Therefore, the results of this dissertation together with the existing literature suggest that the mid-DLPFC and the IPCS are involved during clustering, organising and chunking (modality independent) information during the maintenance in a WM task. The RP musicians seemed to use their knowledge about musical regularities to cluster, chunk and organise the key information. This was reflected in a better behavioural performance for the key sequences, and a stronger involvement of brain areas, which are associated with strategy based organisation of information.

The rehearsal of the key sequences also engaged stronger the premotor cortex bilaterally. This is interesting in the following context: Nonmusicians showed a stronger activation of the premotor cortex during the verbal rehearsal, when compared to the tonal rehearsal. This was interpreted as a more automatic transformation of the verbal sensory input into a motor program, which can be used to rehearse the syllables subvocally (see Chapter 10.5.2.2). This difference was not observed in RP musicians, indicating an easier access to tonal motor representation in RP musicians than nonmusicians, which could be due to their almost daily practise of mapping tones to motor performance (e.g., auditory feedback when they play their instrument). Considering this, it seems plausible that the premotor cortex was more strongly activated for key sequences, because usually most of the RP musicians play their pieces in a certain tonality, i.e. this is what they practise and therefore they should have motor programs, which are more strongly connected to the tonal sensory input to support the rehearsal of the key sequences.

In contrast to what was stated in Hypothesis 3, Broca's area was not more strongly activated during key compared to non-key sequences, although, studies which investigated the violation of verbal and musical structure, showed the involvement of the Broca's area for verbal material (Friederici, 2002) and the pars opercularis bilaterally for musical stimuli (Maess et al., 2001; Tillmann et al., 2003). Several reasons could account for this different finding. Firstly, Maess et al. (2001) and also Tillmann et al. (2003) used musical stimuli that built up strong expectations about the musical progression, which were violated. In the present study the auditory stimuli did not have the potential to build up such context (e.g., the non-key sequences are unstructured in terms of musical regularities), and therefore no expectations were built up or violated. Secondly, in the above mentioned studies (Maess et al., 2001; Tillmann et al., 2003) chords were used, whereas in Experiment 3 sequences of sine wave tones were presented. The present musical stimuli presumably may have been too abstract (sine wave tones) and the tonal context too subtle. This would explain why no activation in the pars opercularis was observed.

11.5.2.4 Comparison of tonal perception between RP musicians and nonmusicians

Comparing the tonal perception between both groups, the RP musicians showed a stronger activation spread over the left SMG/posterior STG. In contrast, nonmusicians did not show a stronger activation compared to RP musicians during the tonal perception.

The involvement of the SMG in WM has already been described, though, this area has been shown to be stronger involved during verbal than during tonal WM tasks (Celsis et al., 1999). But, as already pointed out above, the SMG has been shown to play an important role during tonal WM (Gaab, Gaser et al., 2003), especially in RP musicians (Gaab & Schlaug, 2003). In a subsequent fMRI study, Gaab and Schlaug (2003) reported an increased activation of the SMG bilaterally during the perceptual period of this tonal WM task in RP musicians compared to nonmusicians, although the performance was matched between both groups. Therefore, this study together with the discussed results indicate that the SMG is involved in tonal WM, especially in RP musicians, and is already involved during the tonal perception in WM processes, which points to the use of a strategy during early perceptual processes of WM.

Pantev et al. (1998) showed in an MEG study, that dipole moments for piano tones in the auditory cortex in musicians were enlarged, compared to those of nonmusicians. These results have been supported by Schneider et al. (2002), who showed enhanced activity in primary auditory cortex in professional musicians compared to nonmusicians when listening to sine wave tones, as well as an enlarged Heschl's gyrus in musicians. This indicates differences during the perception of tonal material and related functional activation in auditory cortex

between musicians and nonmusicians. The above mentioned MEG studies (Pantev et al., 1998; Schneider et al., 2002) together with the present dissertation indicate differences in the perception in RP musicians compared to nonmusicians. In this fMRI study the difference was not located in the primary but secondary auditory cortex, in contrast to the MEG studies (Pantev et al., 1998; Schneider et al., 2002), which is presumably due to the different methods used. Jancke et al. (2001) showed that after a frequency training not only the behavioural performance of the participants was improved, but additionally they showed a change in the activation pattern in the secondary auditory areas. This functional reorganisation after the musical training might also be the reason for the different functional pattern in RP musicians and nonmusicians during tonal perception.

11.5.2.5 Comparison of tonal rehearsal between RP musicians and nonmusicians

The RP musicians appeared to display stronger activation of a mostly left pronounced network, including the insular cortex bilaterally, the left PMd, and the left SPL and IPS/IPL during the tonal rehearsal. The results support the assumption of Hypothesis 4. When lowering the threshold ($z > 2.58$), the RP musicians showed stronger activation of (pre-)motor areas bilaterally.

In the present study, the left *insula* showed stronger activation during the verbal rehearsal in nonmusicians, compared to the tonal rehearsal. When comparing the tonal rehearsal between nonmusicians and RP musicians, the RP musicians displayed stronger activation of the insular cortex bilaterally. The insula has been described to play an important role during the processing of auditory language and music information (Bamiou et al., 2003; Friederici et al., 2003; Rumsey et al., 1997), as well as during verbal WM (for an overview see Bamiou et al., 2003). The results of the present study indicate that the insular cortex shows a stronger involvement during verbal WM in nonmusicians, compared to tonal WM. Furthermore, it supports the notion that WM processes related to tonal and verbal material are more similar in RP musicians.

The RP musicians showed a stronger activation of *premotor areas* during the tonal rehearsal when compared to the nonmusicians. Learning to play an instrument also includes an extensive motor training, which leads, as described in Chapter 4, to anatomical (Amunts et al., 1997; Gaser & Schlaug, 2003) and functional (Hund-Georgiadis & von Cramon, 1999; Jancke et al., 2000; Krings et al., 2000) differences related to (pre-)motor areas between musicians and nonmusicians. Meister et al. (2004) reported that musicians activated the premotor cortex bilaterally while they imagined to play their instrument. Gaser and Schlaug

(2003) showed in a VBM study a positive correlation between grey matter and status of musicianship (nonmusician, amateur musician or professional musician) in primary motor and premotor areas bilaterally.

Additionally, when musicians learn to play their instrument, they have to associate a motor action (e.g., pressing a key) with an auditory feedback to control their performance and to correct it if necessary. Therefore, during the course of their musical training musicians establish a strong connection between a motor action and an auditory input. This is exactly what was described in several studies. Haslinger et al. (2005) observed that piano players show a stronger activation of the premotor cortex bilaterally, compared to nonmusicians, when they observed piano related movements. Furthermore, in the study conducted by Haslinger et al. (2005) musicians also showed an increased activation of primary and secondary auditory cortex, compared to nonmusicians, when they observed these silent piano playing movements. This underlines the strong link between auditory sensory input and motor action. Bangert et al. (2005) investigated to what extent the auditory and motor networks are automatically linked in musicians. They used a paradigm in which musicians and nonmusicians either passively listened to music (acoustic task) or performed silent finger movements (motion task). During the acoustic task, the musicians showed stronger activation in frontal, temporal as well as parietal regions (left STG, left PMv, Broca's area, left SMA, and left IPL) compared to the nonmusicians, whereas in the motion task musicians showed stronger activation of the PMv bilaterally, the right M1 and the left SMA. During both tasks musicians showed activation of a left-lateralised network, including frontal, temporal, and parietal areas. This network was not activated in nonmusicians. This study supports the strong connection between cerebral networks related to auditory and motor processing in musicians. These results were supported by Lotze et al. (2003) who compared the motor activation between professional and amateur musicians during the performance and the imagination of a movement. Professional musicians showed stronger activation of the primary auditory cortex during the execution of a movement, indicating a strong auditory-motor association in professional musicians. Using MEG, Haueisen and Knösche (2001) found that the perception of well-practised piano pieces evoked activity in the primary motor cortex, again supporting the strong link between the auditory stimuli and the motor performance in musicians. When lowering the threshold ($z > 2.58$) in the comparison of tonal rehearsal between RP musicians and nonmusicians, the RP musicians in Experiment 3B displayed increased activation of the right STG, also supporting this strong auditory-motor association in RP musicians.

Schubotz and von Cramon (2002) showed, that the premotor cortex is not only active during movement planning, but also during the presentation of a sensory stimulus, which indicates that the lateral premotor cortex obtains a representation of sensory stimulation (sensory somatotopy). The authors reported, that sensory and motor representations are heavily connected, and might even involve partially the same neural networks, mainly premotor and parietal regions (Schubotz & von Cramon, 2002; Schubotz, von Cramon, & Lohmann, 2003). It is important to analyse the result of the increased activation in the premotor cortex during the tonal rehearsal in RP musicians, compared to nonmusicians, in the right context. Nonmusicians showed a stronger involvement of the premotor cortex bilaterally during the verbal rehearsal, compared to the tonal rehearsal. This stronger activation of premotor cortex was interpreted as an indication for a more automatic connection between the sensory input and a motor representation to rehearse the syllables internally in nonmusicians, compared to tonal material (see Chapter 10.5.2.2). RP musicians, in contrast, did not show a stronger activation of premotor areas during the verbal rehearsal when compared to the tonal rehearsal. Based on the assumption that the code in the phonological loop of WM is motoric (for an overview see Baddeley, 1992, 2003; Wilson, 2001), the finding that RP musicians showed a stronger involvement of left premotor cortex during tonal rehearsal compared to nonmusicians, supports the hypothesis that RP musicians have a stronger association between the tonal sensory input and the motor representation compared to nonmusicians, which might be comparable to that of verbal material. This is most probably due to the musical training over years for the RP musicians, when they learn to associate a tonal sensory input with the corresponding motor program (e.g., press a certain key and hear the corresponding tone). This result supports the findings of adaptive changes and plasticity in the brains of musicians, which are due to their musical training (Elbert et al., 1995; Haslinger et al., 2005; Koelsch et al., 1999; Munte et al., 2002; Pantev et al., 1998; Schneider et al., 2002; see Chapter 4.2).

When comparing the functional activation pattern between RP musicians and nonmusicians during the tonal rehearsal, the left *SPL* and the left *IPS/IPL* were more strongly activated in RP musicians. Olesen et al. (2004) reported an increase of activation of the *SPL* and *IPL* bilaterally after a training of a spatial WM task. In nonmusicians the left *SPL* and *IPL* were more strongly activated during the verbal, compared to the tonal condition, which could be explained by alternative theories (see Chapter 10.5.2.2 and Fig. 11.9). As already discussed in Chapter 10.5.2.2, the functions of the *IPL* as an association area, are manifold (e.g., phonological store of verbal WM, attention, motor representations etc.). The phonological store provides temporary storage of acoustic or speech-based information (Baddeley, 1992),

and is thought to be located in the IPL (e.g., Baddeley, 2003; Braver et al., 1997; Crottaz-Herbette et al., 2004; Gruber & von Cramon, 2003; Henson et al., 2000; Paulesu et al., 1993;

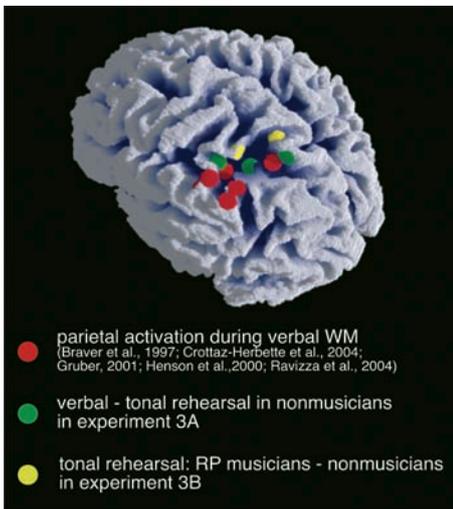


Fig. 11.9: WM related left parietal Activations

Ravizza et al., 2004; see Fig. 11.9). An explanation might be that RP musicians can use this phonological store more effectively for tones, which is due to their musical training.

The explanation that more attention (Corbetta & Shulman, 2002) could be involved in RP musicians is unlikely, because then the tonal task should have required more attention and therefore should have produced an increase in the activation of the IPL in nonmusicians or in RP musicians. In addition, the IPL also plays an important role during

motor related tasks and motor control (Fogassi et al., 2005; Petrides & Pandya, 1984; Rizzolatti et al., 1997; Rizzolatti & Luppino, 2001; Rizzolatti et al., 1998), i.e. it connects sensory information with information necessary for a motor response (Fogassi et al., 2005; Sakata et al., 1997). This interpretation would fit nicely with the increased premotor activations in RP musicians during the tonal rehearsal, which indicates a stronger connection between tonal sensory input and motor representations for tones in RP musicians. A stronger activation of the SPL was also observed in RP musicians when compared to AP musicians in Experiment 1 (see Chapter 7.5.3), which seems to be related to the function of the SPL in multimodal sensory integration (Sergent et al., 1992; Stewart et al., 2003). Multimodal sensory integration combined with motor planning, preparation, and output is of great importance for an instrumental musician. Additionally, it has been shown that the SPL is involved in musicians during the imagination of playing an instrument (Langheim et al., 2002; Meister et al., 2004). Therefore, the enhanced activation of right SPL in RP musicians, compared to nonmusicians, is interpreted as a multimodal encoding strategy for auditory information (e.g., associating tones with visual and/or motor representations). Activation of the SPL and IPS has also been demonstrated during verbal (Awh et al., 1996; Crottaz-Herbette et al., 2004; Gruber, 2001; Gruber & von Cramon, 2003) and tonal WM tasks in nonmusicians (Gaab, Gaser et al., 2003; Zatorre et al., 1994), indicating an important role of this area during WM processes.

To conclude, there are following possibilities to interpret the stronger parietal activation in RP musicians during tonal rehearsal: (i) an enhanced use of the phonological store in RP musicians (Baddeley, 2003; Crottaz-Herbette et al., 2004; Gruber & von Cramon, 2003; Henson et al., 2000; Olesen et al., 2004; Ravizza et al., 2004), (ii) it is related to motor representations (Fogassi et al., 2005; Petrides & Pandya, 1984; Rizzolatti et al., 1997; Rizzolatti & Luppino, 2001; Rizzolatti et al., 1998) or (iii) visual-spatial mapping in RP musicians, compared to nonmusicians (Gaser & Schlaug, 2003; Sergent et al., 1992; Stewart et al., 2003). Because the present study cannot distinguish between these possibilities, further research is necessary.

The nonmusicians showed stronger activations of the left *angular gyrus* during the tonal rehearsal, when compared to the RP musicians. This area has also been more strongly activated in nonmusicians during the tonal rehearsal, when compared to the verbal rehearsal and is usually known to be involved during language, especially during semantic processing (Binder et al., 2003; Binder et al., 2005; Friederici, 2002; Poldrack et al., 2001). Notwithstanding, activation of this area has been observed during various tasks (see Chapter 10.5.2.2), which makes it challenging to interpret this result. One possible explanation would be that nonmusicians use a special strategy to remember the tones, e.g., involving the association of spatial information (Baciu et al., 1999; Blanch et al., 2004; Chambers et al., 2004). The left *frontopolar area*, the left *cingulate gyrus* as well as the left *medial frontal gyrus*, which have been more strongly activated in nonmusicians during the tonal rehearsal, when compared to the RP musicians, might reflect a different strategy in nonmusicians to rehearse the tones or an enhanced monitoring during this task (Y. Kondo et al., 2005; Ullsperger & von Cramon, 2004).

11.6 Summary

Experiment 3B was designed to examine if musical expertise has an influence on perception and WM related processes for tonal stimuli. RP musicians performed a verbal and tonal WM task and were compared with nonmusicians.

It is important to note that this fMRI experiment compared verbal and tonal WM in nonmusicians and RP musicians using the same auditory stimuli for both groups.

Even RP musicians showed a significant difference between tonal and verbal stimuli, indicating that also for RP musicians the verbal sequences were easier to perform. RP musicians showed, as hypothesised, a significantly superior performance for the tones,

compared to the nonmusicians. This result is in accordance with the literature (for an overview see Carterette & Kendall, 1999), and interpreted to result from musical training.

Verbal and tonal rehearsal in RP musicians – During the verbal, as well as during the tonal rehearsal, RP musicians activated a neural network, including the left pars opercularis, the insular cortex bilaterally, the pre-SMA bilaterally, the premotor cortex bilaterally, the left SPL and IPS (including the IPL as well), and the cerebellum. These areas are known to subserve WM tasks (Awh et al., 1996; Baddeley, 2003; Crottaz-Herbette et al., 2004; Gruber, 2001; Gruber & von Cramon, 2003; Jonides et al., 1998; Paulesu et al., 1993; Ravizza et al., 2004; Smith & Jonides, 1998) and have also been involved in the nonmusicians (see Chapter 10.5.2.2). Importantly, in contrast to the nonmusicians, the tonal rehearsal did not show a weaker activation network in the RP musicians, which was interpreted as the consequence of a more similar process in RP musicians when rehearsing tonal and verbal information. Additionally, the verbal rehearsal in RP musicians revealed, as in nonmusicians, a stronger activation of Broca's area. This underlines the hypothesis that Broca's area is more strongly involved during the WM rehearsal of verbal material (see Experiment 3A). An interesting finding was that in RP musicians the premotor areas did not show a stronger involvement during the verbal rehearsal, compared to the tonal rehearsal, in contrast to nonmusicians. This appears to be due to the strong associations in RP musicians between the sensory input when listening to tones and the according motor representation (Bangert et al., 2005; Haslinger et al., 2005; Haueisen & Knosche, 2001; Lotze et al., 2003), which are presumably comparable to those of verbal material.

