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The Neuroanatomical Overlap of Syntax Processing in
Music and Language - Evidence from Lesion and
Intracranial ERP Studies

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Zusammenfassung

Einleitung

Die Gemeinsamkeiten von Sprache und Musik als die beiden Hauptkanäle menschlicher (akustischer) Kommunikation stehen schon seit langer Zeit im Fokus der Wissenschaften. Überlegungen und Befunde reichen von gemeinsamen evolutionären Wurzeln (z.B. S. Brown, 2000; Darwin, 1871/1989; Fitch, 2006; Rousseau, 1781/1998), über ähnliche Struktureigenschaften (z.B. Fitch, 2006; Lerdahl & Jackendoff, 1983), bis hin zu vergleichbaren kognitiven und neurophysiologischen Vorgängen bei der Wahrnehmung von Sprache und Musik (z.B. S. Brown, Martinez, & Parsons, 2006; Koelsch & Siebel, 2005; Patel, 2003a).

Die vorliegende Dissertation beschäftigt sich im Speziellen mit Syntax als einem Aspekt, den beide Domänen innehaben. Sowohl Sprache als auch Musik bestehen aus Einzelelementen (z.B. Phonemen und Wörtern in Sprache, Tönen und Akkorden in Musik), deren regelhafte Kombination zu Sätzen oder musikalischen Phrasen syntaktischen Prinzipien unterliegt. Es wird angenommen, dass die Dekodierung von Struktur in Sprache und Musik sehr ähnliche kognitive Operationen involviert und ähnliche neuronale Verarbeitungsprozesse in Gang setzt. Diese These wird von einer Reihe empirischer Arbeiten gestützt, die z.B. zeigen konnten, dass die gleichzeitige Präsentation syntaktischer Fehler in beiden Modalitäten zur Konkurrenz der Verarbeitungsprozesse um kognitive und neuronale Ressourcen führt (Fedorenko, Patel, Casasanto, Winawer, & Gibson, 2007; Koelsch, Gunter, Wittfoth, & Sammler, 2005; Slevc, Rosenberg, & Patel, 2007; Steinbeis & Koelsch, 2008b). Des Weiteren gibt es Hinweise auf Transfereffekte zwischen beiden Domänen, z.B. den Einfluss von musikalischem Training auf sprachliche Fähigkeiten (Jentschke, 2007; Schlaug, Marchina, & Norton, 2008), oder eine verminderte Sensibilität für musiksyntaktische Irregularitäten bei Personen mit entwicklungsbedingten oder erworbenen Sprachstörungen (Jentschke, Koelsch, Sallat, & Friederici, 2008; Patel, Iversen, Wassenaar, & Hagoort, 2008).

Es wird vermutet, dass diese funktionelle Interaktion auf anatomische Schnittpunkte des neuronalen Sprach- und Musiknetzwerkes zurückgeführt werden kann. Anhaltspunkte dafür liefern fMRT-Studien und Quellmodellierungen von MEG-Daten, die ähnliche Aktivierungsmuster während der Verarbeitung von Phrasenstrukturverletzungen in Sätzen (Friederici & Kotz, 2003) und harmonischen Regelverletzungen in Akkordfolgen (Koelsch, 2005) berichteten.

Ziel der vorliegenden Arbeit war, diese *neuroanatomischen* Zusammenhänge der Syntaxverarbeitung in Sprache und Musik genauer darzulegen und somit die wachsende Literatur zum *funktionellen* Zusammenhang der beiden Domänen zu ergänzen. Im Besonderen fokussierte die Arbeit auf den inferioren Frontallappen (Gyrus Frontalis Inferior, GFI) sowie den superioren Temporallappen (Gyrus Temporalis Superior, GTS) als Hirnregionen, die höchstwahrscheinlich modalitätsübergreifend an der Verarbeitung von Syntax in Sprache und Musik beteiligt sind (Koelsch, 2006).

Um die neurophysiologischen Korrelate dieser Verarbeitungsprozesse zeitlich hoch aufgelöst abbilden zu können, wurde die Methode der ereigniskorrelierten Potenziale (EKP) angewandt. Als Indikatoren für sprachliche Syntaxverarbeitung wurde die ELAN (Early Left Anterior Negativity; Friederici, Pfeifer, & Hahne, 1993), für musikalische Syntaxverarbeitung die ERAN (Early Right Anterior Negativity; Koelsch, Gunter, Friederici, & Schröger, 2000) gewählt, die durch Phrasenstrukturverletzungen in Sätzen einerseits und harmonisch unerwartete Akkorde in Akkordfolgen andererseits ausgelöst werden. Der anatomische Ursprung dieser Komponenten wurde in Experiment 1B für die ERAN mittels einer Läsionsstudie untersucht. In Experiment 2B wurden räumlich hochauflösende intrakranielle EEG-Ableitungen in Epilepsiepatienten vorgenommen und eine Quelllokalisierung für die elektrokortikalen Äquivalente der ELAN und ERAN durchgeführt.

Experimentelle Befunde und Diskussion

In den **Experimenten 1A und 2A** wurde neues musikalisches Stimulusmaterial für die Durchführung der Patientenstudien in psychoakustischer, behavioraler und elektrophysiologischer Hinsicht in gesunden Probanden evaluiert. Hauptaugenmerk dieser Studien war, psychoakustische Störvariablen wie z.B. "sensorische Dissonanz" zwischen harmonisch irregulären Akkorden und dem vorangehenden musikalischen Kontext weitestgehend auszuschließen (Experiment 1A) bzw. zu kontrollieren (Experiment 2A), um eine Interpretation der Patientendaten sicher als Überlappung kognitiver (statt sensorischer) Prozesse

zu gewährleisten (siehe auch Koelsch, Jentschke, Sammler, & Mietchen, 2007; Koelsch & Sammler, 2008).

Experiment 1B ging der Frage nach, ob Läsionen in Hirnarealen, die grundlegend an der Verarbeitung sprachlicher Syntax beteiligt sind, zu vergleichbaren Defiziten in der musikalischen Syntaxverarbeitung führen. Dazu wurde die ERAN in zwei Patientengruppen mit Hirnläsionen in klassischen “Spracharealen”, d.h. mit Kernläsionen im linken GFI ($N = 6$) oder dem linken anterioren GTS ($N = 7$), untersucht und mit Daten gesunder Kontrollprobanden verglichen.

Tatsächlich zeigte sich bei den Patienten mit Läsionen im linken GFI eine veränderte Topographie der ERAN, die stärker frontal und nominell stärker rechtslateralisiert war. Außerdem war die Amplitude der ERAN in Abhängigkeit vom Zeitpunkt der Läsion reduziert und die Fähigkeit der Patienten, harmonisch abweichende Akkorde zu erkennen, beeinträchtigt. Zusammengenommen stützen diese Befunde die grundlegende Rolle des linken GFI in der Verarbeitung musikalischer Syntax. Im Kontext früherer Berichte zur essenziellen Rolle dieses Areals in der Verarbeitung sprachlicher Syntax (Friederici & Kotz, 2003), kann dieses Ergebnis im Sinne einer Überschneidung der sprachlichen und musikalischen Syntaxverarbeitung im linken GFI gewertet werden.

Bei Patienten mit Kernläsionen im linken anterioren GTS konnten keine Hinweise auf Defizite in der Verarbeitung musikalischer Syntax festgestellt werden. Diese Daten könnten einerseits auf die Unabhängigkeit musikalischer Syntaxverarbeitung von der Funktionalität des linken anterioren GTS hinweisen, andererseits jedoch auch auf massive Reorganisationsprozesse zurückzuführen sein, die seit der Hirnverletzung (durchschnittlich 7 Jahre vor Datenerhebung) gewirkt haben. Damit bleibt in diesem Experiment die Frage nach der funktionellen Relevanz des GTS für musikalische Syntaxverarbeitung vorerst ungeklärt, ebenso die Frage nach einer modalitätsübergreifenden Funktion dieses Areals für die Wahrnehmung syntaktischer Regelverletzungen.

In **Experiment 2B** wurde die musikalische und sprachliche Syntaxverarbeitung innerhalb von Versuchsteilnehmern ($N = 9$) verglichen, bei denen elektrokortikale Potenziale von subduralen Gitterelektroden abgeleitet wurden, die zur prächirurgischen Epilepsiediagnostik in perisylvischen Hirnregionen implantiert waren. Hauptableitungsbereich war hier der Temporalappen und der inferiore Saum des GFI der linken oder rechten Hemisphäre. Die elektrokortikalen Äquivalente der ERAN und ELAN wurden bestimmt und deren Generatoren mit Hilfe verteilter Quellmodellierung lokalisiert (Knösche, Maess, & Friederici, 1999).

Intrakraniale Effekte sprachlicher und musikalischer Strukturverletzungen wurden im GTS, sowie (stärker für Musik) auch im GFI nachgewiesen, unabhängig davon ob die Ableitung

in der linken oder rechten Hemisphäre erfolgte. Die genaue Lage der Quellmaxima zeigte eine starke interindividuelle Variabilität. Auf Einzelfallebene zeigten sich deutliche Überschneidungen der Hirnaktivität für Sprache und Musik im GTS, sowie Anhaltspunkte für einen links frontalen Überlappungsbereich. Für rechts frontale Areale bleibt diese Frage aufgrund der vorwiegend temporalen Elektrodenlagen, d.h. der sehr knappen Abdeckung des Frontallappens, vorerst offen.

Zusammenfassend kann festgehalten werden, dass Syntaxverarbeitung sowohl in Sprache als auch in Musik überlappende Operationen im linken GFI sowie bilateralen GTS auslöst. Diese Strukturen stellen somit höchstwahrscheinlich die anatomischen Schnittstellen dar, die den eingangs beschriebenen funktionellen Zusammenhängen zumindest teilweise zugrunde liegen. Als modalitätsübergreifende Funktionen des linken GFI werden syntaktische Arbeitsgedächtnisprozesse sowie die Dekodierung und Integration der hierarchischen Struktur sequenzieller Information (wie Sprache und Musik) diskutiert, die möglicherweise auch auf weitere Modalitäten wie die Wahrnehmung und Ausführung von Bewegungen und Handlungen übertragen werden könnten. Als modalitätsübergreifende Funktion des GTS wird die Analyse und Integration der spektrotemporalen Merkmale auditorischer Information, möglicherweise basierend auf Gruppierungsmechanismen gemäß der Gestaltprinzipien, vorgeschlagen. Im Sinne neuronaler Vernetzung würden diese Mechanismen dem Aufbau einer Repräsentation von Sprache und Musik dienen, die höheren kognitiven Verarbeitungsschritten, z.B. im GFI, zugeführt werden können.

Introduction

Language and music are two primary channels of human auditory communication, and their similarities have long interested scholars. Views and debates reach from common evolutionary roots (C. M. Brown, Hagoort, & Chwilla, 2000; Darwin, 1871/1989; Rousseau, 1781/1998), through comparable “design features” (Fitch, 2006; Lerdahl & Jackendoff, 1983), to similar cognitive mechanisms during the perception and production of speech and music (S. Brown et al., 2006; Koelsch & Siebel, 2005; Patel, 2003a).

Language and music perception are no unitary phenomena, but involve a cascade of intricately related sub-processes. The present dissertation focuses on *syntax* as one aspect that is central to both domains. Although nobody would ever confuse a Mozart sonata and a political speech, they are, in fact, both sequences of discrete elements that are arranged according to a set of “syntactic” rules to form meaningful structures. Neurocognitive theories proposed that music and speech, despite their different contents, share procedural parsing processes (Patel, 2003a). Evidence for shared operations comes from behavioural and ERP studies that reported resource competition effects as soon as syntactic errors were concurrently presented in music and language (e.g., Koelsch, Gunter, et al., 2005; Slevc et al., 2007; Steinbeis & Koelsch, 2008b). Furthermore, musical training was found to enhance musical as well as linguistic syntax processing (Jentschke, Koelsch, & Friederici, 2005), whereas developmental or acquired agrammatical disorders were accompanied by parallel deficits in the processing of musical syntax (Jentschke et al., 2008; Patel et al., 2008).

These functional interactions are thought to rely on a partial overlap of the neural networks supporting musical and linguistic syntax processing. Frontal brain areas (Koelsch, 2005; Patel, 2003a) as well as the superior temporal lobe (Koelsch, 2006) are discussed as likely candidates interfacing syntax processing within both domains.

The present dissertation set out to explicitly test the hypothesis of a co-localisation of musical and linguistic syntax processing within the inferior frontal (IFG) and the superior temporal gyrus (STG), aiming to specify the neural substrate underlying the apparent functional

interactions between both domains. To this end, event-related potentials (ERP) were recorded in an auditory sentence comprehension paradigm (Friederici et al., 1993) and a chord sequence paradigm (Koelsch et al., 2000). The neuroanatomical correlates of ERP components that reflect syntactic structure building in language (ELAN) and music (ERAN) were analysed by means of a lesion study (for the ERAN; Experiment 1), as well as by source modelling of the intracranial equivalents of the ELAN and ERAN recorded from subdural grid-electrodes (Experiment 2).