Key and non-key – To further investigate the effect of musical training on a tonal WM task key sequences (structured according to musical regularities) and non-key (unstructured according to musical regularities) sequences were designed. Key sequences were thought to trigger the use of a strategy in RP musicians in order to rehearse/store the tones. The RP musicians, in contrast to the nonmusicians, displayed a superior performance for the key sequences, when compared to the non-key sequences. This was reflected in a stronger activation of the right mid-DLPFC, the right IPCS, and the premotor cortex bilaterally during the key rehearsal when compared to the non-key rehearsal. In this context it is interesting to note that these areas have been reported to support a strategy based rehearsal (with spatial and verbal material; Bor et al., 2003; Petrides, 2000a; Savage et al., 2001), including the organisation, clustering, and chunking of the material to be memorised. Therefore, the RP musicians appeared to use their knowledge of musical regularities to organise, cluster, and chunk the key sequences, which is reflected in this functional pattern.

Comparison of tonal rehearsal between RP musicians and nonmusicians – As stated in the hypotheses, a difference in the functional activation pattern during the WM for tones was observed between nonmusicians and RP musicians, indicating functional plasticity and adaptation in the brain of musicians (Munte et al., 2002; Pantev et al., 2003; Schlaug, 2001). The RP musicians, compared to the nonmusicians, appeared to display stronger activation of a mostly left pronounced network, including the insular cortex bilaterally, the left PMd, and the left SPL and IPS/IPL during the tonal rehearsal. These activations indicate a different WM related strategy for tonal information in RP musicians, which is most presumably due to the musical training. Importantly, the results of Experiment 3B suggest that RP musicians have a stronger association between the tonal sensory input and the motor representation of this tonal event (Bangert et al., 2005; Haslinger et al., 2005; Haueisen & Knosche, 2001; Lotze et al., 2003). Therefore, this stronger association between the sensory tonal stimulus and the motor action, which was interpreted as a consequence of the musical training (listening to a tone while pressing a key), would make it easier for RP musicians to internally rehearse these tonal information and therefore to maintain it in WM. This process in RP musicians is likely, in contrast to nonmusicians, comparable to the rehearsal of verbal information. The results gained by Experiment 3B point to one important and basic mechanism of verbal (and tonal) WM: to translate the sensory verbal or tonal event into a rehearsable motor representation.

Chapter 12

Experiment 3C – The Influence of Absolute Pitch on Tonal WM Processes

12.1 Introduction

By comparing AP musicians to RP musicians it was intended to explore if the ability of AP has an influence on the cognitive processes (e.g., the degree of involvement) and the neural organisation of WM (see Chapter 5.5.2). In contrast to Experiment 1, the frequencies of all sine wave tones corresponded to the frequencies of the tones of the Western musical scale. Additionally, tonal WM was investigated using incongruent and congruent sequences²³, to explore the underlying mechanisms and neural correlates of AP (see Chapter 9.3.2). Zatorre and Beckett (1989) claimed, that AP musicians do not necessarily have to label the tones, whereas other studies found that AP musicians only show a superior performance to RP musicians during tonal WM tasks when they are able to label the tones (Siegel, 1974; Takeuchi & Hulse, 1993). In Experiments 1 and 2 (see Chapters 7 and 8) this question was investigated, although the tones used did not always correspond to the frequencies of the Western musical scale²⁴. Therefore, the present experiment was designed to examine this issue using only tones which corresponded to the frequencies of the Western musical scale. Using fMRI, areas involved in the perception and in tonal WM processes could be disentangled. With the use of the tonal incongruent and congruent sequences it was intended to analyse, whether the verbal labelling process is automatic (behavioural difference between the congruent and incongruent condition) or not (no behavioural difference between congruent and incongruent sequences), i.e. if musicians show an ‘auditory Stroop effect’ for the incongruent sequences (Itoh et al., 2005; Miyazaki, 1999). Furthermore, the brain areas involved in this process in AP musicians were of interest.

12.2 Hypotheses

1. AP musicians were hypothesised to show a better behavioural performance during the tonal WM task, compared to RP musicians (Hantz et al., 1992; Siegel, 1974; see Chapters 7 and 8).

²³ See chapter 9.3.2 - congruent sequences: the frequency of the sine wave tone corresponded to the simultaneously presented note name, incongruent sequences: the frequency of the sine wave tone did not correspond to the simultaneously presented note name

²⁴ The distractor tones used in experiment 1 did not correspond to the frequencies of the tones of the Western musical scale, and in experiment 2 microtones were used ($\frac{1}{4}$ semitone steps).

2. AP musicians were assumed to show a superior tonal WM performance for the congruent compared to the incongruent stimuli (Itoh et al., 2005; Miyazaki, 1999; Siegel, 1974).
3. The functional pattern involved during the rehearsal of tonal incongruent sequences was hypothesised to differ from the one involved during the rehearsal of the tones of the congruent sequences. During the tonal rehearsal of the incongruent, compared to the congruent, sequences AP musicians were thought to display a stronger activation in the left posterior DLPFC (Zatorre et al., 1998), because this area is thought to be responsible for the association of tones and the according names of the tones (during the tonal incongruent sequences AP musicians have to associate actively the tones to the corresponding verbal label), and an additional activation of the PT during the tonal incongruent, compared to the tonal congruent, sequences was hypothesised (Itoh et al., 2005).
4. AP musicians were hypothesised to display a stronger activation of the left STS during the perception of the tones compared to RP musicians (see Chapter 7.5.3).
5. Functional differences between RP musicians and AP musicians during the tonal rehearsal were hypothesised to become manifest in a stronger involvement of the PT (Itoh et al., 2005; Luders et al., 2004; Ohnishi et al., 2001; Schlaug, Jancke, Huang, & Steinmetz, 1995) and the left posterior DLPFC (Ohnishi et al., 2001; Zatorre et al., 1998) in AP musicians, whereas the RP musicians were assumed to display an enhanced activation of classical WM areas, e.g., the ventrolateral prefrontal cortex and parietal areas (Itoh et al., 2005; Klein et al., 1984; Zatorre et al., 1998).

12.3 Methods

12.3.1 Participants and AP Testing

Eight musicians (3 male) were assigned to the AP group after performing the two AP tests (see below). AP musicians were recruited from the “University of Music and Theatre Mendelsohn Bartholdy” in Leipzig. The age ranged within the AP group from 21 to 33 years, resulting in a mean age of 25.38 years ($SEM = 1.61$) years.

Following limitations in the AP group were accepted because of the rareness of this phenomenon: (i) one participant was older than 30 years, (ii) two left-handed AP musicians were included and (iii) seven of the AP musicians were not native German speakers, but they spoke German fluently and were familiar with the German note names.

AP was confirmed using two established test (Keenan et al., 2001), in which participants had to name sine wave tones (see Chapters 7.3.1 and 8.3.1). AP musicians were asked to answer

within 3 s. Five AP musicians performed over 90% in the first test, the other three performed over 80%.

Participants were asked to fill out a Musical Experience/AP questionnaire (see Appendix: Musical Experience and AP questionnaire) to gather information about their musical experience and their AP ability.

The AP musicians were compared with a group of RP musicians ($N = 8$) of Experiment 3B, which were matched for gender and age.

12.3.2 Stimuli, Experimental Design, Image Acquisition and Processing

The stimuli, experimental design, fMRI paradigm, as well as image acquisition and processing are described in Chapter 9.3. To gather further information about the AP ability an additional condition for the AP musicians during tonal WM was implemented: a congruent and an incongruent condition (see Chapter 9.3.2).

12.4 Results

12.4.1 Behavioural Data

Musical Experience/AP questionnaire – RP musicians started their musical training at a mean age of 6.19 years ($SEM = 0.25$ years), whereas the musical commencement of AP musicians started at the mean age of 5.94 years ($SEM = 0.31$ years). An independent-samples t -test did not reveal a significant difference between both groups concerning the age of musical commencement ($t(22) = -0.611, p = .548$).

AP test – AP musicians named 92.07% ($SEM = 2.19\%$) correctly in the AP test 1, and 81.51% ($SEM = 5.56\%$) in AP test 2. Thereof, 83.17% ($SEM = 5.37\%$) in AP test 1 and 68.75% ($SEM = 9.51\%$) in AP test 2 were given correctly within 3 seconds after the end of the tone. AP musicians needed on average 1416 ms²⁵ ($SEM = 453$ ms) to name the sine wave tones in AP test 1, and 2024 ms ($SEM = 902$ ms) in AP test 2.

Verbal vs. tonal rehearsal – AP musicians performed 91.72% ($SEM = 1.42\%$) correctly during the verbal and 81.09% ($SEM = 4.17\%$) during the tonal condition. The RT for the verbal condition was 1637 ms ($SEM = 127$ ms) and for the tonal condition 1673 ms ($SEM = 143$ ms) (see Appendix Tab. A.2 and A.3). The AP musicians showed, by applying a paired-samples t -test, a significantly higher performance in terms of percentage of CR for the verbal sequences, compared to the tonal sequences ($t(7) = -2.822, p = .026$), however, there was no difference between both types of stimuli for the RT ($t(7) = 0.618, p = .556$).

²⁵ RT = between the the end of the tone and the button press

Key vs. non-key – A paired-samples *t*-test revealed no differences between key (CR: $M = 81.56\%$, $SEM = 3.44\%$; RT: $M = 1655$ ms, $SEM = 137$ ms) and non-key (CR: $M = 80.63\%$, $SEM = 5.86\%$; RT: $M = 1691$ ms, $SEM = 152$ ms) sequences concerning the percentage of CR ($t(7) = 0.197$, $p = .850$) or the RT ($t(7) = -0.777$, $p = .463$).

Incongruent vs. congruent – AP musicians performed 77.81% ($SEM = 4.99\%$) correctly during the tonal incongruent condition and 84.38% ($SEM = 4.22\%$) during the tonal congruent condition. The RT was on average 1699 ms ($SEM = 134$ ms) for the tonal incongruent and 1648 ms ($SEM = 156$ ms) for the tonal congruent condition. No significant difference (paired-samples *t*-test) was observed for the percentage of CR ($t(7) = -1.649$, $p = .143$) or the RT ($t(7) = 0.987$, $p = .357$) between the tonal incongruent and the tonal congruent condition (see Appendix Tab. A.2 and A.3).

AP musicians compared to RP musicians and nonmusicians – To investigate potential differences between the groups (nonmusicians, RP musicians and AP musicians) a one-way-ANOVA was applied and subsequently Scheffé post-hoc tests (SPHT) were calculated. The results are summarised in table A.4 of the Appendix.

No significant difference in percentage of CR for the verbal condition between the AP and RP musicians were observed ($F(2,38) = 2.548$, $p = .092$; SPHT: $p = .564$).

AP musicians showed a significantly higher percentage of CR for the tonal sequences, compared to RP musicians ($F(2,38) = 19.404$, $p = .000$; SPHT: $p = .029$), although there was no significant difference between the RT for this condition between both groups ($F(2,38) = 4.413$, $p = .019$; SPHT: $p = .921$). In addition, there was no behavioural difference between RP musicians and AP musicians for the key and non-key sequences (see Appendix Tab. A.4). Importantly, the AP musicians showed a significantly higher percentage of CR during the tonal congruent sequences than the RP musicians ($F(2,38) = 24.542$, $p = .000$; SPHT: $p = .001$), whereas this was not observed during the tonal incongruent condition ($F(2,38) = 11.095$, $p = .000$; SPHT: $p = .429$). No significant difference between both groups was displayed for the RT of the tonal congruent ($F(2,38) = 4.086$, $p = .025$; SPHT: $p = .987$) and tonal incongruent sequences ($F(2,38) = 4.703$, $p = .015$; SPHT: $p = .831$).

Correlations – The age of musical commencement did not correlate with the performance in AP test 1 or 2 (see Appendix Tab. A.5). The age at which AP was detected did not correlate with the performance in the AP tests 1 ($r = -.572$, $p = .138$) or 2 ($r = -.517$, $p = .190$), but it showed a significantly negative correlation between the performance in the AP test, which only regarded answers within 3 seconds as correct (for AP test 1 ($r = -.764$, $p = .027$) and AP test 2 ($r = -.889$, $p = .003$)). In addition, the age at which AP was detected was significantly

positively correlated with the RT in AP test 1 ($r = .730, p = .040$) and AP test 2 ($r = .803, p = .016$).

The performance during the tonal condition was not significantly correlated to AP performance (see Appendix Tab. A.5). Furthermore, only the performance in the AP test 1 correlated with the performance in the tonal WM task in some conditions:

- It correlated positively with the CR during the tonal incongruent sequences ($r = .731, p = .039$),
- it was negatively correlated with the RT in the tonal incongruent condition ($r = -.832, p = .010$),
- it correlated negatively with the RT in the tonal congruent condition ($r = -.843, p = .009$), and
- it did not correlate with the correct answers during the tonal congruent sequences ($r = .656, p = .077$).

12.4.2 fMRI Data

Tonal perception vs. silence in AP musicians – The tonal perception ($z > 3.09, k = 20, SR = 15$) activated the STG bilaterally (see Appendix Fig. A.6 and Tab. A.16).

Tonal rehearsal vs. pink noise nonrehearsal in AP musicians – During the tonal rehearsal ($z > 2.58, k = 10, SR = 10$) AP musicians activated a neural network including the left pars orbitalis and pars opercularis, the right insular cortex, the left pre-SMA, the premotor cortex bilaterally, the left IPL and IPS, the left SMG, the right hippocampus and the cerebellum bilaterally (see Fig. 12.1 and Appendix Tab. A.16).

Incongruent vs. congruent perception in AP musicians – The perception of the tones of the incongruent sequences, compared to the perception of the tones of the congruent sequences ($z > 2.58, k = 6, SR = 10$), engaged more strongly the STS and the STG bilaterally (see Fig. 12.2 and Tab. 12.1). The perception of the tones of the congruent sequences ($z > 2.58, k = 6, SR = 10$) did not show enhanced activation when compared to the perception of the tones of the incongruent sequences.

Incongruent vs. congruent rehearsal in AP musicians – Whereas the rehearsal of the tones of the incongruent sequences, contrasted against the rehearsal of the tones of the congruent sequences ($z > 2.58, k = 6, SR = 10$) activated the left parahippocampal gyrus and the right cerebellum more strongly, the rehearsal of the tones of the congruent sequences showed

stronger activation of the IFG bilaterally, as well as the right STG and the left STS when compared to the rehearsal of tones of the incongruent sequences (see Fig. 12.3 and Tab. 12.1).

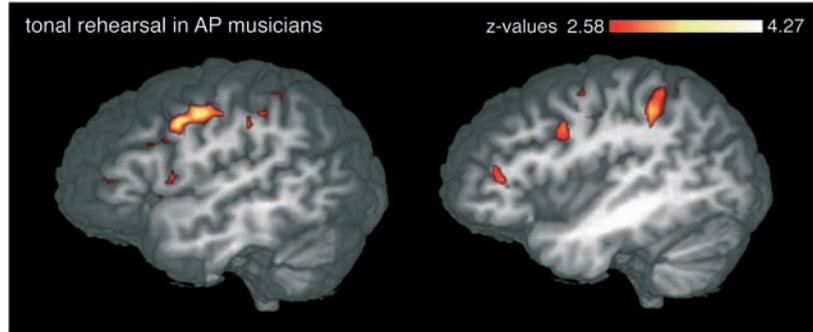


Fig. 12.1: Tonal Rehearsal vs. pink noise Nonreh. in AP musicians ($z > 2.58$, $k = 10$, $SR = 10$)

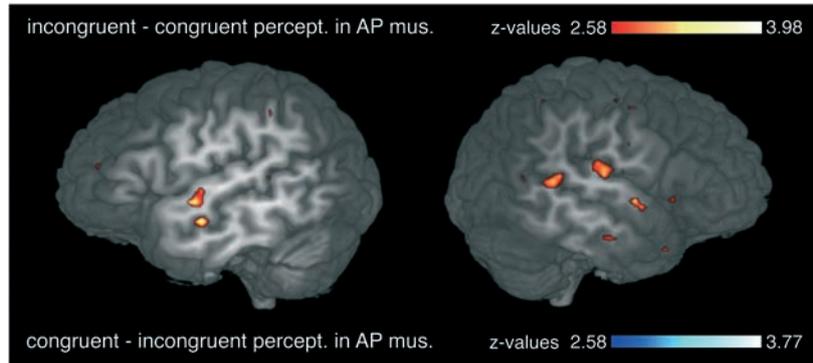


Fig. 12.2: Tonal incongruent vs. congruent Perception in AP musicians ($z > 2.58$, $k = 6$, $SR = 10$)

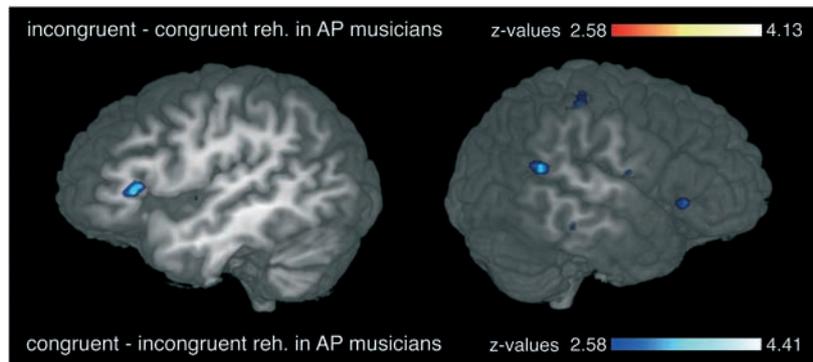


Fig. 12.3: Tonal incongruent vs. congruent Rehearsal in AP musicians ($z > 2.58$, $k = 6$, $SR = 10$)

Tab. 12.1: Comparison of incongruent and congruent Perception/Rehearsal of Tones in AP musicians

area	left hemisphere					right hemisphere				
	BA	x	y	z	z-value	BA	x	y	z	z-value
<i>AP musicians: incongruent – congruent perception ($z > 2.58, k = 6, SR = 10$)</i>										
frontopolar area						10	7	51	12	3.47
cingulate gyrus	24	-5	-12	36	3.82	24/31	13	-15	39	3.90
paracentral lobule						5	10	-36	48	3.45
SMG	40	-38	-33	24	3.75					
STG/postcentral gyrus						40/42	55	-18	15	3.47
anterior STG	22	-47	-9	0	3.74	22	52	-3	0	3.98
STS	21/22	-53	-9	-9	3.80	21/22	58	-42	9	3.63
ITG						20/21	40	-15	-15	3.01
cuneus	18	-5	-75	18	2.87					
	18	-2	-84	12	3.04					
fusiform gyrus						19/36	34	-42	-9	3.67
<i>AP musicians: congruent – incongruent perception ($z > 2.58, k = 6, SR = 10$)</i>										
n.s.										
<i>AP musicians: incongruent – congruent rehearsal ($z > 2.58, k = 6, SR = 10$)</i>										
parahippocampal gyrus	30	-26	-45	3	3.79					
cerebellum							4	-45	-3	3.35
<i>AP musicians: congruent – incongruent rehearsal ($z > 2.58, k = 6, SR = 10$)</i>										
IFG	45	-47	24	6	4.19	46	37	33	9	3.30
	46	-41	33	12	3.04	47	28	33	-9	3.26
						47	25	15	-12	3.30
insular cortex							34	-9	-6	3.31
							28	24	3	3.82
cingulate gyrus	25	-8	12	-9	3.51					
pre-SMA						6	4	15	63	3.25
postcentral gyrus						43	61	-6	15	3.83
IPS	7/40	-26	-54	42	3.19	40	52	-30	48	3.42
SMG	40	-62	-36	30	4.41	40	49	-39	21	3.24
anterior STG						38	37	15	-21	3.80
						38	34	0	-15	3.34
posterior STG						22	55	-48	15	3.59
anterior STS	20/21	-44	3	-27	3.05					
lingual gyrus	19	-23	-60	0	3.14					
capsula interna							13	6	6	3.24
putamen							16	15	-6	3.06
brainstem		-5	-27	-21	3.43					
cerebellum		-17	-51	-24	4.01					

Tonal perception contrasted against pink noise perception: RP musicians vs. AP musicians –

During the tonal perception ($z > 2.58, k = 6, SR = 10$) the RP musicians showed stronger activation of the right cingulate gyrus, the right pars triangularis and the cuneus bilaterally, whereas the AP musicians showed stronger activations of the left SMA and the left posterior STG/STS (see Fig. 12.4 and Tab. 12.2).

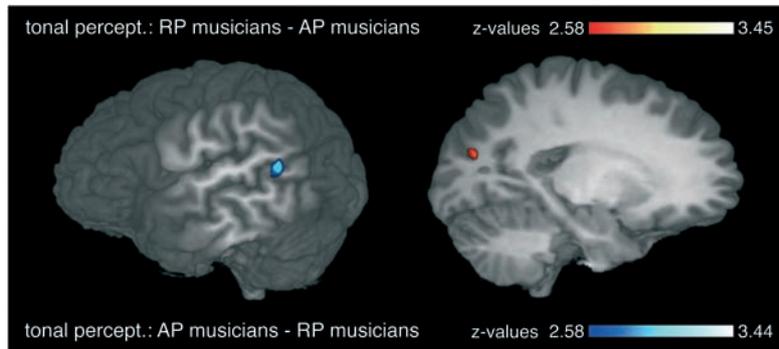


Fig. 12.4: Comparison of tonal Perception between RP and AP musicians ($z > 2.58$, $k = 6$, $SR = 10$)

Tonal rehearsal contrasted against pink noise nonrehearsal: AP musicians vs. RP musicians

– During the tonal rehearsal, which was contrasted against pink noise nonrehearsal ($z > 2.58$, $k = 6$, $SR = 10$), the RP musicians showed stronger activation of the left pre-SMA, the left middle frontal gyrus, the left pars orbitalis and the left MTG, whereas the AP musicians showed stronger activations of the right IFG (BA 44/45), the left hippocampus/parahippocampal gyrus, and the right cerebellum (see Fig. 12.5 and Tab. 12.2). The right hippocampus was more strongly activated in AP musicians, compared to RP musicians, when lowering the threshold ($z > 2.58$, $k = 4$, $SR = 10$, Talairach coordinates: 25 -33 0).

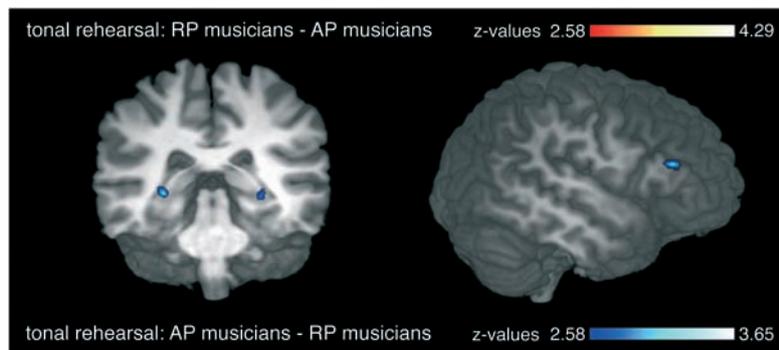


Fig. 12.5: Comparison of tonal Rehearsal between RP and AP musicians ($z > 2.58$, $k = 6$, $SR = 10$)

Tab. 12.2: Comparison of Activations during tonal Perception/Rehearsal between RP mus. and AP mus.

area	left hemisphere					right hemisphere				
	BA	x	y	z	z-value	BA	x	y	z	z-value
<i>RP musicians – AP musicians: tonal perception – pink noise perception ($z > 2.58, k = 6, SR = 10$)</i>										
pars triangularis	45	40	30	6	2.84					
cingulate gyrus	24	7	27	0	3.46					
corpus callosum		-14	-42	18	3.10					
cuneus	18	-14	-84	24	3.07	18	16	-78	21	2.95
<i>AP musicians – RP musicians: tonal perception – pink noise perception ($z > 2.58, k = 6, SR = 10$)</i>										
SMA	6	-5	-9	60	3.16					
posterior STG/STS	21/22	-59	-51	15	3.38					
<i>RP musicians – AP musicians: tonal rehearsal – pink noise nonrehearsal ($z > 2.58, k = 6, SR = 10$)</i>										
pre-SMA	6	-2	12	60	3.33					
middle frontal gyrus	9	-20	36	30	3.71					
pars orbitalis/IFG	47	-29	33	-3	4.29					
MTG	21	-56	-21	-12	3.30					
<i>AP musicians – RP musicians: tonal rehearsal – pink noise nonrehearsal ($z > 2.58, k = 6, SR = 10$)</i>										
IFG	44/45	49	27	18	3.40					
hippocampus/parahip. g.	27	-26	-30	0	3.04					
cerebellum						25	-63	-30		3.44

12.5 Discussion

12.5.1 Behavioural Data

Musical Experience/AP questionnaire – As in the previous AP experiments (Experiments 1 and 2; see Chapters 7.4.1 and 8.4) no difference was observed in the age of musical commencement between AP and RP musicians. Therefore, the data in the present study does not support the assumption that an early musical training facilitates the development of AP as suggested by the literature (e.g., Baharloo et al., 1998; Miyazaki, 1988; Russo et al., 2003; Takeuchi & Hulse, 1993). However, there are some ideas that it is not only important that musical training is given at a very early age, but also how this musical training is designed. Usually, musical training focuses on the relative pitch dimension, which can even inhibit the development of AP (Levitin & Zatorre, 2003). Therefore, it might be crucial to learn to associate musical note names with certain pitches in order to develop AP (Levitin & Zatorre, 2003; Takeuchi & Hulse, 1993; Vitouch, 2003).

Verbal vs. tonal in AP musicians – Like nonmusicians and RP musicians, AP musicians showed a better performance during the verbal condition, compared to the tonal condition. Even though AP musicians showed the best performance during the tonal condition, compared to nonmusicians and RP musicians, they still performed better in the verbal, compared to the tonal, task. This implicates that they might have an advantage when they would label tones verbally.

Key vs. non-key in AP musicians – In contrast to the musicians without AP, the AP musicians showed no significant difference between the key and the non-key sequences. Therefore, it is

suggested that AP musicians did not use knowledge about musical regularities, like RP musicians, to memorise the tonal sequences (see Chapter 11.5.2.3).

Incongruent vs. congruent within AP musicians – In contrast to what was postulated in Hypothesis 2, AP musicians did not show a significant difference between tonal incongruent and congruent sequences, although there was a tendency towards a better performance during the tonal congruent compared to the incongruent sequences. However, different studies reported a superior performance for AP musicians for incongruent sequences, when compared to congruent sequences (Itoh et al., 2005; Miyazaki, 1999; Zakay, Roziner, & Ben-Arzi, 1984). Zakay et al. (1984) showed that the RT for AP musicians increased, when they had to name a pitch sung on a wrong note name than a spoken note name. Miyazaki (1999) observed an analogue of a (visual) Stroop effect in the behavioural performance when AP musicians were asked to name incongruent and congruent syllable-tone pairs, that is AP musicians were faster in naming the pitches of the tones in the congruent condition. Additionally, Itoh et al. (2005) observed that AP musicians were slower when they had to name the pitches during an incongruent trial. The difference between the percentage of CR in the congruent and incongruent in this experiment presumably did not reach significance, due to the small group size of the AP musicians.

AP musicians compared to RP musicians and nonmusicians – The fact that no behavioural differences were observed between the groups during the verbal condition implicates, that there are no major differences for phonemic WM between the groups.

As stated in Hypothesis 1, AP musicians performed significantly better during the tonal condition compared to RP musicians. In Experiment 1, the AP musicians showed a significantly superior performance during the tonal WM task, when an outlier (one AP musician) was excluded. In this experiment the target tones corresponded to the frequency of the Western musical scale, while the distractor tones did not. Additionally, the frequency range within one auditory sequence was wider (compared to Experiment 2), making the use of verbal labelling in AP musicians more probable. In Experiment 2, microtones ($\frac{1}{4}$ steps) were used in a WM task, and no significant performance difference was observed between AP and RP musicians. In Experiment 3, when tones were used, which corresponded to frequencies of the Western musical scale, the AP musicians outperformed the RP musicians. Therefore, Experiments 1, 2 and 3C indicate that AP musicians have a superior memory for tonal stimuli, but only when the frequencies of the tones corresponded to the frequencies of the Western musical scale.

Strikingly, this difference during the tonal WM task between AP and RP musicians in Experiment 3C was due to the tonal WM performance during the congruent sequences, where AP musicians showed a significantly better performance compared to RP musicians, while there was no difference observed between both groups during the tonal incongruent condition. This indicates, that AP musicians outperform RP musicians during a tonal WM task only when they can label these tones. Therefore, this supports the above mentioned results, that AP musicians presumably label pitches automatically (Itoh et al., 2005; Miyazaki, 1999; Zakay et al., 1984). Due to the small group size AP musicians might not show a significant difference between tonal incongruent and congruent sequences in the present study. Interestingly, a positive correlation between the tonal WM performance in the AP test and in the incongruent condition indicated that AP musicians rely less on this verbal labelling system with increased AP ability.

AP test – AP musicians performed better for the AP test 1, which only comprised tones from one octave. This result is in accordance with the literature, where it was reported that AP musicians show superior performance when naming tones of the middle register (AP test 1), compared to lower or higher registers (AP test 2) (Miyazaki, 1989; Takeuchi & Hulse, 1993). In addition, the AP test distinguished between AP musicians and musicians without AP.

Correlations with AP performance – A significant negative correlation between the AP age (when was the AP discovered) and the performance within 3 seconds in both AP tests was observed, whereas the age of musical commencement did not correlate with either the percent of CR nor with the RT in the AP tests. This suggests (i) that it is important at what age AP is detected and (ii) AP is faster and more automatic when it is discovered early. On the other hand, it is also conceivable that good AP is present very early in life. There was no correlation found between the age of musical commencement and the AP ability. Numerous AP studies reported a significant negative correlation between the age of musical commencement and AP performance and therefore emphasised the importance of an early musical training for the development of AP (e.g., Baharloo et al., 1998; Miyazaki, 1988; Russo et al., 2003; Takeuchi & Hulse, 1993). But, Levitin and Zatorre (2003) pointed out that early musical training is not indispensable for the acquisition of AP, because musical training enhances the ability of relative pitch, whereas only a ‘pitch-to-name’ association training, in which a particular auditory stimulus is consistently assigned to a certain category would train the AP ability.

It is very interesting that good AP performance in AP test 1 was positively correlated with the tonal WM performance during the incongruent sequences, indicating that AP musicians who showed a superior performance during the AP test were not getting confused that easily during the tonal incongruent condition. Itoh et al. (2005) observed the opposite behaviour in an auditory Stroop task: The better the AP ability, the more interference during an incongruent pitch-syllable condition was observed. The data from the present study suggest that good AP musicians do not seem to rely on verbal labelling strategies that strongly.

12.5.2 fMRI Data

12.5.2.1 Tonal Perception and Rehearsal in AP musicians

During the tonal perception scans, AP musicians showed activation of the STG bilaterally, and an activation of an extratemporal network, which is comparable to the one observed in RP musicians (see Chapter 11.4.2). During the tonal rehearsal, AP musicians activated neural areas, comparable to the activations observed in RP musicians (see Chapter 11.4.2) and nonmusicians (see Chapter 10.4.2), including the left IFG, the right insular cortex, the premotor cortex bilaterally, the left IPS and IPL, and the cerebellum bilaterally. This network is known to be involved in WM tasks (e.g., Awh et al., 1996; Baddeley, 2003; Crottaz-Herbette et al., 2004; Gruber & von Cramon, 2003; Kirschen et al., 2005; Ravizza et al., 2004; see Chapters 3.3 and 10.5.2.2). However, AP musicians showed, in contrast to the other groups, also activation of the right hippocampus.

12.5.2.2 Incongruent and Congruent Perception and Rehearsal in AP musicians

The perception of the tones of the incongruent sequences, compared with the perception of the tones of the congruent sequences, engaged more strongly the STS and the STG bilaterally in AP musicians. This enhanced activation of the STG and STS cannot be due to amplitude differences in the stimuli, because the same stimuli were used for the incongruent and congruent sequences (in a different composite) and the stimuli were matched for loudness. Studies showed that the activation of the auditory cortex can be modulated by *attention*: The more attention was employed to solve a certain auditory task, the more activation was reported for the primary and secondary auditory cortices (Grady et al., 1997; Jancke et al., 1999; Mitchell et al., 2005; Petkov et al., 2004; Pugh et al., 1996). Therefore, the enhanced activation of the STG and STS during the perception of the tones of the incongruent sequences might be associated with increased top-down attention, which is used to spot or detect the incongruence. This result is in accordance with an auditory Stroop task conducted with AP musicians by Itoh et al. (2005). In an ERP study the authors asked AP musicians to

name either the pitch or the syllable of a sung note name and observed a left posterior-temporal negativity ('AP negativity' with a latency of 150 ms), which was more pronounced (without reaching significance) during the incongruent condition for pitch naming, which they interpreted as verbal labelling processes or pitch-to-name association. The short latency also points to the conclusion that AP already influences early perceptual processes. Furthermore, the authors observed a prolonged RT during the pitch and syllable naming, indicating the automaticity of this pitch naming process (Itoh et al., 2005). The STS seems to play an important role during the perception of tones in AP musicians, because it was also observed to be more strongly involved in AP musicians during tonal perception, when compared to RP musicians (see Chapter 7.5.3), which was interpreted as an indication for a more categorical perception in AP musicians for tones, compared to RP musicians (Binder et al., 2000; Dehaene-Lambertz et al., 2005; Liebenthal et al., 2005; Mottonen et al., 2006; see Fig. 12.6).