The first part of this dissertation comprises theoretical, methodological and empirical background information. **Chapter 1** will present a neurocognitive model of language comprehension demonstrating the complex interplay of sub-processes involved in speech perception. Furthermore, this chapter will introduce two primary brain regions of syntax processing in speech: The inferior frontal gyrus (IFG) and the superior temporal gyrus (STG). **Chapter 2** will describe a neurocognitive model of music perception exhibiting a similar complexity of processing components as the language model. Furthermore, the role of the IFG and STG in syntax processing in music will be reviewed. **Chapter 3** will shed light on the similarities and differences between language comprehension and music perception. Particularly their relationship with respect to “syntax processing” will be highlighted, and the research questions of the present dissertation will be elaborated. The ERP methodology, the special case of intracranial recordings as well as the lesion approach will be introduced and critically discussed in **Chapter 4**.

In the second part of this dissertation, two main experiments and their pilot studies will be presented. Experiment 1 was conducted to investigate musical syntax processing in patients with brain lesions in areas that are known to be involved in linguistic syntax processing, i.e., the left IFG and the left anterior STG. **Chapter 5** will introduce the empirical and methodological background of this study, **Chapter 6** will present the psychoacoustic, behavioural and electrophysiological evaluation of the stimulus material employed in this project, and **Chapter 7** will describe and discuss the results of the actual lesion study. Experiment 2 was conducted to investigate the neuroanatomical overlap of musical and linguistic syntax processing in a within-subject design. Electrocortical equivalents of the ELAN and ERAN recorded from subdural electrodes in patients with pharmaco-resistant epilepsy were localised and compared. **Chapter 8** will give a short introduction into this work, **Chapter 9** will present an EEG pilot study that evaluated the stimulus material designed for this project, and **Chapter 10** will describe and discuss the actual intracranial ERP study and its outcome. In **Chapter 11** the results of the two experiments will be summarised and discussed with respect to the prevailing literature.

Part I

Theoretical and Empirical Background

Chapter 1

Language Perception

The functional architecture and the neuroanatomical underpinnings of human language processing have been topics of intense investigation since the seminal works of Broca, Wernicke and Lichtheim in the second half of the 19th century (Broca, 1861; Lichtheim, 1885; Wernicke, 1874). Since then, a number of claims, models, and theories on *where* and *how* language is processed in the human brain have been established, substantially revised, and partly abandoned. Thus, despite this broad interest in language processing and the large efforts made to clarify this issue, the organisation of language comprehension is still not fully understood. The following sections seek to sketch some core points of our present knowledge. First, a neurocognitive model of auditory sentence comprehension will be introduced (Friederici, 2002, 2006c; Friederici & Kotz, 2003) describing the functional components and temporal dynamics of language processing. In the second part of the chapter, the neuroanatomical architecture of the language network will be discussed with special emphasis on two brain structures thought to subserve syntax processing: The left inferior frontal gyrus (IFG) and the anterior temporal lobe (ATL).

1.1 A Neurocognitive Model of Language Processing

During sentence comprehension, a number of sub-processes come into play from the initial auditory or visual input to the final understanding of the sentence's meaning. Prevalent psycholinguistic models of sentence comprehension may be divided into two groups, the main difference being whether they assume a serial progression of subsequent processing steps or an interactive or parallel activation of these sub-processes (for a review see Pickering & van Gompel, 2006).

In the following, a neurocognitive model of sentence comprehension will be introduced that reconciles both views (Friederici, 2002, 2006c; Friederici & Kotz, 2003, see Figure 1.1). The model combines information on temporal, functional and neurotopological aspects of auditory speech perception obtained by a large number of EEG, MEG, fMRI, and PET studies. The model is organised into 4 phases aligned in an incremental serial order. Phonological processes (Phase 0) precede 3 phases of sentence comprehension: Initial syntactic structure building (Phase 1), followed by semantic processes and thematic role assignment (Phase 2), and completed by processes of integration, reanalysis and repair (Phase 3). The authors emphasise that the model partly supports syntax-first models (Phase 1-2), but provides at the same time clear evidence for an interaction of the different types of information during the final processing phase (Phase 3). The following sections describe the single phases in more detail.

1.1.1 Phase 0 - Phonological Analysis

Phase 0 of the model includes the series of neural processes from auditory input to speech recognition that precede the initial syntactic and semantic processing steps (for more details on speech perception at the sublexical level see, e.g., Griffiths & Warren, 2002; Hickok & Poeppel, 2000; Scott & Johnsrude, 2003). That is, Phase 0 subsumes the primary acoustic analysis of the speech signal within the primary and secondary auditory cortex and the planum temporale (PT), the identification of phonemes within the mid-STG, as well as phonological segmentation and sequencing thought to involve the superior-posterior portion of Brodman's area (BA) 44 within the IFG (see also Hickok & Poeppel, 2007, for a review on the involvement of the STS in phonological segmentation). A neurophysiological correlate of these processes is, amongst others, the N100.

1.1.2 Phase 1 - Initial Syntactic Structure Building

Phase 1 comprises the build-up of an initial phrase-structure of the sentence based on word-category information. Each incoming word is immediately integrated into the current structure according to the syntactic principles of the current language. These first-pass parsing processes are thought to be very fast and highly automatic in nature. If the parser encounters an element belonging to a word-category that violates the syntactic rules, the word cannot be integrated into the established phrase-structure. These difficulties are reflected by a negative ERP component with a frontal, mainly left lateralised scalp distribution peaking between 150 and 200 ms after onset of an incorrect word - the Early Left Anterior Negativ-

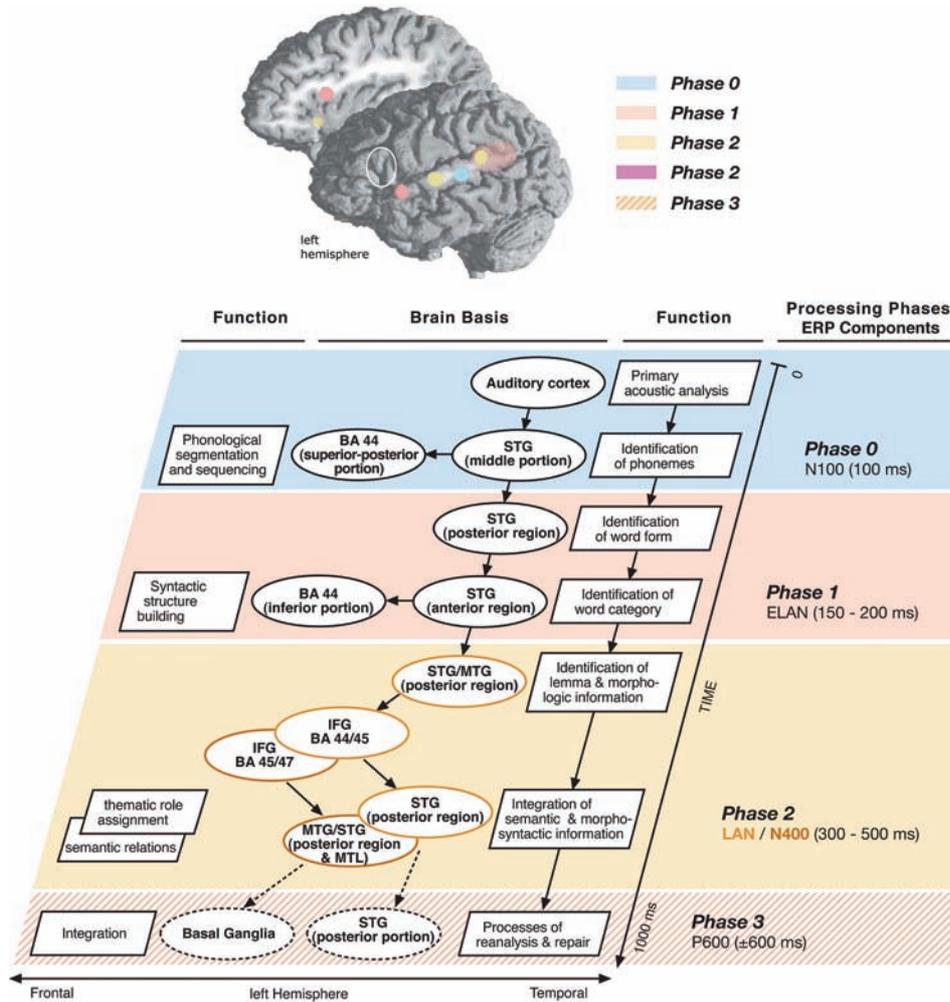


Figure 1.1: A neurocognitive model of sentence comprehension (taken from Friederici & Kotz, 2003). After an initial stage of auditory and phonological processing (Phase 0) mainly involving auditory areas and the middle STG, the model proposes three phases of sentence comprehension: Phase 1 supported by anterior temporal and inferior frontal brain areas describes the build-up of an initial phrase-structure based on word-category information. Parsing difficulties at this stage normally elicit an Early Left Anterior Negativity (ELAN) around 150 - 200 ms. Phase 2 at around 300 - 500 ms after onset of a word contains independent morphosyntactic and semantic processes supported by a variety of temporal and frontal brain structures. This processing stage can be investigated by means of the Left Anterior Negativity (LAN, following morphosyntactic errors) and the N400 (which is larger for semantically inappropriate stimuli). In Phase 3, syntactic and lexical-semantic processes are thought to interact with each other. Conceptually, Phase 3 represents the integration of incoming elements into the established context and repair processes if necessary. Integration difficulties are reflected by a P600 and thought to involve posterior temporal areas and the basal ganglia (BG).

ity (ELAN; e.g., Friederici et al., 1993; Friederici, 1995, 2002; Hahne & Friederici, 1999; Kubota, Ferrari, & Roberts, 2003).¹

The processes of early structure building are thought to be subserved by anterior temporal brain areas, as well as by inferior frontal brain structures (e.g., the inferior frontal gyrus and the deep frontal operculum). This assumption is mainly based on MEG source localisations of the ELAN (Friederici, Wang, Herrmann, Maess, & Oertel, 2000; Gross et al., 1998; Knösche et al., 1999). Additionally, studies with brain lesioned patients showed an attenuation or absence of the ELAN if anterior temporal or inferior frontal brain areas were damaged after cerebral stroke (Friederici, Hahne, & von Cramon, 1998; Friederici, von Cramon, & Kotz, 1999; Friederici & Kotz, 2003; Kotz, von Cramon, & Friederici, 2003). It is assumed that the temporal areas provide information about the different words' categories, whereas the IFG builds the structure of the incoming elements based on this information.

1.1.3 Phase 2 - Lexical Access, Morphosyntactic Processing and Thematic Role Assignment

While Phase 1 solely relies on word-category information, in Phase 2 the meaning and morphosyntactic information of the words (e.g., gender, case) is accessed in order to determine their relation and thematic roles (i.e., agent, object, recipient). It is suggested that these semantic and syntactic processing streams act in parallel but independent from each other. Two ERP components are considered as indicators of the semantic and syntactic analysis in Phase 2: The N400 and the Left Anterior Negativity (LAN).

The N400 is taken as the classical marker of semantic processing, first observed by Kutas and Hillyard more than 30 years ago (Kutas & Hillyard, 1980b, 1984). The N400 is a negativity with centro-parietal scalp distribution generally observed in a time window from 300 to 500 ms (relative to word onset). Its amplitude is sensitive to the semantic fit of the incoming word with the preceding context. The neuroanatomical substrates underlying the N400 are thought to be organised in a widespread cerebral network within both hemispheres (e.g., Maess, Herrmann, Hahne, Nakamura, & Friederici, 2006) as revealed by intracranial or subdural recordings (Halgren et al., 1994, 1994; McCarthy, Nobre, Bentin, & Spencer, 1995; P. Meyer et al., 2005; Nobre & McCarthy, 1995) as well as MEG and EEG source localisation methods. This latter method mostly identified a network of sources, includ-

¹Note that depending on the point at which word-category can be accessed (e.g., within the prefix or the suffix of the word), the onset of the ELAN may occur earlier or later. A number of studies using words with late word-category availability (e.g., "*Das Metall wurde zur Veredelung ...*" vs. "*Das Metall wurde zur veredelt ...*") reported Left Anterior Negativities around 300 to 400 ms after onset of the critical word which could be interpreted as delayed ELAN effects (e.g., Münte, Heinze, & Mangun, 1993).

ing, e.g., areas close to the auditory cortex (e.g., Helenius et al., 2002; Mäkelä, Mäkinen, Nikkiä, Ilmoniemi, & Tiitinen, 2001), the ventral portion of the left inferior frontal gyrus (BA 45/47), the anterior STG (BA 22), posterior MTG (BA 21), inferior temporal gyrus (ITG; BA 20) etc. (e.g., Halgren et al., 2002; Maess et al., 2006). These distributed sources coincide with the widespread brain activations found in fMRI and PET studies during semantic processing (e.g., Hickok & Poeppel, 2007; Spitsyna, Warren, Scott, Turkheimer, & Wise, 2006; Vigneau et al., 2006, see also section 1.2).

A second ERP component associated with Phase 2 is the Left Anterior Negativity (LAN; Coulson, King, & Kutas, 1998). The LAN is considered as an indicator of morphosyntactic processes. It occurs between 300 and 500 ms if the parser encounters violations of, for instance, article-noun gender agreement (e.g., in sentences like “*Er trinkt den_m kühlen_m Bier_n.*”; Gunter, Friederici, & Schriefers, 2000; Koelsch, Gunter, et al., 2005), or violations of subject-verb agreement (e.g., “*Der Junge_{3s} singst_{2s} ein Lied.*”; Angrilli et al., 2002; Gunter, Stowe, & Mulder, 1997; Rossi, Gugler, Hahne, & Friederici, 2005). The neural generators of the LAN are still largely unexplored, and the existing literature draws a rather inconsistent picture reporting the involvement of either temporal (Shtyrov, Pulvermüller, Näätänen, & Ilmoniemi, 2003) or frontal sources (Pulvermüller & Shtyrov, 2003).

1.1.4 Phase 3 - Integration, Reanalysis and Repair

In the final phase of the model, the structural, semantic and thematic representation established in the previous processing steps are integrated. If the integration is successful, full comprehension takes place. Otherwise, the parser detects a mismatch and reanalyses the established structure, e.g., in garden-path sentences like “*When Mary was knitting the socks fell to the floor.*”. If no reanalysis is possible, repair processes come into play. These re-computation processes are typically reflected by a late positivity with centro-parietal scalp distribution and a peak latency between 600 and 1000 ms - the P600 (e.g., Friederici, Hahne, & Mecklinger, 1996; Osterhout, Holcomb, & Swinney, 1994).

To date, the neuroanatomical bases of the P600 are only sparsely explored. Since late ERP components like the P600 mostly rely on distributed sources, the estimation of its generators by means of mathematical procedures like dipole fitting is highly unreliable. The poor temporal resolution of imaging methods like fMRI or PET on the other hand precludes the separation of these late processes from earlier structure building, morphosyntactic and semantic processes. However, lesion studies point to the importance of the basal ganglia (BG) in these late processes. When presented with sentences like “*Der Fisch wurde im geangelt.*”, patients with BG lesions or Parkinson’s disease (including a degeneration of

the dopamine neurons in the BG) show an ELAN (see Phase 1), but no P600, reflecting a deficient ability to integrate, reanalyse or repair incoming items into an established context (e.g., Friederici et al., 1999; Friederici, Kotz, Werheid, Hein, & von Cramon, 2003; Frisch, Kotz, von Cramon, & Friederici, 2003; Kotz, Frisch, Cramon, & Friederici, 2003).

1.2 The Neuroanatomy of Language Processing

The electrophysiological evidence cited in the previous section argues that language comprehension is based on at least three functionally distinct subsystems - phonological, syntactic, and lexical knowledge - as reflected by the distinct ERP components elicited by either sub-process. Assuming an internal modularity of the language system, it has been postulated that these sub-processes rely on distinct brain areas. The identification of the brain structures supporting different aspects of language comprehension has been the major focus of a large number of studies (reviewed in, e.g., Démonet, Thierry, & Cardebat, 2005; Kaan & Swaab, 2002) and a series of functional anatomic models of language (e.g., Friederici, 2002, 2006b; Friederici & Alter, 2004; Hagoort, 2005; Hickok & Poeppel, 2000, 2007; Price, 2000; Scott, Blank, Rosen, & Wise, 2000; Shalom & Poeppel, 2008; Ullman, 2001) has been developed since the “classical” views of Broca, Wernicke and Lichtheim (Broca, 1861; Lichtheim, 1885; Wernicke, 1874).

Despite their focus on different levels of language comprehension [*prelexical* (e.g., Scott et al., 2000) vs. *word level* (e.g., Price, 2000) vs. *sentence level* (e.g., Friederici, 2002)] or production (e.g., Indefrey & Levelt, 2004), and their different major concerns [e.g., the distinction of a ventral and a dorsal stream supporting lexical-semantic processes and auditory-motor integration respectively (Hickok & Poeppel, 2000, 2007), the temporal ordering of different sub-processes (Friederici, 2002, 2006b; Friederici & Kotz, 2003), or the distinction of processes relying on declarative vs. procedural memory resources (Ullman, 2001), the reports agree on the involvement of a mainly left lateralised fronto-temporo-parietal neural network in human speech perception (but see Friederici & Alter, 2004; Friederici, von Cramon, & Kotz, 2007, for a bilateral model of auditory sentence comprehension incorporating prosodic processing). The view on the exact functional segregation of these brain areas and their complex interplay partly depends on the focus of the respective model. The following sections will sketch some of the actual debates on two brain structures known to be substantially involved in human language comprehension - the frontal and the temporal lobe - with a special focus on their role in syntax processing.

1.2.1 The Role of the Inferior Frontal Gyrus (IFG)

Apparently, the IFG is a heterogeneous brain area, which has been suggested by several lines of evidence. Based on the cytoarchitectonic map of Brodmann (1912), three microanatomically (an probably also functionally) distinct subdivisions of the IFG are assumed: BA 44 (roughly corresponding to the pars opercularis), BA 45 (\approx pars triangularis), and BA 47 (\approx pars orbitalis). This view has been basically confirmed and extended (suggesting a further subdivision of BA 44 and BA 45) by modern cyto- and receptorarchitectonic mappings (Amunts et al., 1999; Amunts & Willmes, 2006; Amunts & Zilles, 2006). A recent parcellation of Broca's area based on the connectivity pattern of the putative subregions equally discerned several subdivisions roughly corresponding to BA 44, BA 45, and the adjacent deep frontal operculum (Anwander, Tittgemeyer, Cramon, Friederici, & Knösche, 2007).

Following the assumption that microanatomically distinct brain areas support different functions it may not come as a surprise that IFG activations are observed during various linguistic and also non-linguistic tasks (e.g., Bookheimer, 2002; Grodzinsky & Amunts, 2006). Regarding language studies, the involvement of the IFG has been shown during phonological, syntactic, and semantic processing (see Bookheimer, 2002; Vigneau et al., 2006, for a review), however, the local maxima of the effects appeared to differ between these aspects of language processing: There is growing evidence that BA 47 and 45 are mainly involved in semantic processing, that BA 45 and 44 contribute to syntactic processing, and finally, that BA 44 and parts of BA 6 play a role in phonological processing (Bookheimer, 2002; Devlin, Matthews, & Rushworth, 2003; Friederici, 2002; Hagoort, 2005; Poldrack et al., 1999; Vigneau et al., 2006). Based on these findings, Hagoort (2005) recently proposed to assume an anterior-ventral to posterior-dorsal gradient of left IFG functions. The following paragraphs will summarise some of the core findings on syntax processing within the left IFG.

Syntax processing historically has been described as the cardinal function of the left IFG. This hypothesis was put forward by the beginning of the 1980's (e.g., Berndt & Caramazza, 1980) when it became apparent that patients with lesions in Broca's area (encompassing areas BA 44 and 45 of the left IFG; Amunts et al., 1999; Amunts & Zilles, 2006) are impaired when comprehending sentences which can only be correctly interpreted by relying on syntactic information such as in "*The dog that scratched the cat chased the bird.*" (e.g., Caplan & Futter, 1986; Caramazza & Zurif, 1976; Schwartz, Lenhart, & Lawrence-Sharland, 1980). This clinical finding has found strong support in a number of imaging studies showing increased activations within Broca's area with increasing syntactic complexity due to, e.g., non-canonical word order or long-distance dependencies (e.g., Ben-

Shachar, Hendler, Kahn, Ben-Bashat, & Grodzinsky, 2003; Bornkessel, Zysset, Friederici, von Cramon, & Schlesewsky, 2005; Caplan, Alpert, & Waters, 1998, 1999; Fiebach, Schlesewsky, Lohmann, Cramon, & Friederici, 2005; Friederici, Bahlmann, Heim, Schubotz, & Anwander, 2006; Friederici, Fiebach, Schlesewsky, Bornkessel, & von Cramon, 2006; Grewe et al., 2005; Just, Carpenter, Keller, Eddy, & Thulborn, 1996; Röder, Stock, Neville, Bien, & Rösler, 2002; Stromswold, Caplan, Alpert, & Rauch, 1996). Other evidence for the involvement of the frontal operculum in syntax processing comes from studies using delexicalised syntactic speech (jabberwocky, e.g., “*The mumphy folofel fonged the apole trecon.*”) or syntactic prose (e.g., “*The infuriated water grabbed the justified dream.*”) both forcing the parser to focus on syntactic aspects of sentence processing exclusively (e.g., Friederici, Meyer, & von Cramon, 2000a; Moro et al., 2001). Similarly, a number of studies contrasting syntactically correct vs. incorrect sentences found activations within the IFG or the adjacent deep frontal operculum (e.g., Embick, Marantz, Miyashita, O’Neil, & Sakai, 2000; Friederici, Rüschemeyer, Hahne, & Fiebach, 2003; M. Meyer, Friederici, & von Cramon, 2000; Newman, Just, Keller, Roth, & Carpenter, 2003; Ni et al., 2000). In this context it should be mentioned that several studies point to a functional dissociation of the lateral IFG (BA 44/45) and the deep frontal operculum, supporting the processing of non-local and local dependencies respectively (e.g., Friederici, 2004, 2006a; Friederici, Bahlmann, et al., 2006).

In spite of this apparently converging empirical evidence, several authors have raised concerns about the exact role of the IFG in syntactic processing. This debate has been opened when observing that despite poor comprehension of complex syntactic constructions Broca’s aphasics were still sensitive to grammatical structure (e.g., Berndt, Salasoo, Mitchum, & Blumstein, 1988; Linebarger, Schwartz, & Saffran, 1983). Furthermore, a number of imaging studies on syntactic processing failed to observe activations in the IFG proper (reviewed by Kaan & Swaab, 2002). There are two views to account for these inconsistencies: First, the IFG may be involved only in higher-order syntactic operations like the processing of permutations and transformations (Ben-Shachar et al., 2003; Ben-Shachar, Palti, & Grodzinsky, 2004; Grodzinsky, 2000), the processing of recursions (e.g., Friederici, 2004; Friederici, Bahlmann, et al., 2006), or linearisation (e.g., Bornkessel et al., 2005; Grewe et al., 2005). Another view argues that activations within Broca’s area rather depend on the higher working memory load or storage demands engendered by more complex sentences (e.g., Fiebach et al., 2005; Kaan & Swaab, 2002; Stowe, Haverkort, & Zwarts, 2005) which would be in line with studies on verbal working memory ascribing the articulatory rehearsal process (a major mechanism of the phonological loop) to the left IFG (e.g., Baddeley, 2003; Paulesu, Frith, & Frackowiak, 1993). Recent approaches attempt to combine this conflicting evidence by assuming the existence of a specialised *syntactic*

working memory system - as a part of the syntactic processing system - which is located within the left IFG (BA 44/45; e.g., Caplan et al., 1999; Caplan, Alpert, Waters, & Olivieri, 2000; Fiebach, Schlesewsky, & Friederici, 2001; Fiebach, Vos, & Friederici, 2004; Fiebach et al., 2005; Vigneau et al., 2006). However, research is going on attempting to tease apart linguistic complexity and working memory load (e.g., Friederici, Fiebach, et al., 2006).

In a recent trend, a number of models aimed at establishing a unifying framework for the complex functional pattern of the IFG. Several authors argue more or less conjointly for a superordinate procedural (rather than conceptual) function of the IFG in phonological, syntactic and semantic processes: With this respect, Hagoort (2005) coined the term *unification* as the major role of the left IFG, i.e., the binding of basic components (either phonological, syntactic, or semantic in nature) into larger structures. Shalom and Poeppel (2008) introduced the term *synthesising* to likewise describe the combination of elementary (phonological, syntactic, or semantic) items achieved by the IFG. These assumptions are in line with Friederici (2002) stating that the IFG subserves the construction of semantic and syntactic *relations*, and Ullman (2001) assigning the IFG to a *procedural* (rather than declarative) memory system.