When the rehearsal of tones of the congruent condition was compared to the rehearsal of tones during the incongruent condition, the congruent rehearsal activated more strongly the IFG bilaterally (left: BA 45/46, right: 46/47). Therefore, the results do not support Hypothesis 3, where it was assumed that during the incongruent rehearsal the AP musicians show an increased activation of the left DLPFC and the left PT (Itoh et al., 2005; Zatorre et al., 1998). In addition, the frontal activation was more posterior to that observed by Zatorre et al. (1998). Though, the IFG (particularly the left IFG) has been shown to be involved during verbal WM during this dissertation (see Chapters 9.5.2.2, 10.5.2.2, and 11.5.2.2), which is supported by the literature (Awh et al., 1996; Chen & Desmond, 2005; Fiez et al., 1996; Gruber, 2001; Gruber & von Cramon, 2003; Paulesu et al., 1993; Ravizza et al., 2004), whereas other studies showed that this area supports semantic processing (Friederici, 2002; Friederici, Opitz et al., 2000). It seems highly likely that AP musicians used the additional verbal information while rehearsing the pitches of the congruent sequences. This was presumably not possible for the incongruent sequences, because here the additional rehearsal of verbal labels would have been ineffective, even disadvantageous, because the 'wrong' note names could cause interference *within* one WM system (Deutsch, 1970)). This is supported by the fact that during the rehearsal of tones of the congruent sequences a stronger involvement of areas, that are known from verbal WM tasks, namely the right pre-SMA, the right insular cortex, the IPL bilaterally, and the left cerebellum, were observed. Two factors seem to emphasise the automaticity of the verbal labelling process in the present experiment: (a) the involvement of basic auditory areas and (b) the behavioural tendency for the

AP musicians to show a superior performance during the tonal congruent sequences. The correlation analysis showed that with increasing AP ability the AP musicians were less dependent on this verbal labelling.

The stronger involvement of the right parahippocampal gyrus (stronger during the tonal incongruent compared to the tonal congruent rehearsal) presumably reflects the access of the internal template from long-term memory (LTM) and is discussed below (see the comparison between AP musicians and RP musicians for tonal sequences). The behavioural data indicate a tendency for a

superior performance during tonal WM for the congruent compared to the incongruent sequences. It seems that the STG/STS is strongly involved in the detection of incongruence during the perception phase, and then during the rehearsal of the tones of the congruent sequences, which were, in tendency, easier for the AP musicians.

Because auditory perceptual areas are involved in the detection of incongruence, it appears that also the process of AP is based on early and basic perceptual areas. This result also fits with the findings in Experiment 1, that the left STS is more strongly involved in AP musicians during the perception of tonal stimuli, compared to RP musicians, which was interpreted as a more categorical perception in AP musicians (Binder et al., 2000; Dehaene-Lambertz et al., 2005; Jancke et al., 2002; Liebenthal et al., 2005; Mottonen et al., 2006; see Chapters 7.5.3 and 12.5.2.3).

All in all, it appears that (i) AP musicians detected the incongruence (behavioural differences, stronger activation of the STG and STS during the perception of tones of the incongruent sequences) and (ii) they used verbal labelling during the rehearsal of the tones of the congruent sequences (stronger activation of the IFG bilaterally). Importantly, concerning the verbal labelling process, the behavioural data show that the better the AP performance, the less the AP musician were dependent on this process.

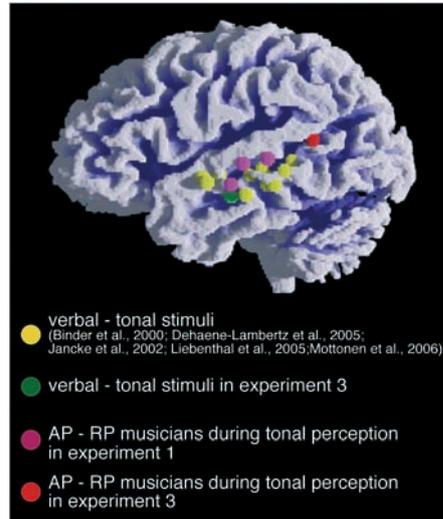


Fig. 12.6: Left STS Activation during different Comparisons

12.5.2.3 Tonal Perception and Rehearsal between AP musicians and RP musicians

During the *tonal perception*, the RP musicians showed mainly increased activation of the right pars triangularis and the cuneus bilaterally. The activation of these areas might indicate a stronger involvement of WM areas (Baddeley, 2003) as well as the use of a visual strategy (Kosslyn et al., 2001) in RP musicians compared to AP musicians. In contrast, the AP musicians displayed stronger activation of the left STG/STS, as formulated in Hypothesis 4. A stronger activation of the left STS in AP musicians, when compared to RP musicians, during the perceptual period of a tonal WM tasks was also observed in Experiment 1 (see Chapter 7.5.3), although the location of the STS activation in Experiment 1 (Talairach coordinates: -61 -18 -4) is posterior to the activation observed in Experiment 3C (Talairach coordinates: -59 -51 15) (see Fig. 12.6). The STS is a quite large structure and in the literature different coordinates²⁶ during the comparison between verbal and tonal perception were reported (see Fig. 12.6). Therefore, future studies are necessary to examine the functions of the different parts of the STS. The stronger activation of STS in AP musicians observed in Experiment 1 was interpreted as the result of a more phonemic/categorical perception of the tones, compared to RP musicians. The result of Experiment 3C supports the findings of the stronger involvement of the left STS found in Experiment 1. Therefore, the results of this dissertation indicate that AP relies on very basic and early perceptual processes. The involvement of the STS indicates a more categorical perception of tonal material in AP musicians, comparable to verbal perception. However, further investigation is necessary to clarify the role of categorical perception in AP musicians. The main finding when comparing the *tonal rehearsal* between AP and RP musicians, was the increased activation of the right pars opercularis/pars triangularis and the left hippocampus (at a lower threshold bilateral activation of the hippocampus was observed) in AP musicians during the tonal rehearsal, compared to the RP musicians. Verbal WM has been reported to enhance activation of the left IFG (Awh et al., 1996; Chen & Desmond, 2005; Fiez et al., 1996; Gruber, 2001; Gruber & von Cramon, 2003; Paulesu et al., 1993; Ravizza et al., 2004; see Chapter 9.5.2.2), but language processes also involve areas in the right hemisphere (Jung-Beeman, 2005), therefore it is tempting to speculate that the stronger activation of the right IFG in AP musicians during the tonal rehearsal, when compared to RP musicians, reflects verbal labelling processes. Nonetheless, this activation is challenging to

²⁶ Talairach coordinates of stronger activations in the STS during verbal perception, compared to tonal perception, observed in different studies: -61 -39 2 (Mottonen et al., 2006), -60 -8 -3 and -56 -31 3 (Liebenthal et al., 2005), -60 -36 -4 (Dehaene-Lambertz et al., 2005), -56 -24 -8 and -56 -32 0 (Jancke et al., 2002), -52 -42 6 and -58 -7 -1 (Binder et al., 2000).

interpret, because two of the eight AP musicians were left-handed, what is likely to have an influence on the lateralisation of this activation. Further research is needed to clarify this issue.

The left hippocampus/parahippocampal gyrus was more strongly activated in AP musicians during the tonal rehearsal compared to RP musicians. The results concerning the hippocampus in relation to memory functions are still contradictory. Some studies showed that the hippocampus is involved in storing information (Ergorul & Eichenbaum, 2004; Sakurai, 2002; Suzuki & Clayton, 2000), some authors even argue that the hippocampus is inhibited during the recall of remote memories (Frankland & Bontempi, 2005) and others propose that the recall, and therefore the decoding, of information is dependent on the hippocampal formation (including the entorhinal, perirhinal and parahippocampal gyrus) (Brown & Aggleton, 2001; Dobbins, Rice, Wagner, & Schacter, 2003; Eldridge, Knowlton, Furmanski, Bookheimer, & Engel, 2000). For instance, Meltzer and Constable (2005) showed in an fMRI study bilateral activation of the hippocampus during the encoding as well as during the recall of paired associate words. These activations were observed to be stronger in those participants during the recall, who showed a better memory performance. Therefore, these authors argued that the hippocampus is entangled during the recall and the encoding of associative memories. Besides, Eichenbaum (2000) suggested that the hippocampus is involved in the formation of relational representations and for the recall of semantic information, as well as recognition and associative memory. A study by Ranganath, Cohen, and Brozinsky (2005) furthermore indicated that the combined activation of the ventral prefrontal cortex, including the triangular gyrus and hippocampus, mediate the formation of LTM information. Given these results, one might assume that the activation of the left (at a lower threshold bilateral) hippocampal formation reflects the access of the internal representation of tones, respectively pitches, and the activation of the right pars opercularis/triangularis the rehearsal of the associated tone names.

RP musicians showed stronger activations of areas usually involved in WM tasks, e.g., the left pre-SMA, the left middle frontal gyrus, the left pars orbitalis as well as the left MTG, which were also more strongly activated in RP musicians during the tonal rehearsal, contrasted against the verbal rehearsal (see Tab. 11.2), which indicates a different strategy during tonal WM processes in RP musicians.

12.6 Summary

By comparing AP musicians to RP musicians it was possible to explore, if the ability of AP has an influence on the cognitive processes (e.g., the degree of involvement) and the neural organisation of WM, because this question is still discussed contradictory in the literature (e.g., Hirose et al., 2002; Itoh et al., 2005; Klein et al., 1984; Zatorre et al., 1998).

Behavioural data – AP musicians did not show a significant performance difference for the tones of the incongruent compared to tones of the congruent sequences, though a trend towards the better performance for congruent sequences was observed, indicating an auditory Stroop effect.

AP musicians showed a better performance during the tonal condition, when compared to the RP musicians. Strikingly, this difference was due to the tonal WM performance during the congruent sequences, where AP musicians showed a significantly better performance compared to RP musicians, while there was no difference between both groups during the tonal incongruent condition. This suggests that the AP musicians in this experiment outperformed RP musicians during this tonal WM task only when they were able to label the tones verbally (or could use the verbal information provided in the congruent condition). A positive correlation between the tonal WM performance in the AP test and in the incongruent condition indicated that AP musicians rely less on this verbal labelling system with increasing AP ability.

Tonal rehearsal in AP musicians – During the tonal rehearsal, AP musicians activated a neural network comprising known WM areas, including the left IFG, the right insular cortex, the left pre-SMA, the premotor cortex bilaterally, the left IPL and IPS, the left SMG, the right hippocampus, and the cerebellum bilaterally (e.g., Baddeley, 2003; Crottaz-Herbette et al., 2004; Gruber & von Cramon, 2003; Henson et al., 2000; Jonides et al., 1998; Kirschen et al., 2005; Ravizza et al., 2004). AP musicians displayed a stronger activation of the right hippocampus in this contrast, which might reflect the access to the internal (presumably tonal) template information (Brown & Aggleton, 2001; Dobbins et al., 2003; Eldridge et al., 2000).

Incongruent and congruent sequences in AP musicians – The perception of tones of the incongruent sequences, compared with the perception of the tones of the congruent sequences, mainly engaged more strongly the STS and the STG bilaterally. Because the activation of the STG is modulated by attention (Grady et al., 1997; Jancke et al., 1999; Mitchell et al., 2005; Petkov et al., 2004; Pugh et al., 1996), this appears to reflect increased top-down attention as a consequence of the detection of incongruence. During the comparison of the rehearsal of tones of the congruent with the incongruent sequences, stronger activation

of the IFG bilaterally was observed during the rehearsal of tones of the congruent sequences. This was interpreted as an additional use of the verbal information during the rehearsal of the tones of the congruent sequences. Interestingly, AP musicians seemed to detect the incongruence (behavioural differences, stronger activation of the STG and STS during the perception of tones of the incongruent sequences) and (ii) to use verbal labelling during the tonal rehearsal of the congruent sequences (stronger activation of the IFG bilaterally). On the other hand, concerning the verbal labelling process, the behavioural data showed as well that the better the AP performance, the less the AP musician were dependent on this process.

Tonal perception: AP vs. RP musicians – During the tonal perception AP musicians showed stronger activation of the left STG/STS than RP musicians. The STS was also more strongly activated in Experiment 1 when AP musicians were compared to RP musicians during tonal perception. It is important to note that the STS was also stronger involved when verbal and tonal perception were compared in Experiment 3. This was interpreted as a more categorical, possibly comparable with verbal, perception in AP musicians. Additionally, the STS is also more strongly involved during the detection of incongruence in AP musicians (see above). Together, these results indicate that AP relies on a very basic and early perceptual process, and is not only including later cognitive stages.

Tonal rehearsal: AP vs. RP musicians – The tonal rehearsal between RP musicians and AP musicians was compared to evaluate, whether AP musicians show less WM involvement during tonal WM, which is still a matter of discussion (e.g., Hantz et al., 1992; Hirose et al., 2002; Itoh et al., 2005; Klein et al., 1984; Zatorre et al., 1998). When comparing the tonal rehearsal between AP and RP musicians, the AP musicians showed an increased activation of the left (at a lower threshold bilateral) hippocampus compared to the RP musicians. Activation of the hippocampus was also observed during the tonal rehearsal in AP musicians contrasted against the pink noise nonrehearsal condition. The hippocampal activation was interpreted as an access to the internal tonal information, due to the fact that studies showed activation of the hippocampus during the recall of information (Brown & Aggleton, 2001; Dobbins et al., 2003; Eldridge et al., 2000). The result, therefore, indicate the following: AP musicians perceive tones categorically (comparable to verbal information), and AP is not only influencing the perception of tones, but also WM processes related to tonal information, suggesting an idea how AP “works”.

Chapter 13

Summary and General Discussion

The purpose of this dissertation was to investigate and compare the perception and WM processes of different auditory stimuli (verbal and tonal) in different groups of participants (nonmusicians, RP musicians, and AP musicians) using fMRI, with the main focus on tonal WM processes.

One advantage of this dissertation is that with the same stimulus material (auditory verbal and tonal sequences) very different groups (in terms of their ‘tonal experience’) were investigated (Experiments 3A-3C), resulting in a high comparability of results between the groups. Furthermore, a large pool of participants (105 participants with 34 AP musicians, 54 RP musicians and 17 nonmusicians) was investigated in this dissertation. The main results discussed in this chapter are summarised and visualised in Fig. 13.1.

13.1 Language and Music

Because there are many open questions concerning the neural correlates of *language and music*, this dissertation aimed to investigate the neural correlates of verbal and tonal perception and *working memory (WM)* processes. WM is essential for understanding language and music, because both unfold over time, so that the already heard auditory information needs to be maintained to build up a context. Until now, WM processes related to tonal stimuli have not received as much research attention as verbal WM processes, therefore potential differences and similarities in the neural patterns underlying verbal and tonal stimuli have remained elusive.

Perception of verbal and tonal stimuli – In accordance with the literature and as hypothesised, stronger activation of the STS and STG was observed during the verbal, compared to the tonal perception (see Fig. 13.1), although participants were always presented with both stimuli simultaneously (Experiment 3). This activation has been reported in the literature (Binder et al., 2000; Dehaene-Lambertz et al., 2005; Jancke et al., 2002; Liebenthal et al., 2005; Mottonen et al., 2006), and was assumed to be due to a phonemic/categorical perception of the verbal material (Liebenthal et al., 2005; Mottonen et al., 2006).

Comparison of WM for tonal and verbal material – This question was mainly investigated in nonmusicians, because this allowed a broad generalisation (Experiment 3A). During the verbal rehearsal nonmusicians activated a cerebral network, including the left mid-DLPFC,

the pars opercularis/premotor cortex bilaterally, the left pre-SMA, the IPS bilaterally, the left IPL, as well as the cerebellum bilaterally. These areas have been reported to be involved in verbal WM tasks (Awh et al., 1996; Baddeley, 2003; Crottaz-Herbette et al., 2004; Gruber, 2001; Gruber & von Cramon, 2003; Henson et al., 2000; Paulesu et al., 1993; Smith & Jonides, 1998). Notably, a quite similar network was activated during the rehearsal of sine wave tones, including the left pars orbitalis, the left pre-SMA, the left PMv, and the right cerebellum. Therefore, the verbal and the tonal rehearsal activated a WM network, but the strength of activation differed in nonmusicians: During the verbal rehearsal stronger activations were observed, compared to the tonal rehearsal. When comparing the verbal directly against the tonal rehearsal, most importantly Broca's area, the premotor areas bilaterally, and the left IPL and SPL were more strongly involved during verbal WM (see Fig. 13.1).

Broca's area is mainly involved in the processing of language (for an overview see Friederici, 2002) and verbal WM (Awh et al., 1996; Chen & Desmond, 2005; Fiez et al., 1996; Gruber, 2001; Gruber & von Cramon, 2003; Paulesu et al., 1993; Ravizza et al., 2004), and more specifically this area is known to be involved in the processing of verbal (Friederici, 2002; Friederici, Meyer et al., 2000) and musical syntax (Koelsch, 2005; Koelsch, Fritz et al., 2005; Maess et al., 2001; Tillmann et al., 2003). Since the auditory stimuli used in the present experiments did not contain any syntactical information, this proposes a special role for Broca's area during verbal WM (see Fig. 13.1).

Because the internal verbal rehearsal is thought to be comparable with subvocal speech (Baddeley, 2003; Baddeley et al., 1998; Wilson, 2001), the stronger activation of the premotor areas appears to reflect a stronger association between the sensory stimulus and the associated motor representation in the verbal modality. This motor representation presumably can be used to rehearse the verbal information internally, comparable or similar to, the motor program used to articulate the syllable aloud. The assumed functions of the IPL and SPL are manifold, including the neural correlate of the phonological store, attention, motor functions, etc. (e.g., Baddeley, 2003; Cabeza & Nyberg, 2000; Corbetta & Shulman, 2002; Culham & Kanwisher, 2001; Fogassi & Luppino, 2005; Rizzolatti & Luppino, 2001). One interpretation is that the left IPL, which was more strongly activated in nonmusicians during the verbal compared to the tonal rehearsal, indicates a unique role for the phonological store for verbal material (Baddeley, 2003; Braver et al., 1997; Crottaz-Herbette et al., 2004; Gruber & von Cramon, 2003; Paulesu et al., 1993; Ravizza et al., 2004). Alternatively, the IPL might be engaged in motor representations (Fogassi et al., 2005; Fogassi & Luppino, 2005; Rizzolatti & Luppino, 2001), which would fit nicely with the interpretation of the premotor areas.