On an even more domain-general level, these views would also be applicable to non-linguistic material, whenever discrete elements are arranged into sequences, thus, accounting for reports on inferior frontal activations during music perception (e.g., Janata, Tillmann, & Bharucha, 2002; Koelsch, Schröger, & Gunter, 2002; Koelsch & Siebel, 2005; Satoh, Takeda, Nagata, Hatazawa, & Kuzuhara, 2001; Tillmann, Janata, & Bharucha, 2003; Tillmann, Koelsch, et al., 2006). These considerations will be discussed in more detail in Chapters 2 and 3.

1.2.2 The Role of the Anterior Temporal Lobe (ATL)

Another brain area playing a key role in language comprehension is the temporal lobe (e.g., Vigneau et al., 2006). Due to its special relevance for the present dissertation, the following paragraphs will mainly focus on the functional significance of the anterior temporal lobe (ATL; anterior of Heschl's gyrus), while only a short overview over posterior temporal lobe functions will be given.

The posterior temporal lobe (PTL) including Wernicke's area (roughly located within the posterior STG) subserves a variety of tasks associated with language comprehension. The posterior superior temporal plane (STP) including the planum temporale (PT) bilaterally achieves the spectrotemporal analysis of the incoming (linguistic or non-linguistic) signal, building an initial sound-based representation of speech which is objected to higher-order

cognitive processes later on (e.g., Griffiths & Warren, 2002; Hickok & Poeppel, 2000; J. E. Warren, Wise, & Warren, 2005). Beyond this early stage of speech sound recognition, opinions converge on the importance of the STS in phonological processing (e.g., Binder, 2000; Indefrey & Levelt, 2004; Liebenthal, Binder, Spitzer, Possing, & Medler, 2005; Möttönen et al., 2006; Scott et al., 2000), since the STS is specifically activated when encountering signals containing phonemic information compared with a variety of non-speech sounds (reviewed in Hickok & Poeppel, 2007).² More broadly, the (right) superior temporal region has been associated with prosodic processing in speech perception (e.g., Friederici & Alter, 2004; M. Meyer, Alter, Friederici, Lohmann, & von Cramon, 2002; M. Meyer, Steinhauer, Alter, Friederici, & von Cramon, 2004). The posterior middle temporal gyrus (MTG) has been proposed as a region supporting the mapping between the sound-based representation established by the STP and STS and meaning, i.e., widely distributed lexical-semantic representations and concepts (e.g., Binder et al., 1997; Binder, 2000; Hickok & Poeppel, 2007; Rissman, Eliassen, & Blumstein, 2003). This view is corroborated, e.g., by recent large-scale patient studies using voxel-based lesion-symptom mapping (VLSM; Bates et al., 2003; Dronkers, Wilkins, Valin, Redfern, & Jaeger, 2004) showing that damage to the posterior MTG causes severe deficits of word-level comprehension.

Unlike traditional views locating the core regions of language comprehension in posterior superior temporal brain areas (Wernicke, 1874), recent theories emphasise the functional significance of the anterior temporal lobe (ATL) in speech perception. Various accounts of the role of the ATL in sentence comprehension have been proposed. In one theory, the ATL is thought to play a crucial role in lexical-semantic processing, most often as part of a larger temporo-parietal neural network (e.g., Hickok & Poeppel, 2007; Spitsyna et al., 2006). This idea is primarily motivated by clinical research with patients suffering from semantic dementia, a disease caused by a (most often bilateral) degeneration of the ATL (e.g., Nestor, Fryer, & Hodges, 2006; K. Patterson, Nestor, & Rogers, 2007). One of the most prominent symptoms of semantic dementia is a progressive deterioration of receptive and expressive vocabulary, i.e., a progressive failure to name objects, concepts or people across all modalities (anomia; K. Patterson et al., 2007).

Most relevant for the present dissertation are claims made by other theories namely that the ATL is mainly involved in (low-level) syntactic processes. This assumption is supported by several lines of evidence: Neuropsychological studies have demonstrated that damage to

²Several authors propose a rostral stream of processing in the left temporal lobe (e.g., Liebenthal et al., 2005; Scott, 2005). Along its length - running from primary auditory areas in the posterior STP to more anterior and ventral areas in the STG and STS - this pathway has been shown to be increasingly sensitive to phonemic information and more complex, high-level constructs inherent in intelligible speech compared to non-speech sounds.

the ATL including the anterior portion of the superior temporal gyrus (STG; BA 22) causes deficiencies in comprehending complex morphosyntactic structures (Dronkers, Wilkins, Van Valin Jr., Redfern, & Jaeger, 1994; Grossman et al., 1998). Corroboratingly, it was found that the amplitude of the Early Left Anterior Negativity (ELAN - reflecting the initial phrase-structure building based on word-category information; see section 1.1.2) is abolished in patients with left anterior temporal lobe lesions (Kotz, von Cramon, & Friederici, 2003). This finding coincides with previous MEG studies in healthy subjects, localising the major neural generators of the ELAN within anterior temporal (planum polare) and inferior frontal brain areas (Friederici, Wang, et al., 2000; Knösche et al., 1999).

Additional evidence implicating the ATL in syntactic processing comes from functional imaging studies approaching this issue from different angles (for a review see Kaan & Swaab, 2002). Thus, greater ATL activation was found for sentences (containing a syntactic structure) than for lists of unrelated (e.g., Friederici, Meyer, & von Cramon, 2000b; Humphries, Love, Swinney, & Hickok, 2005; Humphries, Binder, Medler, & Liebenthal, 2006; Mazoyer, Tzourio, Frak, & Syrota, 1993) or related words (i.e., scrambled sentences, containing no syntactic structure; e.g., Humphries et al., 2005, 2006; Vandenberghe, Nobre, & Price, 2002). This finding even holds when delexicalised speech (i.e., jabberwocky or syntactic prose; see section 1.2.1) is contrasted against pseudoword lists (Friederici, Meyer, & von Cramon, 2000b; Humphries et al., 2006; Mazoyer et al., 1993; M. Meyer et al., 2000), or when sentences are contrasted against rotated speech (Spitsyna et al., 2006) or meaningful sequences of environmental sounds (Humphries, Willard, Buchsbaum, & Hickok, 2001) arguing in favour of a superiority of syntactic over semantic processing in the ATL. Additionally, the ATL has been more strongly activated by sentences with syntactic violations than by correct sentences (Friederici, Rüschemeyer, et al., 2003; M. Meyer et al., 2000; Rüschemeyer, Fiebach, Kempe, & Friederici, 2005), and has been shown to be selectively responsive to syntactic priming (Noppeney & Price, 2004) suggesting further that syntactic rather than semantic manipulations modulate the ATL activity.

Taken together, the temporal lobe represents a major component of the human language network (e.g., Friederici, 2002; Hickok & Poeppel, 2007; Spitsyna et al., 2006; Vigneau et al., 2006) covering several processing steps from the initial auditory analysis of the incoming signal in the STP via phonological processes in the STS and sound-to-meaning mapping in the MTG leading to higher-order syntactic and semantic processes in the ATL most presumably in conjunction with inferior frontal lobe areas (connected through the fasciculus uncinatus). As pointed out above, the ATL appears to play a major role in syntactic processing, even if it has also shown sensitivity to semantic tasks (e.g., Vandenberghe et al., 2002). In an attempt to combine these findings, several authors recently proposed that the ATL,

more specifically the temporal pole region, subserves the composition of sentence meaning from a syntactic combination of meaningful words (i.e., compositional semantics; Stowe et al., 2005; Vandenberghe et al., 2002).

In a recently published large-scale model of language comprehension, Shalom and Poeppel (2008) integrated the variety of functions described above and proposed that the temporal lobe would primarily deal with memorising (storing) lexical items (including phonological, morphosyntactic, and semantic information) and facilitating their retrieval, as opposed to the frontal lobe that is primarily involved in synthesising these single elements (see also Vigneau et al., 2006). These views are in line with Friederici (2002) and Indefrey and Levelt (2004) claiming that the temporal cortex subserves the retrieval of word-level syntactic information (e.g., the word-category), whereas the frontal cortex is involved in coordinating relations between basic items.

1.3 Summary

Connected speech is a smooth and effortless mode of human communication. However, behind the apparent ease with which we understand language stands a tremendously quick and intricate analysis of the acoustical, phonological, syntactic, lexical, conceptual, and prosodic information conveyed by the signal. In the present chapter, a neurocognitive model of sentence comprehension was presented that relates these sub-processes in a serial way with some interaction at later processing stages (Friederici, 2006b; Friederici & Kotz, 2003).

In the second part of the chapter, two core regions of the distributed language comprehension network - the IFG and the ATL - were introduced. Keeping their functional heterogeneity in mind, their special role in syntax processing was highlighted. The ideas recently formulated by Shalom and Poeppel (2008) and supported by other authors (e.g., Friederici, 2002; Hagoort, 2005; Indefrey & Levelt, 2004; Ullman, 2001; Vigneau et al., 2006) were thereby taken as unifying framework, stating that the ATL is mainly involved in encoding or retrieving lexical (i.e., phonological, syntactic, and semantic) information, whereas the IFG is primarily concerned with the build-up of relations between these constituent elements.

From these findings the question arises, whether these processes are specific to language processing, or whether some of them act also during the processing of non-speech sequences of elements, like for instance tones or chords in musical pieces. To further elucidate this issue, Chapter 2 will give an overview over temporal and neuroanatomical aspects of music processing before both modalities, language and music, will be compared in Chapter 3.

Chapter 2

Music Perception

While language comprehension has been a core issue of neuropsychological research for more than one and a half century now, the first studies on the neurocognitive architecture of music processing date back hardly one and a half decade. Since then, a multitude of articles, reviews and books have been published, demonstrating the growing interest in the neural mechanisms of music processing and the beginning of intense and systematic investigation (e.g., Peretz, 2006). By now, considerable progress has been made in deciphering the functional architecture of music processing, however, we are still way back from understanding the whole ensemble of neuronal mechanisms underlying music appreciation, from the initial perception of a single tone to the large-scale processing of whole symphonies. The first part of the present chapter aims to give an overview about some of the core findings in these fields by exemplarily introducing one neurocognitive model of music perception (Koelsch & Siebel, 2005). Due to the special relevance for the present dissertation, a major focus will be placed on electrophysiological and neuroanatomical correlates of harmonic structure building. The second part of this chapter will briefly review the fundamental role of two brain areas in music perception - the temporal lobe (TL) and the inferior frontal gyrus (IFG).

2.1 A Neurocognitive Model of Music Processing

Music perception, like language comprehension, involves a multitude of intricately related brain functions, comprising, e.g., the more or less basic acoustic analysis of the auditory signal (e.g., Patel & Balaban, 2001; Tramo, Shah, & Braidá, 2002; J. D. Warren, Uppenkamp, Patterson, & Griffiths, 2003; Zatorre, 2001), rhythmic (e.g., Krumhansl,

2004; Patel, 2003b), melodic (e.g., Krumhansl, 2004) and harmonic structure building (e.g., Koelsch et al., 2000; Koelsch, Fritz, Schulze, Alsop, & Schlaug, 2005; Tillmann, Koelsch, et al., 2006), meaning extraction (e.g., Koelsch, Kasper, et al., 2004; Steinbeis & Koelsch, 2008a), and emotional appreciation (e.g., Blood, Zatorre, Bermudez, & Evans, 1999; S. Brown, Martinez, & Parsons, 2004; Koelsch, Fritz, Cramon, Müller, & Friederici, 2006).

Due to the relative youth of the neurocognition of music as research field (compared to the field of language), so far only very few models of music perception incorporating these single components have been established (e.g., S. Brown et al., 2006; Koelsch & Siebel, 2005; Peretz & Coltheart, 2003). To give an example: Relying on the concept of modularity of cognitive processes (Fodor, 1983), Peretz and Coltheart (2003) derived a model of the functional architecture of music processing from a large number of case studies in brain-damaged patients with impairments or preservations of specific musical abilities. Based on the logic of double dissociation, the authors identified a number of encapsulated modules organised in two parallel and largely independent subsystems dedicated, e.g., to the melodic analysis of the musical input (i.e., contour, or interval, and the tonal encoding of pitch) or the processing of temporal parameters of music (i.e., rhythm and metre). While providing a valuable framework on the cognitive organisation of music perception, the anatomical precision of this model remains, however, rather coarse (see Liégeois-Chauvel, Peretz, Babai, Laguitton, & Chauvel, 1998; Peretz, 1990; Schuppert, Münte, Wieringa, & Altenmüller, 2000, for attempts to clarify the question of hemispheric specialisation).

The aspect of localisation has been complemented by a more recent neurocognitive model of music perception (Koelsch & Siebel, 2005) developed on the basis of neurophysiological and neuroimaging studies with healthy participants specifying the temporal order as well as the neuroanatomical substrates of the relevant cognitive sub-processes. In the following sections, the model of Koelsch and Siebel (2005) will be taken as a guideline through the complex cascade of processing steps from the perception of single tones to the activation of motor effectors when listening to music (see Figure 2.1). Therein, the processing of structure in music will be explained in more detail.

2.1.1 Early Processing Stages

Subcortical pre-processing. When music reaches our ears, the signal (as any other acoustic information) is mechanically translated into neural activity at the level of the cochlea. On its way through the nuclei of the auditory brainstem (see Nieuwenhuys, Voogd, & Van Huijzen, 1995, for anatomical details) and the thalamus, various temporal (e.g., Griffiths, Uppenkamp, Johnsrude, Josephs, & Patterson, 2001) and spectral properties of the signal

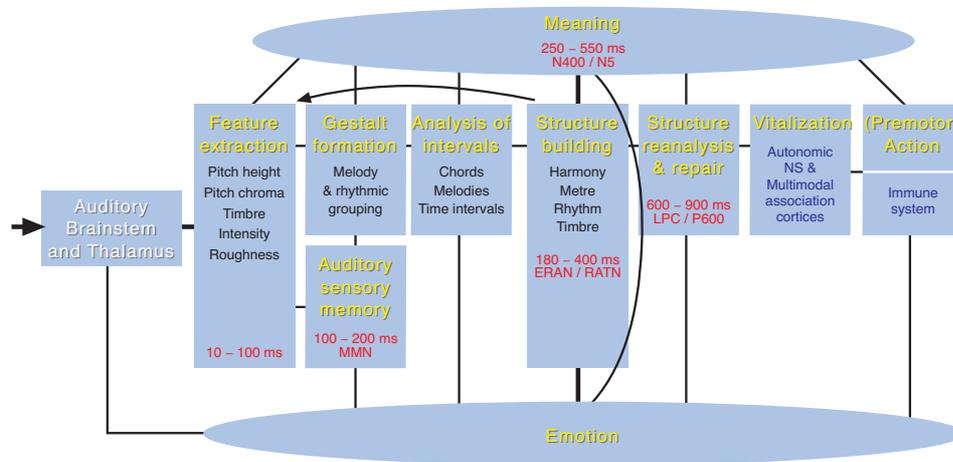


Figure 2.1: A neurocognitive model of music perception. The model relies mainly on data obtained from healthy subjects by means of EEG/MEG and fMRI, thus providing information on the time course as well as on the neuroanatomical correlates of the single processing steps (Koelsch & Siebel, 2005, see text for further explanations).

(e.g., Musacchia, Sams, Skoe, & Kraus, 2007) are analysed, before it reaches the (primary) auditory cortex.

Feature extraction. Within the primary and the adjacent secondary fields (see, e.g., Kaas & Hackett, 2000; Liégeois-Chauvel, Musolino, & Chauvel, 1991; Morosan et al., 2001, for the anatomy of primary and secondary auditory cortex), features of the auditory input, such as pitch height (e.g., Tramo et al., 2002) and pitch chroma (J. D. Warren et al., 2003), roughness (e.g., Fishman et al., 2001), intensity (e.g., Gutschalk, Patterson, Rupp, Uppenkamp, & Scherg, 2002), and timbre (e.g., Menon et al., 2002; J. D. Warren, Jennings, & Griffiths, 2005), are analysed in more detail. The exact underlying mechanisms and localisations of these processes are still under intense investigation, however, a functional asymmetry of the left and the right auditory fields with respect to the processing of temporal and spectral stimulus properties appears to be well established (e.g., Belin et al., 1998; Jamison, Watkins, Bishop, & Matthews, 2006; Zatorre & Belin, 2001; Zatorre, Belin, & Penhune, 2002): That means, even if left and right auditory cortex respond to both parameters, the left auditory cortex appears to be especially tuned to the tracking of rapidly changing acoustic information (in the range of milliseconds) which is most relevant for speech processing. On the other hand, right auditory areas were found to have a higher spectral resolution, vital to music perception.

Grouping of single events. Music relies on relations between elements rather than on absolute values of single elements, requiring mechanisms that allow the melodic and rhythmic grouping of individual tones to form a coherent percept. Since music unfolds over time, it appears plausible that a memory system is needed to transiently store incoming information in order to integrate subsequent tones. The model of Koelsch and Siebel (2005) incorporates an *auditory sensory memory* module to account for these processes. Operations of this system are partially reflected by the Mismatch Negativity (MMN), a component of the event-related potential (ERP; see Chapter 4) peaking around 100-200 ms after the onset of a deviant (i.e., “odd”) tone within a series of standard tones (see Näätänen, Paavilainen, Rinne, & Alho, 2007, for a review). The neural generators of the MMN are located within or in the close vicinity of the primary auditory cortex (e.g., Alho, 1995; Rosburg, Trautner, Dietl, Kral, et al., 2005), but additional frontal sources are debated (e.g., Doeller et al., 2003; Rinne, Alho, Ilmoniemi, Virtanen, & Näätänen, 2000).

Relying on these auditory sensory memory functions, *Gestalt formation* can take place, i.e., the organisation of distinct perceptual elements into a global representation according to general Gestalt principles, such as proximity, similarity, or continuity. Note that these grouping mechanisms are not only relevant for music perception but play a crucial role in auditory scene analysis and auditory stream segregation in everyday life (e.g., Carlyon, 2004; Griffiths & Warren, 2004).

Most presumably closely linked to the global grouping of the single elements, a local *analysis of the relation between these discrete constituents* takes place. This includes (a) a detailed processing of the temporal intervals, and (b) the fine-grained analysis of pitch relations of successively (melody) or simultaneously (harmony) presented tones. As pointed out earlier, there is considerable evidence from lesion studies that melodic and temporal information is processed independently (Peretz & Coltheart, 2003). Furthermore, distinct cerebral areas have been shown to be involved in the build-up of global (Gestalt) and local (interval) relations between single tones. For example, supratemporal brain regions posterior of Heschl’s gyrus, i.e., the planum temporale (PT) are crucial for auditory scene analysis and stream segregation (relying on Gestalt formation, i.e., the identification of auditory objects; e.g., Griffiths & Warren, 2002), whereas the anterior supratemporal plane, i.e., the planum polare (PP) is sensitive to pitch intervals and sound sequences (e.g., R. D. Patterson, Uppenkamp, Johnsrude, & Griffiths, 2002; J. D. Warren et al., 2003; Zatorre, Evans, & Meyer, 1994).

2.1.2 Music-Syntactic Processing

Music is not a random sequence of tones, on the contrary, the organisation of tones and chords within a melody or a harmonic progression is guided by a complex set of (syntactic) regularities as described by music theory. The analysis of these structural relations makes up the next step in the model of Koelsch and Siebel (2005) as shown by the two boxes demarcated as *Structure building* and *Structural reanalysis and repair* (see Figure 2.1). Before turning to the brain signatures of music-syntactic processing, some basic principles of musical structure will be explained. A major focus will be placed on melodic and harmonic structure (see Krumhansl, 2000 for comments on rhythmic structure).

Tones, scales, and chord functions. In Western tonal music, a diatonic scale comprises seven of the twelve chromatic tones of an octave, that are arranged in two half- and five whole-tone steps in various ways.¹ A tonal key exactly determines the tones which belong to a scale, e.g., the C major key determines exclusively the tones C-D-E-F-G-A-B. Note that the tones of a scale are not equivalent but are organised around the first tone of the scale, termed the tonic (i.e., C in C major). The other tones are arranged according to a *hierarchy of stability*,² with the fifth and the third scale tone (i.e., G and E in C major) being most closely related to the tonic, the remaining diatonic tones (i.e., the in-key tones D, F, A, and B in C major) being less related, and the non-diatonic tones (i.e., the out-of-key tones C \sharp , D \sharp , E \sharp , F \sharp , G \sharp , and A \sharp in C major) being least related to the tonic.

Two different keys never consist of exactly the same tones, although they may have tones in common. The number of tones that are shared by two keys determines how closely these keys are related. For instance, G major is very closely related to C major because both keys have six tones in common (i.e., C-D-E-G-A-B), they only differ with respect to one tone (F \sharp in G major instead of F in C major). On the other hand, F \sharp major is very distantly related to C major because both keys only share one tone (i.e., B) and differ with respect to the other six tones (F \sharp -G \sharp -A \sharp -C \sharp -D \sharp -E \sharp in F \sharp major instead of C-D-E-F-G-A in C major). In music theory, this principle of key-relatedness is illustrated by the *circle of fifths* (Figure 2.2).

By simultaneously sounding three tones of a key that are separated by thirds (e.g., C-E-G in C major), in-key chords are formed. Depending on which scale tone a chord is built on, it is associated with a specific *chord function* (Figure 2.3). For example, the in-key chord built on the first scale tone is denoted as tonic [I], and the chords built on the fifth and fourth

¹The order of these half- and whole-tone steps determines, e.g., the mode of the scale, i.e., major or minor.

²The concept of stability relates to the fact that the tones at high levels of the hierarchy are perceived as more final and serve as better completion to melodic phrases than tones at lower levels of the hierarchy that consequently demand resolution to more stable tones in the system.

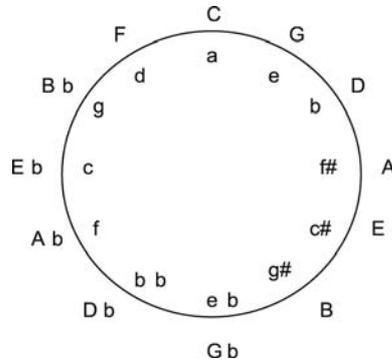


Figure 2.2: The Circle of fifths. The outer upper-case symbols represent major keys, the inner lower-case symbols demark minor keys (i.e., C major and a minor). The closer two keys, the stronger they are harmonically related. For instance C major shares six notes with its neighbouring keys F major and G major, only three notes with E major, and merely one tone with F# major.

tone are termed dominant [V] and subdominant [IV]. Like the tones of a scale, also chord functions are organised according to a hierarchy of stability. Thus, the tonic is the best representative, i.e., the *tonal centre* of a key. The dominant is most closely related to the tonic, followed by the subdominant. These three chords together form the *harmonic core*, i.e., they best establish the key. Further, less related, chord functions are, e.g., supertonic [III], mediant [III], and submediant [VI]. Most importantly, a chord built on the same note may have different functions depending on the key it belongs to. That means, while the major chord built on G serves as tonic chord in G major, it acts as subdominant in D major or as dominant in C major (see Figure 2.3). The interpretation of its actual function, hence, depends heavily on the harmonic context that provides information on the actual key.

The arrangement of chord functions in harmonic progressions is guided by these combined music-theoretical principles of key-relatedness and hierarchy of stability (e.g., Riemann, 1877/1971). Thus, chords are preferably organised as a neat alternation of harmonically distant events and their resolution into more stable events of the harmonic hierarchy. Beginnings and endings of segments are usually marked by such stable tones or chords. For example, a dominant-tonic progression (as part of a cadence) represents the closure of a phrase, not so the reverse tonic-dominant progression.

The cognitive representation of musical structure. Since the 1970's, the mental representation of different aspects of these organising principles of Western tonal music have been investigated in musicians and non-musicians. In a pioneering experiment on the *relation of pitch within a context*, Krumhansl (1979) found that the perception of the 12 tones of the chromatic scale corresponded surprisingly well to the levels of the tonal hierarchy

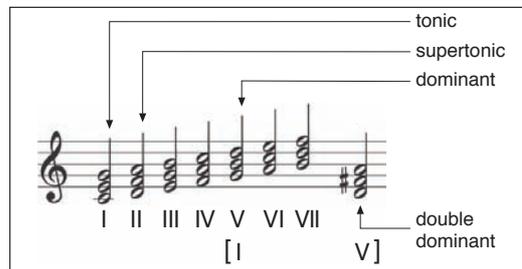


Figure 2.3: Examples of chord functions in C major. The chord built on the first scale tone is termed tonic [I], the chord built on the second scale tone is denoted as supertonic [II], and the chord built on the fifth scale tone as dominant [V]. Note that the dominant of C major represents the tonic in G major (see I in square brackets). The dominant of G major may thus be interpreted as the dominant to the dominant of C major, also termed double dominant (see V in square brackets).

described by music theory. That means, participants subjectively grouped [1] the tones of the tonic chord, [2] the remaining diatonic tones, and [3] the non-diatonic tones. A similar correspondence between mental representation and music-theory has been shown for the *key-relatedness*. Based on probe-tone ratings, Krumhansl and Kessler (1982) computed a four-dimensional spatial map of key-distances that can be depicted as a torus (see Figure 2.4). Notably, dimensions 1 and 2 of the map corresponded fairly well to the circle of fifths (see above). Furthermore, the music-theoretical relationships between major keys and their parallel and relative minor keys were apparent.