However, both interpretations are not contradictory, but suggest an idea how the verbal material might be decoded in the phonological store. The tonal rehearsal showed stronger activation of the left cingulate gyrus and the left angular gyrus (see Fig. 13.1), possibly reflecting evaluatory processes as well as the use of a different strategy (e.g., Baciú et al., 1999; Blanch et al., 2004; Chambers et al., 2004; Y. Kondo et al., 2005).

Interestingly, the results indicate that although the neural networks underlying WM for tonal and verbal stimuli show considerable overlap, there are also areas that seem to be engaged specifically, and/or are more involved in verbal (e.g., Broca's area, premotor cortex bilaterally, left IPL) or tonal (e.g., left angular gyrus) WM processes in nonmusicians. Therefore, the present experiment suggests that the main neural networks related to WM are similar for both types of stimuli, but each network emphasises and/or involves slightly different (neural) subcomponents. Based on the conclusion that verbal material has to be translated from the sensory input into a motor code, which is internally rehearseable, it is tempting to speculate that the ability to translate the sensory tonal information into this internally rehearseable motor representation is also what constitutes the performance in tonal WM tasks. This was further investigated in RP musicians.

13.2 Musicians and Plasticity

The question of differences and similarities concerning the neural correlates of WM was examined in different groups of participants: nonmusicians and RP musicians. Many *musicians* start their musical training at a very early age. This musical practise for many years results in an increased auditory, visual, and somatosensory input, as well as in intensive training of motor functions. Thus, musicians are excellent participants to investigate to what extent the environment can shape the brain, to examine *plasticity* (e.g., Munte et al., 2002; Pantev et al., 2003; Schlaug, 2001). Therefore, musical expertise was expected to be a moderating factor in WM processes for tonal stimuli, which was investigated in this dissertation (Experiment 3B).

During the verbal, as well as during the tonal rehearsal, RP musicians activated a neural network, including the left pars opercularis, the insular cortex bilaterally, the pre-SMA bilaterally, the premotor cortex bilaterally, the left SPL and IPS (activation also spread in the IPL), and the cerebellum. These areas are known to subserve WM tasks (Awh et al., 1996; Baddeley, 2003; Crottaz-Herbette et al., 2004; Gruber, 2001; Gruber & von Cramon, 2003; Henson et al., 2000; Kirschen et al., 2005; Paulesu et al., 1993; Smith & Jonides, 1998) and have also been observed to be involved in the nonmusicians. An interesting finding was that

in contrast to the nonmusicians, the tonal rehearsal did not show a weaker activation in the RP musicians, which is interpreted to be the consequence of a greater similarity between tonal and verbal WM processes in RP musicians. Though, the verbal rehearsal in RP musicians revealed, as in nonmusicians, a stronger activation of Broca's area, which supports the notion established in Experiment 3A that Broca's area is more strongly involved during the WM rehearsal of verbal material (see Fig. 13.1).

Interestingly, in contrast to nonmusicians RP musicians did not show a stronger involvement of the premotor areas during the verbal rehearsal, compared to the tonal rehearsal. Learning to play an instrument also includes an extensive motor training, which leads to anatomical (Amunts et al., 1997; Gaser & Schlaug, 2003) and functional (Hund-Georgiadis & von Cramon, 1999; Jancke et al., 2000; Krings et al., 2000) differences related to (pre-)motor areas between musicians and nonmusicians. Studies indicated that there is a strong association between (pre)motor and auditory areas as a consequence of the musical training, which includes the learning of associations between a motor action (e.g., pressing a key of the piano) and the corresponding auditory stimulus (Bangert et al., 2005; Haslinger et al., 2005; Haueisen & Knosche, 2001; Lotze et al., 2003; Meister et al., 2004). Considering the result that, unlike nonmusicians, RP musicians did not show a stronger premotor activation during the verbal, when compared to the tonal rehearsal, and the stronger involvement of premotor areas in RP musicians during the tonal rehearsal, compared to nonmusicians, this supports the hypothesis that RP musicians have a stronger association between the tonal sensory input and the motor representation, which might be comparable to that of verbal material. This is most probably due to the musical training over years for the RP musicians, when they learn to associate a motor program/action with a corresponding tonal sensory input (e.g., pressing a certain key and listening to the corresponding tone).

During the tonal, compared to the verbal, rehearsal the RP musicians showed a stronger activation of the right SMG. The SMG has been shown to play an important role during tonal WM (Gaab, Gaser et al., 2003), and the present study indicates that the SMG plays an important role in tonal WM, especially in RP musicians (see Fig. 13.1).

The RP musicians, compared to the nonmusicians, appeared to display (besides the left premotor area) stronger activations of a mostly left pronounced network, including the insular cortex bilaterally, the left SPL and IPS/IPL during the tonal rehearsal.

When comparing the functional activation pattern between RP musicians and nonmusicians during the tonal rehearsal, the left *SPL* and the left *IPS/IPL* were more strongly activated in RP musicians (see Fig. 13.1). This is important insofar that in nonmusicians the left *SPL* and

IPL were more strongly activated during the verbal, compared to the tonal condition, which could be explained by alternative theories: e.g., the phonological store of verbal WM, attention, motor representations, etc. (Baddeley, 2003; Braver et al., 1997; Cabeza & Nyberg, 2000; Corbetta & Shulman, 2002; Culham & Kanwisher, 2001; Fogassi & Luppino, 2005; Gruber & von Cramon, 2003; Paulesu et al., 1993; Ravizza et al., 2004; Rizzolatti & Luppino, 2001). There are following possibilities to interpret the stronger parietal activation in RP musicians compared to nonmusicians during tonal rehearsal: (i) an enhanced use of the phonological store in RP musicians for tonal material (Baddeley, 2003; Crottaz-Herbette et al., 2004; Gruber & von Cramon, 2003; Henson et al., 2000; Olesen et al., 2004; Ravizza et al., 2004), (ii) it is related to motor representations (Fogassi et al., 2005; Petrides & Pandya, 1984; Rizzolatti et al., 1997; Rizzolatti & Luppino, 2001; Rizzolatti et al., 1998) or (iii) visual-spatial mapping in RP musicians (Gaser & Schlaug, 2003; Sergent et al., 1992; Stewart et al., 2003).

In any case, these activation differences between RP musicians and nonmusicians are thought to reflect a different WM related strategy for tonal information in RP musicians, presumably due to the musical training. This result supports the findings of adaptive changes and plasticity in the brains of musicians (e.g., Elbert et al., 1995; Koelsch et al., 1999; Munte et al., 2002; Schneider et al., 2002).

Considering the results observed in RP musicians and nonmusicians, the processes underlying verbal and tonal WM seem to be quite similar (translate the sensory auditory event into a rehearseable motor code), when the tonal WM has been trained. The results gained by Experiment 3B point to one important and basic mechanism of verbal (and tonal) WM: to translate the sensory verbal or tonal event into a rehearseable motor representation.

Tonality/strategy based WM - As hypothesised, RP musicians, in contrast to nonmusicians and AP musicians, showed a significant superior performance for the key sequences compared to the non-key sequences, which was also reflected in the activation of additional brain areas during the rehearsal of the key sequences, namely the right mid-DLPFC, the right IPCS, and the premotor cortex bilaterally (see Fig. 13.1). These areas have been shown to be involved in strategy-based WM processes (Bor et al., 2003; Petrides, 2000a, 2005; Savage et al., 2001). Therefore, RP musicians presumably used their explicit and implicit knowledge about musical regularities to cluster, chunk and organise the tonal information to be rehearsed. The stronger premotor activation during key rehearsal is interpreted as a consequence of the tonality: Because usually RP musicians play tonal pieces, they might have stronger motor representations for these sequences.

In contrast to the hypothesis, Broca's area was not more strongly activated during key compared to non-key sequences, although studies, which investigated the violation of verbal and musical structure, showed the involvement of the Broca's area for verbal material (Friederici, 2002), and the pars opercularis bilaterally for musical stimuli (Maess et al., 2001; Tillmann et al., 2003). Several reasons could account for this different finding. Firstly, Maess et al. (2001) and also Tillmann et al. (2003) used musical stimuli that built up strong musicological expectations of the musical progression, which were violated. In the present study the auditory stimuli did not have the potential to build up such a context (e.g., the non-key sequences are unstructured in terms of musical regularities), and therefore no expectations were established or violated. Secondly, in the above mentioned studies (Maess et al., 2001; Tillmann et al., 2003) chords were used, whereas in Experiment 3 sine wave tone sequences were employed, which were presumably too abstract.

This might explain why no activation of the pars opercularis was observed when comparing the key with the non-key rehearsal, but instead areas were activated, which have been shown to be involved during strategy-based WM tasks (Bor et al., 2003; Petrides, 2000a, 2005; Savage et al., 2001). Furthermore it accounts for the finding why no differences (key – non-key) in nonmusicians, neither in the behavioural nor in the functional data, were observed.

13.3 Absolute Pitch

Some musicians possess *absolute pitch (AP)*, i.e. they can name every tone of the Western musical scale without a reference tone (Takeuchi & Hulse, 1993). The neural correlates as well as the underlying perceptual and cognitive mechanisms of AP are still not fully understood. One aim of this dissertation was to explore the involved perceptual and/or cognitive mechanisms and the underlying neural correlates of this rare ability. Because there are still contradictory results concerning the degree of WM involvement in pitch memory tasks in AP musicians (Crummer et al., 1994; Hantz et al., 1995; Hirose et al., 2002; Klein et al., 1984), it was investigated if the ability of AP has an influence on the cognitive processes (degree of involvement) and the neural organisation of WM by comparing AP musicians to RP musicians.

Musical commencement in AP musicians – Although the literature indicates that an early musical training facilitates the development of AP (e.g., Baharloo et al., 1998; Miyazaki, 1988; Russo et al., 2003; Takeuchi & Hulse, 1993) in the experiments, which investigated AP musicians in the present dissertation (Experiments 1, 2 and 3C; $N = 34$ AP musicians) neither a difference in the age of musical commencement between AP and RP musicians, nor

a correlation of the age of musical commencement and the AP ability in AP musicians was observed. Nevertheless, there are some ideas that it is not only important that musical training is given at a very early age, but also *how* this musical training is designed. Usually, musical training focuses on the relative pitch dimension, which can even inhibit the development of AP (Levitin & Zatorre, 2003), i.e. it is presumably crucial to learn to associate musical note names with certain pitches in order to develop AP (Levitin & Zatorre, 2003; Takeuchi & Hulse, 1993; Vitouch, 2003).

On the other hand, the age at which AP was detected was positively correlated with the reaction time of AP musicians in the AP tests, that is the earlier this ability was detected the faster the AP musicians could label the tones in the AP tests, indicating a more automatic and effortless AP ability. The earlier AP is detected the earlier the musicians could train to associate a certain tone to a corresponding category (Levitin & Zatorre, 2003). The data in the present study support the assumption that early learning facilitates the development of AP, but it seems that musical training is not as sufficient as an adapted training of AP (learning to associate tones with certain categories) (Levitin & Zatorre, 2003).

Categorical perception in AP musicians – The fMRI investigation (Experiments 1 and 3C) of the perception of tones in AP and RP musicians indicated that the ability of AP already influences the perception. Importantly, in both studies the AP musicians showed stronger activation of the left STS (although at a somewhat different location; see Fig. 13.1) during the perception. It is interesting to note that the STS has been reported to show stronger activation during the perception of verbal compared to tonal stimuli (Binder et al., 2000; Dehaene-Lambertz et al., 2005; Jancke et al., 2002; Liebenthal et al., 2005; Mottonen et al., 2006), which is thought to be related to the more categorical perception of verbal material (Liebenthal et al., 2005; Mottonen et al., 2006). This result was replicated in the present experiment (Experiment 3): A stronger activation of STS (bilateral) was observed during the perception of the syllables, compared to the tones, although participants always listened to both stimuli simultaneously, but concentrated either on the tones or the syllables. This indicates that the stronger activation of the STS could be due to a top-down effect, modulated by stored verbal templates. This interpretation is also supported by Mottonen et al. (2006). They reported that participants, after they learned to perceive ‘sine wave speech’ as speech, i.e. they learned to categorise the stimuli by developing an internal template, showed stronger activation of the left STS. Therefore, the stronger activation of the STS in AP musicians, when compared to RP musicians, appears to reflect a more categorical perception of tones (comparable to the perception of phonemes in RP musicians or nonmusicians), which could

be modulated by the existence of internal templates for tones in AP musicians (Klein et al., 1984; Zatorre, 2003).

The conclusion that AP already influences early and basic perceptual processes in AP musicians, is furthermore supported by the result that the detection of incongruence between a tone and a verbal stimulus (the name of the note) appears to take place already during the perception and involves basic perceptual areas like the STS and the STG (Experiment 3C).

How automatic is verbal labelling of tones in AP musicians? – It has been suggested in the literature that AP musicians show a superior performance during tonal WM, compared to RP musicians, when they can label the tones verbally (Siegel, 1974; Takeuchi & Hulse, 1993). In the present study AP musicians showed a superior performance during a tonal WM task compared to RP musicians, when the frequency of the tones corresponded to tones of the Western musical scale (see Experiments 1, 2 and 3C). Notably, this indicates that in a tonal WM task AP musicians remember the tones better, if they can assign them to a certain category, e.g., label them verbally. This is additionally underlined by the result that AP musicians displayed a superior performance during the tonal rehearsal of congruent sequences, when compared to RP musicians, whereas this was not the case during the tonal rehearsal of incongruent sequences, suggesting an ‘auditory Stroop effect’ in AP musicians in the incongruent condition. This result is supported by the literature (Itoh et al., 2005; Miyazaki, 1999). That AP musicians have an advantage to label tones verbally was additionally supported by the result that they showed a better performance during the verbal condition, compared to the tonal condition in Experiment 3C. Therefore, this supports the above mentioned results that AP musicians label pitches automatically (Itoh et al., 2005; Miyazaki, 1999; Zakay et al., 1984). Furthermore, a positive correlation between the tonal WM performance in the AP test and in the incongruent condition was observed, indicating that AP musicians are less dependent on this verbal labelling strategy with increasing AP ability.

Interestingly, these results suggest that AP musicians show a better WM performance for tonal stimuli when they can assign the tones to certain categories. Verbal labelling seems to play a role for some AP musicians, but the better the AP the less dependent are the AP musicians on this verbal labelling strategy.

AP and tonal WM – The ability of AP does not only influence the perception of tones, but also the WM for tonal material. During the tonal rehearsal in Experiments 1 and 3C, AP musicians also activated a neural network comprising known WM areas (e.g., IFG,

premotor areas, parietal areas, and cerebellum). The result, that RP musicians show an increased activation of the right SPL/IPS (Experiment 1) and the left pre-SMA, left middle frontal gyrus, the left pars orbitalis, and the left MTG (Experiment 3C) during a tonal WM task, when compared to AP musicians, indicates a difference of WM processes between AP and non-AP musicians. This is in accordance with some results in the literature (because this is still discussed controversially), which assumed differences in WM processes for RP and AP musicians (Crummer et al., 1994; Hantz et al., 1992; Klein et al., 1984; Wayman et al., 1992; Zatorre et al., 1998). E.g., the lack of (or a smaller) P300, which is an electrophysiological index for WM processes (Donchin, 1981; Klein et al., 1984) and has been located in the IPS (Moore et al., 2003), has been reported to be diminished in AP musicians (Crummer et al., 1994; Hantz et al., 1992; Klein et al., 1984; Wayman et al., 1992; Zatorre et al., 1998), because they do not seem to update their WM as frequently due to the internal tonal templates (Zatorre et al., 1998).

The AP musicians showed, when compared to the RP musicians during the tonal rehearsal, an increased activation the left hippocampus (at a lower threshold the hippocampus showed bilateral activation). Activation of the right hippocampus was also observed during the tonal rehearsal in AP musicians, when contrasted against the pink noise nonrehearsal condition. The hippocampal activation is interpreted as an access to the internal template (tonal information), supported by the fact that studies showed activation of the hippocampus during the recall of information (Brown & Aggleton, 2001; Dobbins et al., 2003; Eldridge et al., 2000). Importantly, these results indicate that the neural correlates of WM processes for tonal stimuli differed between RP and AP musicians.

13.4 Overall Summary and Perspectives

All in all, these main results were obtained in the present dissertation:

1. Although the neural networks underlying WM for tonal and verbal stimuli show considerable overlap, there are also areas that seem to be engaged specifically, and/or are more engaged in verbal (e.g., Broca's area, premotor cortex, IPL) or tonal (e.g., angular gyrus) WM processes (see Fig. 13.1). Based on the assumption that verbal material has to be translated from the sensory input into a motor code, which is internally rehearseable, it is assumed that nonmusicians do not have such a strong connection between tonal sensory input and a corresponding motor program as they have for verbal material. This is also reflected in the behavioural data and the functional activation pattern when verbal and tonal rehearsal were compared.

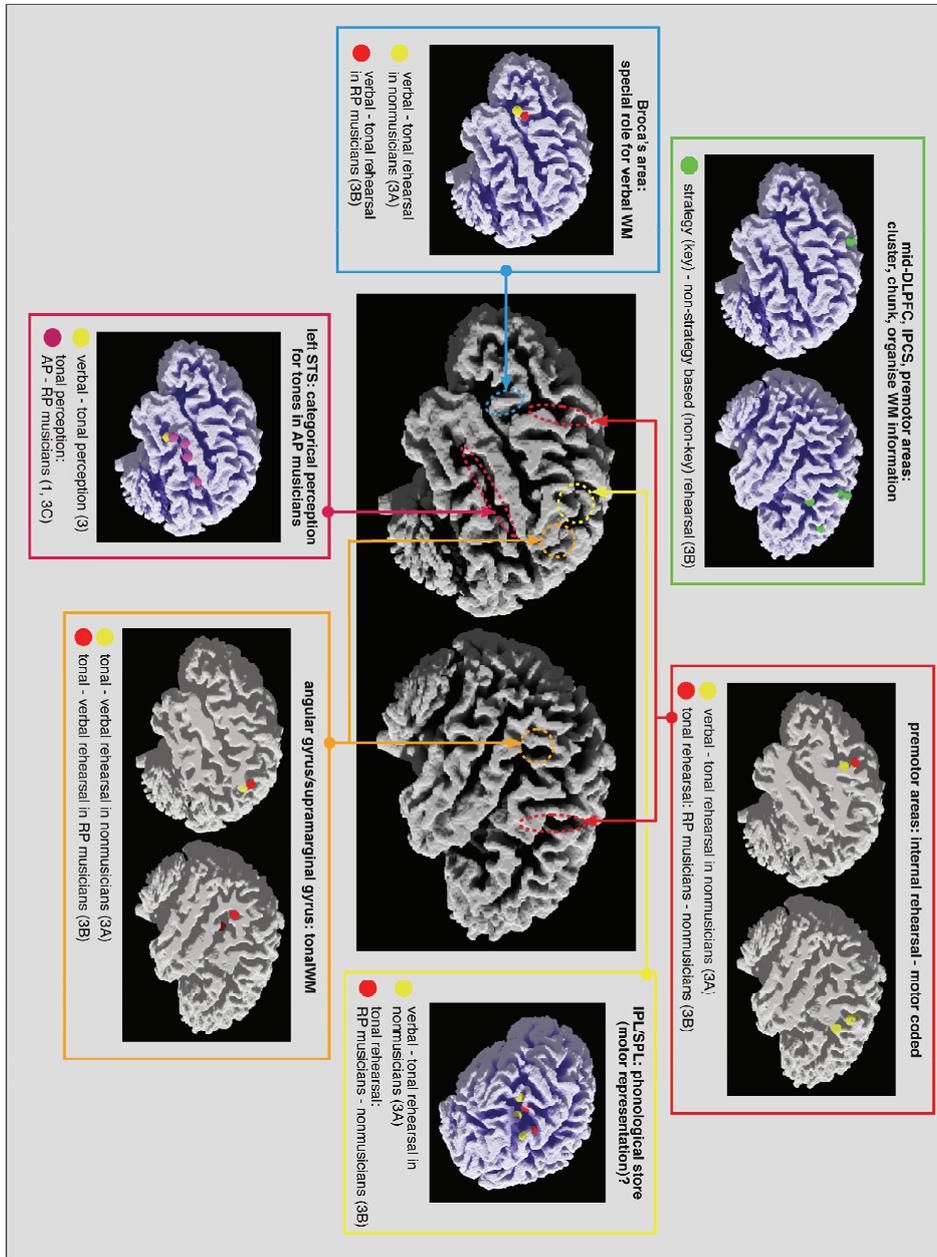


Fig. 13.1: Schematic Summary of main Results

2. Due to their musical training, RP musicians showed a superior performance during the tonal WM task, which might be due to a stronger association between an auditory tonal input and the corresponding motor program to produce such a tone. This was also reflected in the functional pattern (e.g., a stronger involvement of premotor areas during tonal rehearsal in RP musicians compared to nonmusicians; see Fig. 13.1).
3. Results indicate that AP musicians perceive tones more categorically, comparable to the perception of verbal material in non-AP possessors (see Fig. 13.1). Additionally, during the tonal rehearsal AP musicians engage classical WM areas to a lesser degree than RP musicians.

Although the findings of this dissertation shed light on some issues, new questions were raised, which can probably be answered in further experiments.

AP musicians and categorical perception – AP musicians seem to show a superior performance in tonal WM task, when the frequencies of the tones corresponded to the frequencies of the tones of the Western musical scale. It would be interesting to investigate with fMRI whether there are differences in the perception and rehearsal phase between AP and RP musicians when they listen to microtones compared to tones which frequency corresponds to the frequency of the Western musical scale.

Level of difficulty – The experiment consisted of three pairs of conditions, which were interwoven: verbal and tonal, key and non-key, as well as tonal congruent and tonal incongruent. In addition, three different groups of participants (nonmusicians, RP and AP musicians) were investigated. Therefore, there was no possibility to control for the level of difficulty between the tasks or groups. Nevertheless, it would be challenging to design an experiment with tonal and verbal stimuli, which have the same difficulty for nonmusicians.

Parietal activations – This study was not designed to clarify whether the IPL is involved in the storage of verbal information (phonological store), or in attentional mechanisms. However, because the parietal lobe, as a heteromodal association area, is involved in many tasks (Corbetta & Shulman, 2002; Culham & Kanwisher, 2001), it is still an open question whether this area also serves as the neural correlate of the phonological store. Also the question arises, if the Baddeley and Hitch model (Baddeley & Hitch, 1974) can comprehensively account for the full complexity of cognitive and neural organisation of WM processes.

Motor representations – It would be interesting to pursue the question of the premotor involvement in auditory WM. It is conceivable to investigate this with more 'natural' sounds,

e.g., with piano tones in piano players or violin tones in violin players. Another possibility would be to analyse if the premotor involvement is different between piano tones and sine wave tones in piano players. It could be hypothesised that the premotor involvement is stronger for the tones of the instrument played by the musician, because the association between the auditory sensory event and the motor program should be more closely related. Furthermore, it would be interesting to examine whether there is a difference in the premotor cortex activation between different musicians during tonal WM tasks, e.g., comparing singers with piano players. It is plausible that singers might activate different premotor areas (premotor cortex associated with mouth movements) than piano players (premotor cortex associated with hand movements).

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Appendix

Tab. A.1: Design of the Microtones for Experiment 2

name	frequency in Hz	lower frequency	upper frequency	frequency range	frequency 1st tone	frequency 2nd tone	frequency 3rd tone	frequency 4th tone	frequency difference
B	247								
C	262	255	270	15	258.75	262.5	266.25	270	3.75
C#	277	270	286	16	274	278	282	286	4
D	294	286	303	17	290.25	294.5	298.75	303	4.25
D#	311	303	321	18	307.5	311	316	320.5	4.5
E	330	321	340	19	325.75	330.5	335.25	340	4.75
F	349	340	360	20	345	350	355	360	5
F#	370	360	381	21	365.5	370.5	375.75	381	5.25
G	392	381	404	23	386.75	392.5	398.25	404	5.75
G#	415	404	428	24	410	416	422	428	6
A	440	428	453	25	434.25	440.5	446.75	453	6.25
A#	466	453	480	27	459.75	466.5	473.25	480	6.75
B	494	480	509	29	487.25	494.5	501.75	509	7.25
C	523	509	539	30	516.5	524	531.5	539	7.5

Pretest 1 – 4 for Experiment 3

Pretest 1

Stimuli – The frequency of the presented sine wave tones corresponded to the frequency of the tones of the Western musical scale (based on A = 440 Hz) and ranged from 261 Hz (C4) to 523 Hz (C5). The spoken syllables are the names of the tones in German: C, Cis, D, Dis, etc. (in English: C, C#, D, D#). Each stimulus consisted of a spoken syllable and a simultaneously presented sine wave tone. One stimulus had a duration of 400 ms, with a period of 150 ms silence between the tones. Before participants were presented with the auditory sequence, a visual cue indicated whether they should pay attention to the tones or the syllables. Originally it was planned, to include the rehearsal (to investigate the articulatory rehearsal process) and the suppression (to examine the phonological store) (see Chapters 3.1 and 3.2) in the fMRI experiment. Therefore, this pretest was designed to investigate rehearsal and suppression related processes. After the presentation of the auditory sequence, there was a period of silence lasting for 3600 ms, in which the participants were asked to internally rehearse or suppress, depending on the condition, either the tonal or the verbal stimuli. During the rehearsal condition participants were asked to rehearse the tonal or verbal stimuli internally. During the suppression condition they were asked to sing internally a well-known German nursery rhyme. Afterwards a probe stimulus was presented and participants had to indicate by a button press whether this syllable (verbal condition) or this tone (tonal condition) was already played during the sequence. Therefore the experiment consisted of four conditions: (a) syllable rehearsal, (b) syllable suppression, (c) tone rehearsal, and (d) tone suppression.

Participants – Five female nonmusicians participated in this study (mean age = 24.00 years, age range: 20-26 years).

Results – Participants answered 92.5% ($SEM = 2.09\%$) in the verbal rehearsal condition, 72.17% ($SEM = 3.10\%$) in the verbal suppression condition, 79.33% ($SEM = 4.39\%$) in the tonal rehearsal condition, and 46.68% ($SEM = 7.49\%$) in the tonal suppression condition correctly.

Conclusions – Because the percentage of the correct given answers in the tone suppression condition was below chance, it was decided to exclude the suppression condition from this experiment, but to focus on the rehearsal

conditions. This reduction of conditions made the use of a sparse temporal sampling technique possible (see Chapter 6.4). Because it is planned to investigate nonmusicians, RP musicians and AP musicians with one task, to compare these groups, 79.33% correct answers in the tonal rehearsal condition for the nonmusicians were too high, because RP musicians were hypothesised to perform even better.

Pretest 2

Stimuli – This pretest differed from pretest 1 in two ways: (i) only the rehearsal conditions were realised, and (ii) one sequence consists of five instead of four stimuli. The experimental task was the same as in pretest 1.

Participants – Seven nonmusicians (5 female, mean age = 24.86 years, age range: 20-29) took part in this experiment.

Results – In the verbal rehearsal condition participants performed in 82.14% ($SEM = 4.14\%$) and in the tonal rehearsal condition they performed 62.57% ($SEM = 2.00\%$) correctly.

Conclusion – These performance rates are between 100% (ceiling effect) and over 50% (chance level). Because RP musicians and AP musicians are hypothesised to show a better performance during the tonal rehearsal condition, the tonal and verbal sequences were not balanced for their difficulty level.

Pretest 3

This pretest was conducted to test the fMRI paradigm, which was a modified version of a sparse temporal sampling technique, which allows to present the auditory stimulation in the absence of scanner noise (see Chapter 6.4). During one sequence it was planned to scan twice: the first time after the end of the auditory stimulation and the second time after the presentation of the probe stimulus. It was intended to investigate whether there is a selective influence of the scanning noise on either the verbal or tonal rehearsal. The recorded scanning noise (EPI-T1 sequence) was presented for 2 s. It was either scanned once after the auditory presentation of the probe stimulus or twice, after the presentation of auditory sequence (1. scan) and after the presentation of the probe stimulus (2. scan). Four conditions were realised: (a) verbal rehearsal/scan twice (VT), (b) verbal rehearsal/scan once (VO), (c) tonal rehearsal/scan twice (TT), (d) tonal rehearsal/scan once (TO). The rehearsal period (silence period) ranged from 2-4 s.

Participants – 18 nonmusicians (9 female, age range: 18-29 years) took part in this experiment.

Results – Participants showed a performance of 81.01% ($SEM = 2.25\%$) in the VT condition, 81.58% ($SEM = 1.72\%$) in the VO condition, 56.77% ($SEM = 2.05\%$) in the TT condition and 59.38% ($SEM = 1.83\%$) in the TO condition CR. A paired-samples t -test revealed no significant differences between VT and VO ($t(17) = -0.466, p = .647$) and TT and TO ($t(17) = -1.432, p = .170$). More importantly, a one-sample t -test revealed, that the nonmusicians, which took part in this pre-experiment, performed significantly better ($t(17) = 3.308, p = .004$) than chance (50%) in the tonal (TT) condition.

Conclusions – This behavioural experiment revealed two important results: (i) no selective influence of scanning noise on the tonal condition were observed and (ii) nonmusicians are able to perform the task. Based on this pretest a scanning design was developed (see Chapter 9.3.3).

Pretest 4

Stimuli – This pretest was conducted to test the hypothesis if RP musicians show a superior performance for key sequences compared to non-key sequences (see Chapter 4.2).

Participants – Four musicians participated in this experiment (3 female, mean age = 24.00 years, age range: 22-26 years).

Results – In the verbal rehearsal condition the RP musicians performed in 79.75% ($SEM = 10.51\%$) correct, whereas they performed 66.26% ($SEM = 7.24\%$) correct for the tonal rehearsal condition. Regarding the non-key sequences, RP musicians showed a performance of 60.50% ($SEM = 9.06\%$) correct, whereas they performed 71.25% ($SEM = 5.54\%$) correct for the key sequences. This difference between non-key and key sequences was not, as a paired-samples *t*-test showed, significant ($t(3) = -2.867, p = .064$), but already showed a tendency in the hypothesised direction. However, that the result did not reach significance might be a consequence of the small amount of participants.

Conclusion – Every single musicians, who took part in this pretest, showed a trend for a better performance of the key sequences, compared to the non-key sequences. This pretest indicates a potential performance difference in musicians for non-key and key sequences.

Sequences of Experiment 3

Sequences (key vs. non-key and congruent vs. incongruent) were counterbalanced for:

- the position of the target,
- what was same or different (syllable, tone, both, none),
- range of the tones of one sequence,
- the phonological similarity effect,
- if the probe was in/out of the range of the tonal sequence,
- the contour of the sequences (tones and syllables (note name) in one sequence had the same contour),
- interval/distance, and
- no stimuli (phoneme or tone) was repeated during the sequence.

Musical Experience and AP Questionnaire

Following aspects were examined by this questionnaire:

- the musical experience (What instrument(s) do you play?/When was your musical commencement?/formal music instructions (How long do you practice and how long was your active participation (listening, singing, theory) in music (hours/day)?),
- the musical expertise of parents and siblings, and
- absolute pitch (Do you have absolute pitch?/Is you AP dependent on the instrument?).

Behavioural Data

Tab. A.2: Descriptive Statistics of behavioural Results

group condition	nonmusicians (N = 17)		RP musicians (N = 16)		AP musicians (N = 8)		All Groups (N = 41)	
	M	SEM	M	SEM	M	SEM	M	SEM
tonal % correct	56.28%	1.76%	69.53%	2.64%	81.09%	4.17%	66.30%	2.08%
tonal RT	1318 ms	69 ms	1614 ms	90 ms	1673 ms	143 ms	1503 ms	57 ms
key % correct	57.87%	1.65%	72.50%	2.28%	81.56%	3.44%	68.20%	1.94%
key RT	1327 ms	69 ms	1593 ms	82 ms	1655 ms	137 ms	1495 ms	54 ms
non-key % correct	54.70%	2.60%	66.56%	3.32%	80.63%	5.86%	64.38%	2.49%
non-key RT	1308	69 ms	1640 ms	100 ms	1691 ms	152 ms	1512 ms	62 ms
incongruent % correct	55.92%	2.47%	70.94%	3.22%	77.81%	4.99%	66.05%	2.31%
incongruent RT	1316 ms	72 ms	1609 ms	90 ms	1699 ms	134 ms	1505 ms	58 ms
congruent % correct	56.65%	1.63%	68.13%	2.56%	84.38%	4.22%	66.54%	2.14%
congruent RT	1319 ms	67 ms	1623 ms	90 ms	1648 ms	156 ms	1502 ms	58 ms
verbal % correct	84.49%	2.09%	88.13%	1.98%	91.72%	1.42%	87.32%	1.25%
verbal RT	1227 ms	61 ms	1386 ms	66 ms	1637 ms	127 ms	1369 ms	49 ms
AP test 1 % correct	x	x	21.88%	3.25%	92.07%	2.19%	x	x
AP test 1 % correct < 3s	x	x	17.55%	3.12%	83.17%	5.37%	x	x
AP test 1 RT	x	x	2272 ms	385 ms	1416 ms	453 ms	x	x
AP test 2 % correct	x	x	20.57%	2.41%	81.51%	5.56%	x	x
AP test 2 % correct < 3s	x	x	16.28%	2.78%	68.75%	9.51%	x	x
AP test 2 RT	x	x	2351 ms	364 ms	2024 ms	902 ms	x	x