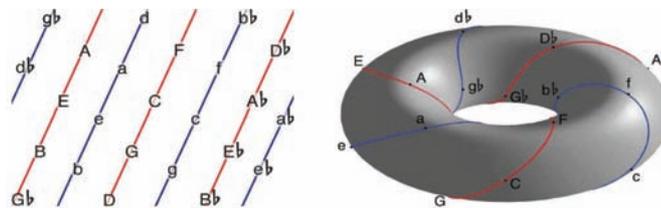


Figure 2.4: Toroidal representation of key distances (according to Krumhansl, 1990) either unfolded (left) or on the surface of a torus (right). Neighbouring keys are related by the circle of fifths (major: red lines, minor: blue lines). Each key is flanked by its relative (e.g., C major - a minor) and parallel (e.g., C major - c minor) minor key. The matching of the opposite edges of the unfolded map will result in the toroidal representation.

In a similar vein, Bharucha and Krumhansl (1983) discovered that perceivers implicitly organised *chords within harmonic progressions* in terms of the hierarchy of stability described by music theory (see above). That means, chords at a lower level of the hierarchy, i.e., harmonically distant from the tonal root, were perceived as tense and demanded resolution to more stable chords of the system (see also Bigand & Parncutt, 1999; Steinbeis, Koelsch, & Sloboda, 2006).

Taken together, these findings demonstrate the existence of an internal representation of tonal structure that matches very well with a number of music-theoretical principals. In particular, the perception of a sequence of tones or chords seems to involve the extraction of the more stable events, that serve as anchor points for less stable events (cf. Bharucha & Krumhansl, 1983; Krumhansl, 1979). Most importantly, these representations were found in musicians and non-musicians alike, suggesting that the ability to process music according to music-syntactic regularities does not derive from intensive musical training (cf. Bigand & Poulin-Charronnat, 2006; Koelsch et al., 2000). On the contrary, as demonstrated by computational modelling, these (implicit) representations are most likely acquired through mere exposure to the Western tonal idiom during every day listening (e.g., Tillmann, Bharucha, & Bigand, 2000).

Musical expectancies and harmonic priming. The implicit knowledge on music-structural principles enables the listener to form expectations on upcoming tones or chords, e.g., to anticipate when unstable chords should resolve to more stable harmonies. The generation of such expectancies has been first described by a study on *harmonic priming*. In this pioneering experiment, Bharucha and Stoeckig (1986) showed that a harmonic context can facilitate (i.e., prime) the processing of a harmonically related event, as reflected by faster and more accurate responses when a chord is closely related to the previous context than when it is distantly related (in terms of distance on the circle of fifths). This result was taken as evidence that a prime context activates the listener's knowledge of Western tonal hierarchies and generates expectancies for related chords to follow (see also Schmuckler, 1989).

The paradigm of harmonic priming (i.e., the speeded decision about a chord following a harmonic context to which it is either closely or distantly related) has become an institution in the research on the cognitive representations of musical structure. The initial findings (Bharucha & Stoeckig, 1986) have been repeatedly replicated and extended by later studies, showing

- that the priming effect relies rather on cognitive than on sensory mechanisms (e.g., Bharucha & Stoeckig, 1987; Bigand, Poulin, Tillmann, Madurell, & D'Adamo, 2003).
- that the expectations are built on the global rather than local context (e.g., Bigand & Pineau, 1997; Bigand & Parncutt, 1999).
- that while related chords benefit from the prime context, less related chords create processing costs (e.g., Tillmann, Janata, Birk, & Bharucha, 2003).

- that harmonic priming acts independently of musical training (e.g., Bigand, 2003).

Furthermore, harmonic priming has been shown to influence the perception of linguistic events, like phonemes (Bigand, Tillmann, Poulin, D'Adamo, & Madurell, 2001) or the meaning of words (Poulin-Charronnat, Bigand, Madurell, & Peereman, 2005). From these combined studies, it may be concluded that musical structures are processed in an irrepres-ible way by automatic processes that most presumably occur as fast as those in the language domain.

ERP correlates of music-syntactic processing. The extraordinary speed with which these processes must necessarily act to decode the rapidly evolving and decaying musical stream, calls for the application of methods that are able to temporally resolve the underlying mechanisms. This requirement has led to a number of EEG studies on this issue. Like the studies on harmonic priming, these experiments most often presented sequences of chords or tones that established a key and were followed by an event that was harmonically either closely or distantly related to the previous context.³ Most often, event-related potentials (ERPs; see Chapter 4) were computed, separately for both types of sequence endings, and compared with each other.

In this vein, the first ERP studies on the processing of melodic and harmonic structure of (previously unheard) music⁴ mainly reported late effects, described as P300 (Besson, Faita, Peretz, Bonnel, & Requin, 1998; Janata, 1995; Regnault, Bigand, & Besson, 2001; see also Beisteiner et al., 1999 for a magnetic P300 observed in an MEG study on harmonic processing), P600 (Patel, Gibson, Ratner, Besson, & Holcomb, 1998), or “late positive component” (LPC; Besson & Faïta, 1995). In the model of Koelsch and Siebel (2005), these ERPs are mainly associated with processes of structural repair and reanalysis once an unexpected chord/tone has been detected (see *Structural reanalysis and repair* in Figure 2.1).

According to Koelsch and Siebel (2005), the detection of an irregular chord, i.e., the viola-tion of the listener’s expectations that are based on the extraction of the tonal centre and the computation of relations between a chord and its context (see *Structure building* in Figure 2.1), is rather reflected by negative ERPs emerging in an earlier time window between 180

³Empirical evidence for “music-syntactic processing” has so far mainly been provided for harmonic and melodic structure (other structural aspects of music comprise rhythmic, metric and timbral organisation).

⁴A number of studies investigated expectancy violations in music by presenting familiar melodies containing either incongruous continuations or unexpected completions (e.g., Besson & Macar, 1987; Paller, McCarthy, & Wood, 1992; Verleger, 1990). Note, that familiar material is not suited to investigate expectancies generated by the compositional principles underlying Western tonal music since these are confounded by expectations based on the learned pitch patterns of the melody. Anyway, the main aim of these studies was not to investigate structure building but semantic processing in music, an issue of intense debate as discussed in Section 2.1.3.

and 400 ms. This assumption finds partial support in the studies cited above. For instance, the data of Besson and Faïta (1995) show an early negativity around 200 ms for incongruous melody endings, however, its functional significance has not been specified by the authors. Likewise, (Patel, Gibson, et al., 1998) reported a right antero-temporal negativity (labelled RATN) around 350 ms after onset of a harmonically inappropriate chord which was thought to possibly reflect the application of music-specific working memory resources or syntactic rules. Apart from this early evidence, a number of more recent ERP studies has demonstrated that violations of harmonic regularities reliably elicit a negativity with a tendential right frontal scalp distribution peaking around 200 ms after onset of the irregular chord (e.g., Koelsch et al., 2000, 2007; Leino, Brattico, Tervaniemi, & Vuust, 2007; Loui, Grent-'t-Jong, Torpey, & Woldorff, 2005; Miranda & Ullman, 2007). This ERP component was labelled ERAN - Early Right Anterior Negativity (e.g., Koelsch et al., 2000; Koelsch, in press).

The ERAN⁵ reflects the computation of the structural relation between an incoming chord and a preceding harmonic context. Notably, this operation appears to be fairly automatic, since the occurrence of the ERAN does not depend on whether the irregular chords are task relevant, or on whether listeners are informed about the irregular chords. The ERAN is even elicited when the participants read a book, play a video game, or track a simultaneously presented speech signal (e.g., Koelsch, Schröger, & Gunter, 2002; Loui et al., 2005; Maidhof & Koelsch, in press), rendering it a valuable tool in the study of young children or patients with brain lesions.

A series of studies showed that the ERAN is shaped by musical training, leading to a considerable increase of its amplitude in adults (e.g., Koelsch, Schmidt, & Kansok, 2002; Koelsch et al., 2007; Koelsch & Sammler, 2008), as well as in children (Jentschke et al., 2005). This finding largely coincides with earlier studies reporting a stronger P300 (Regnault et al., 2001) or LPC (Besson & Faïta, 1995) in trained musicians than in non-musicians. Like-

⁵Due to its apparent similarity to the Mismatch Negativity (MMN), the ERAN has been sometimes denoted as *music-syntactic MMN* (e.g., Koelsch, Maess, Grossmann, & Friederici, 2003; Koelsch, Gunter, Schröger, & Friederici, 2003; Koelsch, Grossmann, et al., 2003). However, its occurrence regardless of deviance probability (unlike the MMN) as well as its strong dependency on a previously established context (see Koelsch, Gunter, et al., 2001) argue in favour of at least partially different cognitive processes underlying the ERAN and the MMN. In a recent review, Koelsch (in press) attributed the major difference of MMN and ERAN to the type of internal representation they are based on: While the MMN is the detection of a mismatch between an incoming event and a representation that is extracted on-line from the acoustic environment (see auditory sensory memory in Section 2.1.1), the ERAN reflects the incongruence between a perceived chord and the implicit knowledge of harmonic principles existing in a long-term memory format. Apart from that, a few authors used labels like *early anterior negativity* (Loui et al., 2005) or *early negativity* (Steinbeis et al., 2006) to describe ERPs in the ERAN time window elicited by harmonic violations. These variants are due to the broader and sometimes rather bilateral than right lateralised topography of the ERAN (see also Leino et al., 2007; Miranda & Ullman, 2007).

wise, the ERAN can also be influenced by short-term exposure, as revealed by a study showing a progressive decrease (but no complete decay) of the ERAN amplitude in the course of two hours of listening to regular and irregular harmonic progressions (Koelsch & Jentschke, 2008).

Neural correlates of music-syntactic processing. The discovery of the ERAN as robust electrophysiological marker of music-syntactic processing raises another pertinent question, namely, which brain areas generate this effect, and more generally, which cerebral structures support music-syntactic analysis? This issue has been addressed by source localisations applied to EEG and MEG data revealing a major contribution of the bilateral inferior frontal gyrus (IFG; Koelsch, Maess, Gunter, & Friederici, 2001; Maess, Koelsch, Gunter, & Friederici, 2001), as well as a possible involvement of the bilateral anterior superior temporal gyrus (aSTG; Koelsch & Friederici, 2003). Most intriguingly, these brain areas have been previously identified as major components of the neural network processing syntax in language (see Chapter 1). Thus, the Early Left Anterior Negativity (ELAN) reflecting structure building in language (see Chapter 1) is equally generated within the inferior frontal lobe and the aSTG (Friederici, Wang, et al., 2000), and shares, furthermore, a number of characteristics with the ERAN, e.g., latency, polarity, and frontal scalp distribution. These findings gave rise to the hypothesis of a partial overlap of the neural networks supporting structure building in music and language which will be investigated in more detail in the present dissertation (see Chapter 3).

Complementary to EEG/MEG source localisations, functional neuroimaging studies provide evidence for a widespread neural network of musical structure building within the temporal, frontal, and parietal lobes. At the level of melodic processing, R. D. Patterson et al. (2002) demonstrated that the anterior STG of the right hemisphere is specifically sensitive to tonal music built according to syntactic regularities as compared to a random organisation of single tones. By presenting a melody that systematically modulated through all major and minor keys, Janata, Birk, et al. (2002) identified an area within the rostromedial prefrontal cortex that is particularly involved in the tracking of key changes. In a study on violations of tonality and/or rhythm (Krumhansl, 2004), bilateral activations of the STG (though with right hemisphere preponderance) were observed. In a related vein, studies on the processing of harmonic (ir)regularities corroboratingly reported activations within the left and right IFG, ventral premotor cortex, and the insula (with right hemisphere preponderance), the anterior/posterior STG/STS, the MTG, as well as the left or right supra-marginal gyrus (SMG; Koelsch, Schröger, & Gunter, 2002; Koelsch & Siebel, 2005; Till-

mann, Janata, & Bharucha, 2003; Tillmann, Koelsch, et al., 2006) supporting the notion of an extensive fronto-temporo-parietal network involved in music-syntactic analysis.

2.1.3 Processing Emotion and Meaning in Music

Emotion. It has been proposed that many musical emotions rely on fulfilled or suspended musical expectations (L. B. Meyer, 1956), e.g., related to structural aspects of music as described above. More precisely, unexpected chords, i.e., chords that are harmonically distant from their tonal root create a feeling of tension and suspense, while the resolution of unstable to stable events is perceived as relaxing (Bigand & Parncutt, 1999; Bigand, Parncutt, & Lerdahl, 1996; Lerdahl & Jackendoff, 1983; Steinbeis et al., 2006).

The model of Koelsch and Siebel (2005) incorporates these findings by highlighting the link between structure building processes and emotion (see Figure 2.1). However, the authors state that emotional processing can take place during all stages of music perception, even already at the level of the thalamus which is directly linked to major components of the emotion circuit (e.g., the amygdala and the medial orbitofrontal cortex). Similarly, basic auditory features like roughness or consonance and dissonance are able to induce emotions (e.g., Blood et al., 1999; Koelsch et al., 2006; Sammler, Grigutsch, Fritz, & Koelsch, 2007).