Tab. A.3: Paired-samples *t*-tests of behavioural Results
(significant differences are emphasised (bold/highlighted in grey))

group condition	nonmusician (N = 17)		RP musician (N = 16)		AP musician (N = 8)		all Groups (N = 41)	
	<i>t</i> -value	<i>p</i> -value	<i>t</i> -value	<i>p</i> -value	<i>t</i> -value	<i>p</i> -value	<i>t</i> -value	<i>p</i> -value
tonal correct (%) – verbal correct (%)	-17.322	.000	-6.003	.000	-2.822	.026	-11.323	.000
tonal RT – verbal RT	2.237	.040	5.626	.000	.618	.556	4.774	.000
key correct (%) – non-key correct (%)	1.241	.232	2.775	.014	.197	.850	2.358	.023
key RT – non-key RT	1.080	.296	-1.289	.217	-.777	.463	-.927	.360
incongruent correct (%) – congruent correct (%)	-.326	.749	1.160	.264	-1.649	.143	-.307	.761
incongruent RT – congruent RT	-.119	.907	-.819	.426	.987	.357	.228	.821

Tab. A.4: Comparison of the behavioural Results between Nonmusicians, RP musicians and AP musicians (significant differences are emphasised (bold/highlighted in grey))

condition	ANOVA		Scheffé post hoc test (SPHT)	
	F	p	groups	p
tonal % correct	$F_{(2,38)} = 19.404$.000	RP – AP	.029
			nonmusicians – AP	.000
tonal RT	$F_{(2,38)} = 4.413$.019	nonmusicians – RP	.001
			RP – AP	.921
key % correct	$F_{(2,38)} = 25.330$.000	nonmusicians – AP	.062
			nonmusicians – RP	.054
key RT	$F_{(2,38)} = 4.018$.026	RP – AP	.055
			nonmusicians – AP	.000
non-key % correct	$F_{(2,38)} = 11.215$.000	nonmusicians – RP	.000
			nonmusicians – AP	.042
non-key RT	$F_{(2,38)} = 4.633$.016	RP – AP	.949
			nonmusicians – AP	.061
incongruent % correct	$F_{(2,38)} = 11.095$.000	nonmusicians – RP	.043
			RP – AP	.429
incongruent RT	$F_{(2,38)} = 4.703$.015	nonmusicians – AP	.001
			nonmusicians – RP	.004
congruent % correct	$F_{(2,38)} = 24.542$.000	RP – AP	.831
			nonmusicians – AP	.041
congruent RT	$F_{(2,38)} = 4.086$.025	nonmusicians – RP	.058
			RP – AP	.001
verbal % correct	$F_{(2,38)} = 2.548$.092	nonmusicians – AP	.000
			nonmusicians – RP	.004
verbal RT	$F_{(2,38)} = 5.898$.006	RP – AP	.987
			nonmusicians – AP	.052
			RP – AP	.564
			nonmusicians – AP	.104
			nonmusicians – RP	.407
			RP – AP	.103
			nonmusicians – AP	.006
			nonmusicians – RP	.277

Tab. A.5: Correlations (Pearson) between behavioural Results for AP musicians (significant correlations are emphasised (bold/highlighted in grey))

	AP age	age of musical commencement	tonal % correct	tonal RT	incongruent % correct	incongruent RT	congruent % correct	congruent RT	AP test 1 % correct	AP test 1 < 3 s % correct	AP test 1 RT	AP test 2 % correct	AP test 2 < 3 s % correct	AP test 2 RT
age of musical commencement	r=.377 p=.357													
tonal % correct	r=-.106 p=.805	r=-.001 p=.998												
tonal RT	r=.169 p=.689	r=-.215, p=.510	r=-.947 p=.000											
incongruent % correct	r=.344, p=.404	r=-.306, p=.461	r=.921 p=.001	r=-.840 p=.009										
incongruent RT	r=.112, p=.791	r=-.163, p=.700	r=-.969 p=.000	r=.985 p=.000	r=-.845 p=.008									
congruent % correct	r=.197, p=.640	r=-.360, p=.382	r=.888 p=.003	r=-.878 p=.004	r=-.638 p=.089	r=-.915 p=.001								
congruent RT	r=.213, p=.612	r=-.253, p=.545	r=-.905 p=.002	r=.989 p=.000	r=-.816 p=.014	r=.948 p=.000	r=-.824 p=.012							
AP test 1 % correct	r=.572, p=.138	r=-.099, p=.815	r=.769 p=.026	r=.849 p=.008	r=-.731 p=.039	r=-.832 p=.010	r=-.843 p=.009	r=-.707 p=.077						
AP test 1 < 3 s % correct	r=.764, p=.027	r=-.186, p=.660	r=.441 p=.274	r=.433 p=.284	r=-.572 p=.138	r=-.437 p=.279	r=-.843 p=.009	r=-.707 p=.077	r=-.399 p=.082					
AP test 1 RT	r=.730, p=.040	r=-.294, p=.480	r=.351 p=.394	r=.292 p=.482	r=-.517, p=.190	r=-.307 p=.459	r=-.420 p=.301	r=-.707 p=.077	r=-.598 p=.118	r=-.967 p=.000				
AP test 2 % correct	r=.517, p=.190	r=-.100, p=.814	r=.243 p=.562	r=-.401 p=.325	r=-.177, p=.674	r=-.264 p=.376	r=-.424 p=.271	r=-.424 p=.271	r=-.069 p=.799	r=.196 p=.642	r=-.082 p=.846			
AP test 2 < 3 s % correct	r=.889, p=.003	r=-.115, p=.786	r=.332 p=.422	r=-.438 p=.277	r=-.447 p=.267	r=-.368 p=.370	r=-.488 p=.128	r=-.488 p=.128	r=.017 p=.964	r=.683 p=.062	r=.651 p=.094	r=.749 p=.032		
AP test 2 RT	r=.803, p=.016	r=-.181, p=.781	r=.277 p=.506	r=.337 p=.414	r=-.463 p=.248	r=.239 p=.368	r=.764 p=.000	r=.764 p=.000	r=.611 p=.108	r=.714 p=.046	r=.727 p=.041	r=.529, p=.426	r=.854, p=.007	

fMRI Data

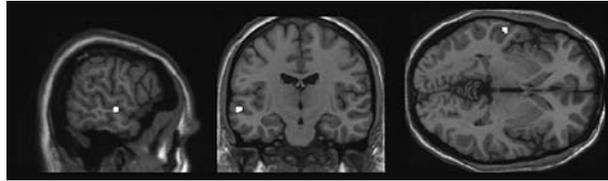


Fig. A.1: AP musicians showed stronger Activation of the left STS (-55 -21 -7) compared to RP musicians (ITPs 0-3, $p < 0.05$, FDR corr., $k = 10$)

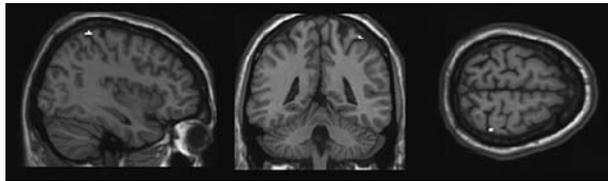


Fig. A.2: RP musicians demonstrated more Activation of the right SPL/IPS (34 -48 55) compared to AP musicians (ITPs 0-6, $p < 0.05$, FDR corr., $k = 10$)

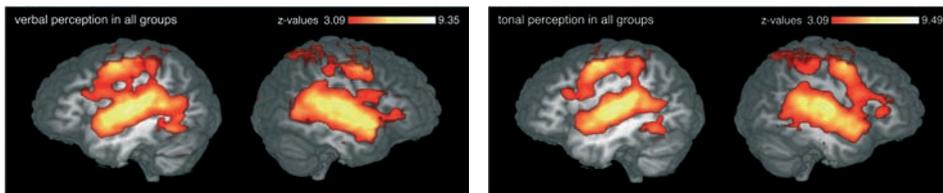


Fig. A.3: Verbal and Tonal Perception vs. Silence in all Groups ($z > 3.09$, $k = 20$, SR = 15)

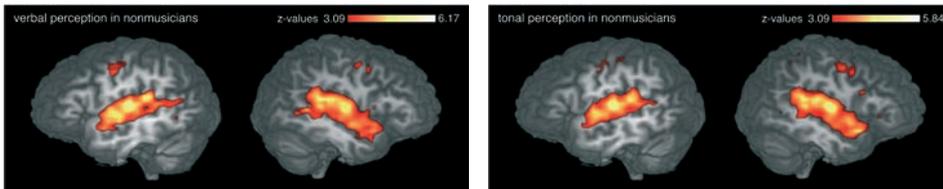


Fig. A.4: Verbal and Tonal Perception vs. Silence in Nonmusicians ($z > 3.09$, $k = 20$, SR = 15)

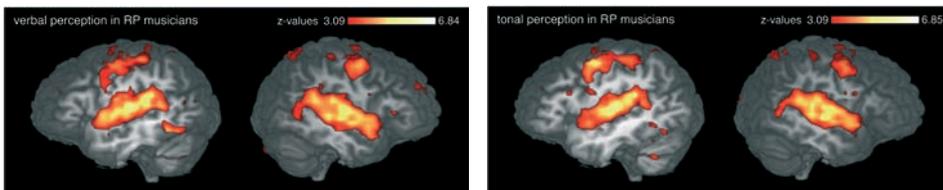


Fig. A.5: Verbal and Tonal Perception vs. Silence in RP musicians ($z > 3.09$, $k = 20$, SR = 15)

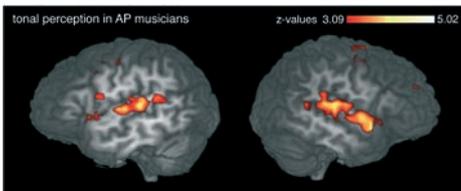


Fig. A.6: Tonal Perception vs. Silence in AP musicians ($z > 3.09$, $k = 20$, SR = 15)

Tab. A.6: Brain Activations for all Groups during verbal and tonal Perception

area	left hemisphere					right hemisphere				
	BA	x	y	z	z-value	BA	x	y	z	z-value
<i>all groups: verbal perception – silence ($z > 3.09, k = 20, SR = 15$)</i>										
frontopolar area						10	25	54	3	4.44
SFG						9	22	51	27	5.10
mid-DLPFC	9	-32	39	30	4.42					
pars opercularis/IFG	44	-44	15	21	4.97	45	34	27	18	4.72
cingulate gyrus	24	-8	15	33	5.60	24	7	12	33	5.43
	31	-5	-39	27	6.22	31	4	-24	42	6.34
SMA	6	-5	-3	57	7.82					
PMd	6	-23	-6	54	5.46	6	22	-6	51	5.22
M1	4	-47	-9	48	6.73	4	46	-6	45	6.97
central sulcus	3/4	-8	-33	63	5.86					
SPL						7	25	-63	54	5.74
						7	34	-42	60	5.05
STG	41	-44	-24	12	9.25	42	40	-18	9	9.34
						42	55	-27	9	9.44
precuneus	7	-2	-75	42	6.68	7	1	-48	63	5.87
cuneus						18	1	-81	15	6.32
putamen		-20	6	12	6.43	16	0	9	9	6.16
cerebellum		-11	-51	-36	4.22	10	-69	-9	6.10	6.10
		-26	-60	-12	6.46	10	-78	-33	4.66	4.66
brainstem						4	-36	-3	7.12	7.12
						7	-33	-21	4.59	4.59
<i>all groups: tonal perception – silence ($z > 3.09, k = 20, SR = 15$)</i>										
Inferior frontal sulcus (IFS)						9/46	37	36	18	5.24
mid-DLPFC	9	-32	39	30	4.16					
cingulate gyrus	23	-2	-30	27	5.43					
SMA	6	-5	-3	57	8.24					
PMd	6	-23	-6	54	5.58					
PMv						6	43	-3	45	7.46
M1	4	-44	-9	48	6.98					
central sulcus	4/5	-8	-33	63	5.28					
SPL	7	-23	-63	45	5.53	7	22	-63	54	5.59
IPS						7/40	28	-54	42	5.19
IPL	40	-41	-39	42	5.34	7/40	37	-42	54	4.98
STG	41	-38	-27	15	9.10	42	55	-27	9	9.50
precuneus						7	4	-65	54	6.70
cuneus	18	-11	-99	18	4.30	18	7	-69	18	5.02
putamen		-20	3	9	6.10	16	6	3	5.93	5.93
thalamus		-14	-27	3	6.95	10	-27	0	7.22	7.22
cerebellum		-29	-60	-15	6.11	10	-69	-9	5.94	5.94
brainstem		-8	-36	-30	5.46	1	-39	-3	6.83	6.83

Tab. A.7: Brain Activations for all Groups during verbal and tonal Rehearsal

area	left hemisphere					right hemisphere				
	BA	x	y	z	z-value	BA	x	y	z	z-value
<i>all groups: verbal rehearsal – pink noise nonrehearsal (z > 3.09, k = 10, SR = 10)</i>										
middle frontal gyrus	10/46	-29	45	9	4.09					
mid-DLPFC	9/46	-41	33	21	5.09	9/46	37	30	21	4.13
pars opercularis/IFG	44	-53	9	9	6.16					
	44	-47	9	24	6.89					
insular cortex		-29	15	9	6.50		31	24	3	5.61
cingulate gyrus						32	10	21	33	5.53
pre-SMA	6	-2	3	57	7.28					
	6	-2	18	45	6.88					
PMd	6	-29	-3	54	5.63	6	28	-6	54	5.55
PMv	6	-47	3	33	6.66	6	43	0	39	4.12
						6	49	6	18	4.60
M1	4	-50	-12	45	6.42	4	31	-21	57	4.88
medial M1	4	-8	-27	63	5.01	4	10	-33	63	4.51
postcentral gyrus						3	31	-27	48	5.05
SPL	7	-26	-57	42	5.44	7	19	-60	57	4.40
IPS	7/40	-35	-45	42	5.89	7/40	28	-57	45	3.97
parahippocampal gyrus						30	28	-45	3	4.82
putamen		-20	-6	12	5.84					
cerebellum		-17	-45	-18	5.01		28	-60	-18	6.33
		-26	-60	-18	3.76		13	-39	-21	4.73
							16	-69	-33	5.00
<i>all groups: tonal rehearsal – pink noise nonrehearsal (z > 3.09, k = 10, SR = 10)</i>										
IFS	46	-44	42	9	3.86					
	9/44	-50	12	27	5.01					
mid-DLPFC	9/46	-41	33	21	4.33					
pars opercularis/IFG	44	-50	9	9	5.48					
insular cortex		-29	15	9	6.15		31	24	0	4.13
pre-SMA	6	-2	3	54	6.96					
PMd	6	-26	0	51	5.26	6	28	-15	60	5.14
PMv	6	-53	3	18	5.46					
M1	4	-50	-9	45	6.29	4	49	-9	42	4.65
postcentral gyrus						3	31	-27	48	5.01
paracentral lobule	6	-8	-27	63	4.97	6	7	-30	60	5.45
SPL	7	-23	-63	51	4.90	7	19	-60	57	4.12
IPL	40	-44	-39	42	5.36					
parahippocampal gyrus						30	28	-42	3	4.61
putamen		-20	0	6	5.10		19	-2	9	4.49
thalamus		-8	-18	3	5.01					
caudate nucleus							7	3	-3	3.52
cerebellum		-17	-66	-6	4.18		13	-39	-21	5.58
		-26	-60	-15	4.11		28	-60	-18	5.87
		-14	-42	-18	5.18					

Tab. A.8: Brain Activations during verbal and tonal Perception in Nonmusicians

area	left hemisphere					right hemisphere				
	BA	x	y	z	z-value	BA	x	y	z	z-value
<i>nonmusicians: verbal perception – silence (z > 3.09, k = 20, SR = 15)</i>										
cingulate gyrus						23	1	-39	24	4.22
SMA	6	-5	-3	57	4.94					
PMd	6	-41	-6	54	4.16					
M1	4	-50	-9	39	3.87	4	46	-6	45	3.73
postcentral gyrus	2	-41	-27	57	3.80					
paracentral lobulus						5	1	-24	48	4.59
SPL						7	25	-63	45	3.62
IPL/IPS						7/40	34	-45	48	3.68
STG	41	-38	-27	15	6.17	42	55	-27	9	6.01
						42	43	-36	15	5.48
						22	55	-9	0	5.80
posterior STS	22/39	-41	-54	15	4.30					
precuneus	7	-2	-60	54	4.09					
	7	-8	-51	39	4.17					
	7	-5	-78	39	4.58					
cuneus						18	10	-75	18	5.00
capsula interna		-14	6	9	5.10		16	0	9	4.29
thalamus		-14	-24	0	4.69		13	-27	0	4.46
brainstem							1	-36	-3	5.36
cerebellum		-8	-60	-12	3.87		16	-54	-18	3.78
<i>nonmusicians: tonal perception – silence (z > 3.09, k = 20, SR = 15)</i>										
cingulate gyrus	23	-2	-27	30	3.90	29	4	-39	21	3.85
posterior insular cortex							43	-15	9	5.52
PMv						6	40	-3	39	4.48
M1	4	-23	-18	48	3.77					
SMA	6	-8	-3	57	5.38					
IPS						7/40	28	-54	42	4.14
STG	41	-38	-27	15	6.01	42	40	-36	15	5.63
						42	55	-27	9	5.88
anterior STG						38	46	6	-12	5.05
posterior MTG	39	-44	-60	15	4.12					
precuneus	7	-2	-60	54	4.00					
putamen		-17	3	6	4.88					
capsula interna							19	-6	9	4.33
brainstem							1	-39	-3	5.08
cerebellum							16	-57	-18	4.35

Tab. A.9: Comparison of Brain Activations during verbal and tonal Perception in Nonmusicians

area	left hemisphere					right hemisphere				
	BA	x	y	z	z-value	BA	x	y	z	z-value
<i>nonmusicians: verbal – tonal perception (z > 3.09, k = 10, SR = 10)</i>										
SFG	10	-11	48	-3	4.04					
middle occipital gyrus	19	-32	-93	3	3.57					
<i>nonmusicians: tonal – verbal perception (z > 3.09, k = 10, SR = 10)</i>										
n.s.										

Tab. A.10: Activated Brain Areas during verbal and tonal Rehearsal in Nonmusicians

area	left hemisphere					right hemisphere				
	BA	x	y	z	z-value	BA	x	y	z	z-value
<i>nonmusicians: verbal rehearsal – pink noise nonrehearsal ($z > 3.09, k = 10, SR = 10$)</i>										
IFS/mid-DLPFC	9/46	-44	30	21	4.52					
mid-DLPFC	9	-44	24	33	4.45					
pars opercularis/PMv	6/44	-50	6	27	5.63	6/44	49	12	21	3.94
insular cortex		-32	24	3	4.34					
PMd	6	-32	-6	54	3.92					
pre-SMA	6	-2	3	57	4.83					
	6	-2	18	45	5.23					
M1	4	-50	-12	45	3.85	4	34	-15	54	4.26
IPS	7/40	-29	-60	48	3.84	7/40	28	-54	42	3.67
	7/40	-26	-54	39	4.26					
IPL	40	-41	-42	54	4.36					
	40	-35	-39	39	5.89					
anterior STG	38	-50	15	-3	3.78					
thalamus		-11	-15	6	3.82					
cerebellum		-8	-48	-9	3.74		22	-66	-18	4.74
		-17	-48	-18	4.00		16	-72	-33	3.72
<i>nonmusicians: tonal rehearsal – pink noise nonrehearsal ($z > 3.09, k = 10, SR = 10$)</i>										
pars orbitalis/IFG	47	-41	27	-3	4.91					
cingulate gyrus	32	-8	18	33	3.42					
pre-SMA	6	-5	3	57	4.58					
	6	-2	18	45	3.50					
PMv	6	-56	0	30	3.87					
	6	-59	3	18	4.17					
M1						4	49	-9	42	3.77
postcentral gyrus	3	-56	-15	30	3.25					
IPL	40	-47	-33	48	3.73					
STS	21/22	-44	-33	0	3.41					
MTG	21	-56	-39	0	3.41					
cerebellum							31	-60	-18	3.92

Tab. A.11: Comparison of activated Brain Areas during verbal and tonal Rehearsal in Nonmusicians

area	left hemisphere					right hemisphere				
	BA	x	y	z	z-value	BA	x	y	z	z-value
<i>nonmusicians: verbal – tonal rehearsal (z > 2.58, k = 10, SR = 10)</i>										
middle frontal gyrus	10/46	-35	45	15	3.18					
IFS/mid-DLPFC	9/45	-38	24	21	3.47	9/46	40	33	21	3.17
pars opercularis	44	-56	12	6	3.79					
insular cortex		-32	24	3	3.96		25	18	6	3.00
posterior corpus callosum		-14	-39	21	3.33					
pre-SMA	6	-11	3	51	3.79					
	6	-2	24	42	3.84					
PMv	6	-44	0	33	4.44	6	25	6	45	3.44
						6	43	6	39	4.35
						6	52	12	27	3.54
SPL	7	-26	-66	51	3.50	7	28	-63	48	3.58
IPS	7/40	-29	-51	39	4.01	7/40	28	-54	42	3.57
IPL	40	-38	-39	42	4.29					
cerebellum							19	-66	-15	2.84
<i>nonmusicians: tonal – verbal rehearsal (z > 2.58, k = 10, SR = 10)</i>										
frontopolar area	10	-20	54	21	3.27					
	10	-17	48	3	3.16					
cingulate gyrus	31	-8	-45	30	3.45					
angular gyrus/SMG	39/40	-47	-60	33	4.29					
posterior MTG						21	52	-51	9	3.02

Tab. A.12: Activated Brain Areas during verbal and tonal Perception in RP musicians

area	left hemisphere					right hemisphere				
	BA	x	y	z	z-value	BA	x	y	z	z-value
RP musicians: verbal perception – silence ($z > 3.09, k = 20, SR = 15$)										
frontopolar area	10	-8	54	0	4.17	10	7	54	3	4.14
IFS						10/46	28	48	15	4.88
mid-DLPFC	9/46	-32	27	30	3.89					
cingulate gyrus	23	-20	-54	9	4.51	23	4	-54	9	3.54
	24	-11	18	27	4.65					
	24/31	-5	-15	36	4.31					
SMA	6	-5	0	54	5.75					
PMd	6	-23	-3	54	4.85	6	19	0	54	4.38
PMv	6	-44	-3	48	5.64	6	31	-9	36	4.37
M 1						4/6	49	-3	45	4.93
paracentral lobule						5/7	1	-42	66	4.34
SPL	7	-20	-66	54	5.23	7	19	-66	60	4.83
IPL	40	-38	-35	51	4.88					
STG	41	-50	-21	12	6.84	42	43	-18	9	6.57
posterior ITG	37	-50	-51	-9	5.45					
precuneus						7	4	-69	27	4.17
cuneus						18	1	-84	15	4.33
lingual gyrus						18	4	-72	0	3.96
thalamus		-11	-30	3	4.80					
brainstem							4	-36	-3	4.54
cerebellum		-29	-60	-12	4.79		4	-30	-30	4.09
		-14	-87	-12	3.94		28	-63	-12	4.26
		-35	-48	-24	4.97		16	-84	-30	3.90
		-47	-66	-30	3.97					
RP musicians: tonal perception – silence ($z > 3.09, k = 20, SR = 15$)										
mid-DLPFC						9/46	34	36	21	3.90
cingulate gyrus	24	-11	18	27	4.29					
pre-SMA						6	1	18	39	4.29
SMA	6	-5	0	57	5.32					
PMd	6	-26	-3	54	4.42	6	25	-9	60	4.35
PMv	6	-44	-3	48	5.50					
M 1						4/6	46	-3	45	5.05
SPL	7	-20	-66	57	5.45					
IPL	40	-41	-36	51	4.63	40	34	-36	42	3.56
STG	22	-56	-36	15	5.89	42	55	-24	12	6.48
	41	-50	-21	12	6.86					
posterior MTG						21/37	52	-57	6	4.36
posterior ITG	37	-56	-60	-3	3.80					
precuneus						7	16	-66	24	3.92
						7	4	-66	57	4.97
cuneus						18	10	-96	21	4.21
						18	1	-84	15	4.42
cingulate gyrus/lingual gyrus	18/23	-20	-54	6	4.92					
thalamus							10	-27	0	4.64
cerebellum		-44	-54	-30	3.87		10	-69	-9	4.28
		-29	-60	-15	4.19		31	-54	-18	3.77
		-32	-39	-24	3.67					

Tab. A.13: Activated Brain Areas during verbal and tonal Rehearsal in RP musicians

area	left hemisphere					right hemisphere				
	BA	x	y	z	z-value	BA	x	y	z	z-value
<i>RP musicians: verbal rehearsal – pink noise nonrehearsal ($z > 3.09, k = 10, SR = 10$)</i>										
inferior frontal junction (IFJ)	6/9/44	-32	3	33	4.00					
pars opercularis	44	-50	9	12	4.83					
insular cortex		-29	21	6	5.24	31	21	3	4.61	
cingulate gyrus	32	-11	24	30	3.61	24/32	13	15	30	4.33
pre-SMA	6	-2	12	48	5.16	6	4	6	54	5.46
PMd	6	-26	0	54	3.60					
	6	-23	6	63	3.36					
	6	-26	-15	57	3.73					
PMv	6	-47	6	36	4.70	6	28	-3	48	4.44
M1						4	25	-21	54	3.81
central sulcus						3/4	7	-27	63	4.17
postcentral gyrus						1/2	40	-27	60	3.58
						3	31	-27	66	3.79
						3	31	-27	48	3.96
SPL	7	-20	-63	57	3.98					
IPS	7/40	-29	-60	45	3.98					
	7/40	-47	-42	57	3.89					
	7/40	-35	-48	48	4.10					
putamen		-20	-6	12	3.78					
cerebellum						25	-63	-15	4.39	
<i>RP musicians: tonal rehearsal – pink noise nonrehearsal ($z > 3.09, k = 10, SR = 10$)</i>										
IFJ	6/9/44	-32	3	30	3.73					
middle frontal gyrus	9	-50	15	33	3.73					
mid-DLPFC	9/46	-44	27	27	3.94					
pars opercularis	44	-56	9	9	3.99					
insular cortex		-29	24	3	4.65	28	15	6	3.46	
		-35	15	9	4.50	31	24	0	3.77	
pre-SMA	6	-5	9	48	4.82	6	1	3	54	4.95
PMd	6	-26	0	51	3.89	6	25	-3	51	3.88
	6	-20	12	60	3.44	6	25	-9	60	4.17
PMv	6	-47	3	36	4.36	6	52	0	39	3.85
	6	-53	3	18	3.93					
M1	4	-47	-9	42	4.52	4/6	34	-15	54	4.79
postcentral gyrus						3	28	-27	45	4.09
SPL	7	-20	-63	54	4.26					
IPS/IPL	7/40	-35	-48	54	4.72					
IPL	40	-44	-39	42	3.71					
putamen		-26	-6	12	4.32					
		-23	0	3	4.00					
caudate nucleus						16	0	21	4.47	
globus pallidus						19	-6	0	4.14	
cerebellum		-5	-66	-9	3.42	28	-69	-12	5.12	
		-20	-66	-9	3.79	43	-63	-18	4.25	
		-17	-36	-12	3.93					
		-17	-51	-12	3.79					
		-23	-42	-21	4.11					

Tab. A.14: Comparison of tonal Perception between RP musicians and Nonmusicians

area	left hemisphere					right hemisphere				
	BA	x	y	z	z-value	BA	x	y	z	z-value
<i>RP musicians – nonmusicians: tonal perception – pink noise perception ($z > 3.09, k = 10, SR = 10$)</i>										
posterior STG/SMG	40/42	-50	-36	18	3.85					
<i>nonmusicians – RP musicians: tonal perception – pink noise perception ($z > 3.09, k = 10, SR = 10$)</i>										
n.s.										

Tab. A.15: Comparison of tonal Rehearsal between RP musicians and Nonmusicians

area	left hemisphere					right hemisphere				
	BA	x	y	z	z-value	BA	x	y	z	z-value
<i>RP musicians – nonmusicians: tonal rehearsal – pink noise nonrehearsal ($z > 2.58, k = 10, SR = 10$)</i>										
middle frontal gyrus	11	-26	33	-6	3.37					
insular cortex		-32	21	6	3.90	31	15	6		3.62
pre-SMA	6	-14	15	48	3.24					
SMA/M1						4/6	7	-27	63	3.92
PMd	6	-23	-6	51	3.50					
PMv ²⁷	6	-47	3	42	3.23					
SPL	7	-17	-57	51	3.60					
IPL/IPS	40	-35	-48	51	4.24					
STG						22	37	-42	12	2.96
putamen							25	3	9	3.03
globus pallidus/putamen							22	-3	0	3.23
caudate nucleus		-11	12	12	3.06					
capsula interna							22	24	9	3.53
<i>nonmusicians – RP musicians: tonal rehearsal – pink noise nonrehearsal ($z > 2.58, k = 10, SR = 10$)</i>										
frontopolar area	10	-2	57	12	4.00	10	10	60	18	4.35
SFG	9/10	-8	57	24	3.27	9	7	54	36	3.08
medial frontal gyrus	9	-5	48	33	3.22					
cingulate gyrus	31	-2	-48	30	2.99					
	24	-2	33	3	4.36					
angular gyrus						39	46	-60	30	3.31
						39	37	-60	36	3.33
MTG/angular gyrus	22/39	-41	-57	24	4.13					
posterior STS						37	52	-54	12	3.08
precuneus						7	1	-63	36	3.18
cerebellum							19	-42	-36	3.49

²⁷ Only reached significance with 9 voxel per cluster.

Tab. A.16: Activated Brain Areas during tonal Perception and tonal Rehearsal in AP musicians

area	left hemisphere					right hemisphere				
	BA	x	y	z	z-value	BA	x	y	z	z-value
<i>AP musicians: tonal perception – silence ($z > 3.09$, $k = 20$, $SR = 15$)</i>										
pre-SMA	6	-2	15	42	4.54					
SMA	6	-5	-3	51	4.65	6	4	-15	69	4.05
PMd						6	19	0	54	3.93
PMv	6	-44	3	33	4.62	6	43	-3	45	4.32
M1	4	-44	-9	51	3.72					
STG	41	-38	-27	12	4.59	41/42	34	-24	9	4.62
	41/42	-50	-18	9	5.02	22/42	55	-30	12	4.62
	42	-56	-33	18	4.40	38	49	6	-9	4.67
anterior STG/IFG	38/44	-47	12	0	3.87					
precuneus/SPL						7	19	-72	51	4.07
putamen/globus pallidus		-20	0	3	3.49					
cerebellum		-29	-57	-15	4.79					
<i>AP musicians: tonal rehearsal – pink noise nonrehearsal ($z > 2.58$, $k = 10$, $SR = 10$)</i>										
pars orbitalis/IFG	45/46	-41	33	9	3.04					
pars opercularis/IFG	44	-44	9	6	2.82					
insular cortex							25	27	0	3.03
cingulate gyrus						32	7	18	36	3.15
pre-SMA	6	-5	6	51	3.90					
PMd	6	-26	0	51	3.82	6	25	-12	51	3.32
						6	13	-12	54	3.12
PMv	6	-56	3	33	4.28					
	6	-32	-3	39	3.80					
IPS	7/40	-29	-57	54	3.22					
IPL	40	-44	-39	42	3.29					
	40	-50	-30	39	2.97					
SMG	40	-26	-51	36	2.98					
hippocampus						25	-36	0		2.81
thalamus		-17	-12	15	3.60					
cerebellum		-17	-42	-24	3.28	22	-63	-15		3.11
						10	-39	-21		3.76
						22	-57	-36		3.98

Abbreviations

A1	Primary Auditory Cortex	MTG	Middle Temporal Gyrus
AEF	Auditory Evoked Fields	N	Total Number in a Sample
AP	Absolute Pitch	NMDA	N-methyl-D-aspartate
BA	Brodmanns Area	NMR	Nuclear Magnetic Resonance
BOLD	Blood Oxygen Level Dependency	n.s.	not significant
CC	Corpus Callosum	PET	Positron Emissions Tomography
CR	Correct Responses	PMd	Dorsolateral Premotor Cortex
DIPC	Dorsal Inferior Parietal Cortex	PMv	Ventrolateral Premotor Cortex
DLPFC	Dorsolateral Prefrontal Cortex	PT	Planum Temporale
EC	Enriched Conditions	RF	Radiofrequency
EEG	Electroencephalogram	ROI	Region of Interest
ELAN	Early Left Anterior Negativity	RP	Relative Pitch
EPI	Echo Planar Imaging	RT	Reaction Time
ERAN	Early Right Anterior Negativity	SD	Standard Deviation
ERP	Event Related Potential	SEM	Standard Error of Mean
FDR	False Discovery Rate	SFG	Superior Frontal Gyrus
FFT	Fast Fourier Transformation	SMA	Supplementary Motor Area
FID	Free Induction Decay	SMG	Supramarginal Gyrus
fMRI	functional Magnetic Resonance Imaging	SNR	Signal-to-Noise Ratio
FOV	Field of View	SPHT	Scheffé Post-Hoc Tests
FWHM	Full Width at Half Maximum	SPL	Superior Parietal Lobe
GLM	General Linear Model	SR	Search Radius
H	Hydrogen	STG	Superior Temporal Gyrus
HG	Heschl's Gyrus	STS	Superior Temporal Sulcus
IC	Impoverished conditions	T	Tesla
IFG	Inferior Frontal Gyrus	TE	Echo Time
IFJ	Inferior Frontal Junction	TO	Tonal rehearsal/scan Once
IFS	Inferior Frontal Sulcus	TR	Repetition Time
IPL	Inferior Parietal Lobe	TT	Tonal rehearsal/scan Once
IPCS	Inferior Precentral Sulcus	VIPC	Ventral Inferior Parietal Cortex
IPS	Intraparietal Sulcus	VBM	Voxel-Based Morphometry
ILPG	Intrasulcal Length of the Precentral Gyrus	VLPFC	Ventrolateral Prefrontal Cortex
ITG	Inferior Temporal Gyrus	VO	Verbal rehearsal/scan Once
ITP	Imaging Time Point	VT	Verbal rehearsal/scan Twice
k	Voxel Extent	WM	Working Memory
LTM	Long Term Memory		
LTP	Long-Term Potentiation		
M	Mean		
MI	Primary Motor Cortex		
MEG	Magnetoencephalography		
MRI	Magnetic Resonance Imaging		

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Dissertationsbezogene bibliographische Daten

Schulze, Katrin

NEURAL CORRELATES OF WORKING MEMORY FOR VERBAL AND TONAL STIMULI IN NON-MUSICIANS AND MUSICIANS WITH AND WITHOUT ABSOLUTE PITCH

Universität Leipzig, Dissertation

203 Seiten, 326 Literaturangaben, 50 Abbildungen, 27 Tabellen

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Leipzig, den 06. Juni 2006

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