Meaning. Although music is regarded as means of communication, opinions as well as empirical evidence on possible “semantics of music” diverge. Early ERP studies concluded that music is unable to transfer meaning in the same way as language (e.g., Besson & Macar, 1987; Besson et al., 1998; Paller et al., 1992; Verleger, 1990). This assumption was mainly based on the failure to elicit an N400 - a classical marker of semantic processing in language (Kutas & Hillyard, 1980a, 1984, see Chapter 1) - by presenting familiar melodies that contained distorted notes thought to be equivalent to semantic violations in sentences. However, more recent priming studies have challenged this view, for example, by showing that a word that semantically mismatches with a previous musical context elicits an N400 that is statistically indistinguishable from the N400 elicited by mismatch words after linguistic prime contexts (Koelsch, Kasper, et al., 2004). These data demonstrate that music can activate representations of meaningful concepts and transfer meaning to a considerably larger degree than previously believed.

Another line of evidence for the processing of meaning in music comes from studies investigating the N5, an ERP with bilateral frontal scalp distribution peaking around 500 ms after onset of an irregular chord, thus, mostly following the ERAN (e.g., Koelsch et al., 2000; Koelsch, 2005). This effect was taken to reflect the integration of the unexpected chord into

the previously established context (e.g., Koelsch et al., 2000; Poulin-Charronnat, Bigand, & Koelsch, 2006). Notably, the N5 is sensitive to the build-up of a harmonic context (Koelsch et al., 2000, Experiment 1) very much like the N400 is sensitive to the establishment of a semantic context during sentence comprehension (Van Petten & Kutas, 1990). Based on this observation, it has been speculated that the N5 may be associated with the “semantic” analysis of tension-resolution patterns in music (e.g., Koelsch, 2005). This idea found strong support in a recent ERP study (Steinbeis & Koelsch, 2008b) showing a competition between N400 and N5 when semantically inappropriate words and syntactically irregular chords were presented simultaneously. Most importantly, these results suggest a strong link between musical structure and meaning, and propose shared neural resources of language and music processing also in the field of semantics.

To summarise, the processing of music is not a monolithic phenomenon, but is composed of a number of intricately related sub-processes, from the basic acoustic analysis through structural, emotional, and semantic analysis, to the activation of the motor system and immune system (Koelsch & Siebel, 2005). Most intriguingly, at several stages music perception parallels very much the processing of language. Particularly musical and linguistic syntax as well as semantics may rely on similar cognitive operations which may be supported by partly overlapping cerebral structures. The present dissertation will particularly investigate the hypothesis of an anatomical overlap of syntax processing in music and language (see Chapter 3). Candidate structures appear to be primarily the inferior frontal gyrus (IFG) as well as the temporal lobe (TL). In the second part of this chapter, the role of these two brain areas in music perception will be shortly reviewed.

2.2 The Neuroanatomy of Music Processing

2.2.1 The Role of the Temporal Lobe (TL)

Lesions of the temporal lobes (TL) lead to a variety of amusic deficits with respect to, e.g., the processing of melodic and temporal aspects of music (e.g., intervals and contour, or rhythm and metre; Ayotte, Peretz, Rousseau, Bard, & Bojanowski, 2000; Liégeois-Chauvel et al., 1998; Peretz, 1990; Schuppert et al., 2000), the perception of timbre (dystimbria; Griffiths et al., 2007; Kohlmetz, Müller, Nager, Münte, & Altenmüller, 2003; Mazzucchi, Marchini, Budai, & Parma, 1982; Samson & Zatorre, 1994; Samson, Zatorre, & Ramsay, 2002), and the recognition and recall of familiar and unfamiliar melodies (e.g., Peretz et al., 1994; Samson & Zatorre, 1991), demonstrating the numerous facets of temporal lobe

functions and its necessity for intact music perception (see Stewart, Kriegstein, Warren, & Griffiths, 2006, for a review).

The temporal lobe is the seat of the auditory cortex that is involved in the analysis of any auditory signal. The different subdivisions of the auditory cortex⁶ are thought to subservise music perception according to a *hierarchy of melodic processing* (e.g., Griffiths et al., 1998; R. D. Patterson et al., 2002). While the primary and secondary auditory cortices are mainly involved in the processing of spectrotemporal features and pitch⁷ of *individual sounds* (e.g., Griffiths et al., 1998; R. D. Patterson et al., 2002; Zatorre, 1988), higher-level processes like the analysis of simple *pitch sequences* involve more distributed regions anterior and posterior of Heschl's gyrus (HG; e.g., Griffiths et al., 1998; Krumhansl, 2004; R. D. Patterson et al., 2002), as well as beyond the temporal lobe (see below). Within this framework, Griffiths (2001) proposed so-called "pitch sequence detection areas" located within the anterior and posterior STG.

The posterior STG has been frequently related to music processing in various ways. First, functional neuroimaging studies corroboratingly reported posterior STG activations when contrasting the passive listening to melodies vs. noise (e.g., Zatorre et al., 1994), or when comparing the processing of harmonically distantly and closely related musical events (e.g., Koelsch, Gunter, et al., 2002; Koelsch, Fritz, et al., 2005; Tillmann, Koelsch, et al., 2006). Second, the function of the planum temporale (PT) within the posterior STG may be shaped by musicianship. For example, Ohnishi et al. (2001) found stronger activations within bilateral PT in musicians than in non-musicians during listening to music. Furthermore, the degree of activation in the left PT correlated with the absolute pitch ability of the musicians (for a corroborating anatomical asymmetry see also Schlaug, Jäncke, Huang, & Steinmetz, 1995). Conversely, patients with unilateral cortectomy of the posterior STG (sparing HG) showed pronounced deficits in the processing of sequential pitch variations, demonstrating the critical role of this region in melody perception (e.g., Liégeois-Chauvel et al., 1998).

⁶The auditory cortex is not a unitary structure as demonstrated, for instance, by cyto-, myelo-, and receptorarchitectonic mappings in macaques (Hackett, Preuss, & Kaas, 2001; Kaas & Hackett, 2000) and humans (Hackett et al., 2001; Morosan et al., 2001). In macaques, three main regions with several subdivisions can be distinguished that are hierarchically interconnected (Kaas & Hackett, 2000): A central *core* (Hackett et al., 2001), a surrounding *belt*, and a lateral *parabelt*. In the human literature, the auditory cortex is frequently subdivided according to functional aspects: The *primary auditory cortex* located within the medial part of Heschl's gyrus (HG; Liégeois-Chauvel et al., 1991; Morosan et al., 2001), the *secondary auditory cortex* located within the lateral portion of HG, and the *auditory association areas* that extend more laterally, posteriorly and anteriorly into the STS, planum temporale (PT) and planum polare (PP) of the superior temporal gyrus (STG).

⁷Note that the term "pitch" denotes a psychological percept rather than the physical attribute of the sound. There is growing evidence that the PAC may be mainly involved in the processing of general spectrotemporal features of the sound, whereas the SAC acts as a "pitch centre" that encodes the percept as opposed to the stimulus properties (e.g., Gutschalk et al., 2002; R. D. Patterson et al., 2002).

However, the posterior STG and particularly the planum temporale (PT) is not specific to music processing but has been associated with various other functions, such as the extraction of pitch height (as opposed to pitch chroma; J. D. Warren et al., 2003), the perception of timbre (Griffiths et al., 2007; Menon et al., 2002; J. D. Warren et al., 2005) and tonal modulations (e.g., Binder, Frost, Hammeke, Rao, & Cox, 1996; Binder et al., 2000; Jäncke, Wüstenberg, Scheich, & Heinze, 2002), the spatial processing of sound (e.g., J. D. Warren & Griffiths, 2003; Zatorre, Bouffard, Ahad, & Belin, 2002), or the processing of speech sounds (e.g., Binder et al., 1996; Hickok, Buchsbaum, Humphries, & Muftuler, 2003; Jäncke et al., 2002, note that the posterior STG in the left hemisphere overlaps with Wernicke's area).

On a more abstract level, Griffiths and Warren (2002) proposed that the PT acts as a “computational hub” that is sensitive to all these kinds of information in order to segregate auditory objects within the highly complex acoustic world. Amongst others, these processes rely on the detection of coherent streams within the auditory scene by grouping elements according to Gestalt principles like (spatial or spectral) proximity, and (temporal or spectral) continuity (e.g., Bregman, 1990; Carlyon, 2004; Griffiths & Warren, 2004). Notably, very similar grouping mechanisms are crucial for music perception, when organising distinct pitches into global representations of musical phrases (see section 2.1.1 and Koelsch & Siebel, 2005).

Apart from the posterior STG, the lesion literature highlights the crucial role of the anterior temporal lobe (ATL) in music processing (e.g., Ayotte et al., 2000; Peretz, 1990; Liégeois-Chauvel et al., 1998; Schuppert et al., 2000). For example, patients with unilateral right ATL excisions (Samson & Zatorre, 1988; Zatorre, 1985) or bilateral ATL damage (Satoh et al., 2005) showed severe deficits when asked to discriminate unfamiliar melodies that differed in one tone. Notably, this impairment was observed in the absence of lesions in HG, demonstrating the crucial role of the ATL in melody processing. Further studies highlighted the importance of the right ATL for tonal working memory. That means, when asked to compare two pitches that were separated by a series of interfering tones, patients with right ATL (but not those with left ATL) excisions performed significantly lower than normal controls (Zatorre & Samson, 1991; see also Zatorre & Halpern, 1993 for similar deficits when patients were asked to compare imagined pitches).⁸ Note that both findings are closely related: Since music unfolds over time, an on-line sensory memory system is evidently

⁸Further experiments consistently observed deficits in the recognition of familiar (e.g., Peretz et al., 1994; Satoh et al., 2005) or novel melodies (e.g., Samson & Zatorre, 1991, 1992; Zatorre, 1985) in patients with either right or left anterior temporal lesions, which was taken to reflect the importance of the bilateral ATL for musical long-term memory. It remains, however, to be clarified whether these deficits were really mnemonic in nature or emerged from a more basic impairment of melody perception. Indeed, in all of these studies, pitch-pattern perception was either deficient (Peretz et al., 1994; Satoh et al., 2005) or not tested (Samson & Zatorre, 1991, 1992; Zatorre, 1985).

necessary to compute the relationships between successive items in order to achieve a stable and coherent internal representation of the melody (see also section 2.1.1).

The functional neuroimaging literature is broadly congruent with the involvement of the ATL in melody processing, even though its exact role still remains to be clarified. For example, the anterior STG consistently showed increased levels of activation as a function of the harmonic distance or relatedness of a tone or chord relative to a previous musical context (e.g., Koelsch, Gunter, et al., 2002; Koelsch, Fritz, et al., 2005; Krumhansl, 2004; Tillmann, Koelsch, et al., 2006), leading to the assumption that the anterior STG may be part of the neural network involved in musical syntax processing (Koelsch, 2006). Another study reported activations in the anterior STG when contrasting the perception of melodic or random pitch sequences against fixed pitch sequences (R. D. Patterson et al., 2002; see also Krumhansl, 2004). However, no difference was found between listening to random pitch patterns (i.e., without syntax) or pitch sequences arranged according to music-theoretical principles (i.e., with syntax), suggesting that the anterior STG may be more generally involved in the processing of pitch patterns, and is possibly less dependent on music-syntactic functions than proposed by experiments using chord sequences paradigms. Future studies are clearly necessary to elucidate this issue.

In sum, the auditory cortices and adjacent association areas in the superior temporal lobes (possibly with a degree of right lateralisation) are crucial for the analysis of pitch and pitch patterns that form the basic modules of music. With the aim to build a coherent representation of a melody, the posterior STG (particularly the PT) may be involved in the grouping of single elements according to Gestalt principles, whereas the anterior STG may provide resources for the short-term retention and computation of relations between successive items of a musical stream. It remains to be specified, in how far these computations rely on perceptual (R. D. Patterson et al., 2002) or music-syntactic principles (Koelsch, Gunter, et al., 2002; Koelsch, Fritz, et al., 2005; Krumhansl, 2004; Tillmann, Koelsch, et al., 2006), and to what extent they may be shaped by the densely interconnected frontal lobes (see next section). Finally, it is important to mention, that these combined processing steps are also required for the analysis of other sounds, such as speech, leading to a considerable similarity of brain activations in temporal lobe areas evoked by speech and music (e.g., Price, Thierry, & Griffiths, 2005).

2.2.2 The Role of the Inferior Frontal Gyrus (IFG)

Another brain area that appears to be crucially involved in music perception is the inferior frontal gyrus (IFG), often along with the ventro-lateral premotor cortex (vlPMC). Mostly

both hemispheres are involved, though often with a degree of right lateralisation. This cerebral region has been found to be activated consistently across a number of music studies investigating, e.g., the processing of music-syntactic relations in melodies (e.g., Krumhansl, 2004; Parsons, 2001; Platel et al., 1997; Zatorre et al., 1994) and chord progressions (e.g., Koelsch, Gunter, et al., 2002; Koelsch, Fritz, et al., 2005; Levitin & Menon, 2003; Maess et al., 2001; Parsons, 2001; Tillmann, Janata, & Bharucha, 2003; Tillmann, Koelsch, et al., 2006), the perception of rhythmic patterns (e.g., Platel et al., 1997; Parsons, 2001; Schubotz, Friederici, & Cramon, 2000), the mental imagery of songs (e.g., Halpern & Zatorre, 1999; Kraemer, Macrae, Green, & Kelley, 2005), and the tracking of one voice in a multi-part composition (Janata, Tillmann, & Bharucha, 2002; Satoh et al., 2001).

On a more abstract level, it has been proposed that the inferior frontal lobe (IFL), particularly the pars opercularis of the IFG (BA 44) and the adjacent vIPMC, is implicated in the processing of musical *structure*, i.e., the analysis of sequential auditory information that is organised according to melodic, harmonic, and rhythmic principles (see, e.g., Koelsch, 2006; Levitin & Menon, 2003). That means, when listening to music, the IFL is thought to identify the structural (rather than perceptual; see section 2.2.1) relationships among the items of the musical sequence (e.g., tones, chords, or beats) and to *integrate* this information according to the implicit knowledge of the listener about music structural principles. Based on these computations, the IFL is further involved in a fast short-term *anticipation* of upcoming events (see section 2.1.2). A mismatch between these predictions and a new element, e.g., a chord that is harmonically distantly related to the previous context, leads to enhanced processing within the IFL (as indicated by stronger activations in fMRI or larger amplitudes of the ERAN in EEG), reflecting the greater difficulty to integrate this element into the established representation.

An alternative, though related, framework of IFG functions concerns its special role in musical working memory. This idea was initially motivated by a study with right frontal lobectomy patients who showed severe deficits in a pitch comparison task as soon as the two target tones were separated by interfering tones (Zatorre & Samson, 1991, similar deficits were found after right anterior temporal lobectomy; see above). Corroboratingly, PET (Zatorre et al., 1994; Zatorre, 2001) and fMRI studies (e.g., Gaab, Gaser, Zaehle, Jäncke, & Schlaug, 2003; Hickok et al., 2003; Koelsch et al., in press; Schulze, 2006) reported activations in inferior frontal and ventro-lateral premotor areas during pitch memory tasks.⁹

Note that this view is compatible with the role of the IFG in structure building, a function that requires the continuous update of the actual mental representation of the melody, which

⁹It has been proposed that these activations reflect subvocal rehearsal processes that may exert a similar function as the “phonological loop” in verbal working memory (Baddeley, 2003; Paulesu et al., 1993).

necessarily involves the storing of information and its permanent manipulation, triggering classical working memory processes. Therefore, the function of the IFG in music perception may be summarised as on-line recognition, integration, and prediction of structured sequences that unfold over time.

Most intriguingly, this role likewise applies to the perception of sequential stimuli other than music, such as language. As outlined in Chapter 1, the IFG is indeed substantially involved in the processing of syntax in language (e.g., Bornkessel et al., 2005; Caplan et al., 1998, 1999; Fiebach et al., 2005; Friederici, Bahlmann, et al., 2006) pointing to a more domain-general function of this brain area in the processing of structured sequences (see Chapter 3 for further details).

2.3 Summary

The present chapter demonstrated that music perception, like language comprehension, is no monolithic entity but involves a cascade of intricately related serial and parallel processing steps. The model of Koelsch and Siebel (2005) was taken as a guideline to briefly summarise our current knowledge on how basic acoustic features of single tones are integrated bit by bit to finally form a meaningful and emotive percept in the listener's mind. Special emphasis was placed on the mechanisms of harmonic structure building as an interface between syntax, emotion and meaning in music.

The second part of the chapter was devoted to two essential brain areas of the distributed music perception network - the anterior temporal and the inferior frontal lobe. Keeping possible differences between both structures in mind, their particular role in the processing of rule-based auditory information was highlighted. In this context, it became apparent how much the mechanisms of music perception resemble those involved during language comprehension, leading to the pertinent question to what extent the processing of music and language may overlap within the ATL and the IFG. This question will be addressed in the following chapter.

Chapter 3

Music and Language

The differences and similarities of music and language as cognitive domains have long interested scholars from philosophy (e.g., Rousseau, 1781/1998), bio- and ethnomusicology (see S. Brown, 2000; Darwin, 1871/1989; Fitch, 2006), or cognitive neuroscience (e.g., S. Brown et al., 2006; von Frankl-Hochwart, 1891; Koelsch, 2005; Patel, 2003a). For example, a longstanding debate in neuropsychology is centred on the domain-specificity or domain-generalness of music and language processing (e.g., von Frankl-Hochwart, 1891; Marin & Perry, 1999). A number of case studies in this field reported on patients with *aphasia without amusia* or, conversely, with *amusia without aphasia* (see Marin & Perry, 1999; Peretz & Coltheart, 2003, for reviews), taken as evidence for a double dissociation, i.e., only little overlap between music and language processing (see also Chapter 5). This conclusion might, however, be premature for two reasons: First, cases of aphasia without amusia are most often exceptional individuals like composers or conductors (e.g., Amaducci, Grassi, & Boller, 2002; Luria, Tsvetkova, & Futer, 1965), calling into question the generalisability of these results, particularly in light of the evidence for substantial functional and anatomical differences between musicians and non-musicians (see Münte, Altenmüller, & Jäncke, 2002, for a review).

Second, as presented in Chapters 1 and 2, both music and language perception are not unitary mental faculties, but represent complex sets of interacting cognitive processes. The prevailing case studies, however, make no claims with respect to these subcomponents, and most often, the global diagnosis of *aphasia without amusia* or vice versa was drawn without testing all of these processes. In fact, regarding the question of domain-specificity separately for the different processing components, music and language appear to show strong parallels at the level of syntax and intonation, but significant divergences at the level of meaning (i.e., semantics) and the discretisation of pitch and time (S. Brown et al., 2006;

Fitch, 2006). In the following sections, the current debates on these differences will be briefly introduced, before turning to major similarities of the two domains with a special focus on syntax processing.

3.1 Differences Between Music and Language

For the listener, music and language are very different. No one would ever confuse a Mozart sonata with a scientific talk. But what makes the difference? Two aspects that considerably diverge between both domains will be exemplarily presented in turn: The prevalence of discrete pitches and isochrony in music and the semanticity of language.

3.1.1 Discrete Pitches and Isochrony

Music refers to a set of discrete pitch categories that are organised in scales¹ and tend to be presented (more or less) isochronically, i.e., with a regular periodic pulse (the beat). These characteristics may be regarded as two of the core features of music. Of course speech also involves pitch modulations as a part of speech prosody (see section 3.2.1), however, these pitches are not related to scales but vary rather continuously. Similarly, there are certainly several styles of speech that are produced in isochrony, e.g., poetry, but these make up only a fraction of natural speech that exhibits most often a more variable accent structure. Most intriguingly, discrete time and pitch make music acoustically more predictable than language, thus, providing the fundament for motor synchronisation within groups of individuals, for example, a couple of dancers or musical ensembles.

3.1.2 Meaning

Meaning is a key feature of language, most often regarded as *the* core difference to music. It is widely agreed that language, can convey propositional meaning, i.e., that each speech symbol refers to the representation of an object. On the other hand, musical elements do not equally map onto discrete semantic meanings (consider for instance C♯ vs. “table”). This does, however, not imply that music has no meaning. Music theorists posit that music employs rather different mechanisms than language to communicate meaning, either via extramusical associations (Koelsch, Kasper, et al., 2004), as for example raised by sound

¹To be more precise, pitch categories are not unique to music. Over half of the world’s languages are “tone languages”, i.e., in which the pitch of a syllable can change its meaning. The crucial difference between pitch categories of tone languages and the discrete pitches of music is, however, that the latter are arranged in scales, whereas the former vary continuously.

patterns that resemble features of objects (like narrow intervals create the impression of narrowness), or the suggestion of a particular mood (e.g., via major or minor mode), or by intrinsic structural properties of music like tension-resolution patterns (L. B. Meyer, 1956; Steinbeis & Koelsch, 2008b, see also Chapter 2.1.3).

3.2 Similarities of Music and Language

From another perspective, music and language may not seem so different. Both are rule-based systems composed of a finite set of discrete sounds (e.g., phonemes in language vs. pitches in music) that are organised into higher-order structures (sentences vs. musical phrases) according to specific rules. The following sections will present two of these structural similarities between music and language: The grouping of elements into phrases, as well as the arrangement of words and chords within sequences according to syntactic principles. Beforehand, the perhaps most obvious similarity between music and language will be described: Melodic contour and speech intonation, sometimes also referred to as “sentence melody”.

3.2.1 Melodic Contour and Speech Intonation

Pitch manipulations are both musically and linguistically relevant. Melodic contour, i.e., the ups and downs in pitch direction of a melody without regard of exact interval size, is a salient feature of music that expresses emotions (Juslin & Laukka, 2003) and determines the internal melodic structure, e.g., by characterising themes, or by marking phrases and boundaries between structural units (see section 3.2.2). In speech, the closest analog to melodic contour is the trajectory of the fundamental frequency (F_0) over time, called *intonation* that expresses emotional (e.g., Kotz, Meyer, et al., 2003) and linguistic functions of speech prosody (e.g., Eckstein & Friederici, 2006; Friederici et al., 2007; M. Meyer et al., 2002).² Although intonation does not depend on a fixed-interval scale as melodic contour, it contributes to marking the boundaries of structural units, as in music (see section 3.2.2). Furthermore, intonation helps distinguishing pragmatic categories of utterances (e.g., statement, question, command), and signalling focus (Patel, Peretz, Tramo, & Labreque, 1998).

Neuropsychological research provides evidence that melodic contour and speech intonation draw on shared cognitive and neural resources. For example, Patel, Peretz, et al. (1998)

²Speech prosody is “the organisational structure of speech” (M. Meyer et al., 2002, p. 74). that is coded by phonetic attributes like intonation, duration, and amplitude.

reported the case of a patient with bilateral temporal and right frontal lesions who exhibited parallel deficits in processing contour information in melodies and the use of intonational cues to decode the focus of a sentence (e.g., “*Sing* now, please.” vs. “*Sing now*, please.”), or to distinguish statements and questions. Further support comes from recent EEG studies showing that musical training can enhance pitch perception in linguistic material (e.g., Besson, Schön, Moreno, Santos, & Magne, 2007; Magne, Schön, & Besson, 2006; Moreno & Besson, 2006; Schön, Magne, & Besson, 2004). Finally, prosodic information in language is processed predominantly in right superior temporal regions (e.g., Friederici & Alter, 2004; M. Meyer et al., 2002, 2004), that means, in brain areas that have been shown to play a functional role in the perception of melodic contour (e.g., Ayotte et al., 2000; Liégeois-Chauvel et al., 1998; Peretz, 1990; Schuppert et al., 2000). Taken together, there is ample evidence to assume a similar processing of melodic contour and intonation in speech, hence, supporting the notion of a partial functional overlap between music and language perception.

3.2.2 Phrasing

Neither language nor music are uniform auditory streams, rather they are structured into phrases to facilitate the processing of the complex sequential input and to reduce working memory demands. In both domains, phrases most often group syntactic units helping the parser to decode the linguistic or musical stream and to resolve ambiguity. In language, this becomes particularly clear when regarding sentences like “The queen said the knight is singing.” Intonational phrasing helps determining who is singing, the queen or the knight. Music is intrinsically ambiguous, as each note or chord can act in different functions depending on the key it belongs to (see Chapter 2.1.2). Beginnings and endings of phrases are typically marked by stable harmonies of the actual key, helping to extract the tonal centre and to disambiguate the functions of tones and chords, thus, crucially guiding how a musical piece is perceived.

As already mentioned in section 3.2.1, phrase boundaries in both domains are marked by very similar prosodic cues such as intonational contour, short pauses, or lengthening of the pre-final syllable or note (language: Steinhauer, Alter, & Friederici, 1999; music: Knösche et al., 2005; Neuhaus, Knösche, & Friederici, 2006). Neuropsychological research indicates that the perception of these phrase boundaries in language and music involves similar cognitive mechanisms and neural resources. For example, the amusic patient described by Patel, Peretz, et al. (1998) exhibited not only marked deficits when asked to discriminate syntactically ambiguous sentences that required the interpretation of intona-

tional phrase boundaries (see example above), but a parallel impairment was also observed in the discrimination of delexicalised melodic-rhythmic counterparts of these sentences (see also Hoyte, Brownell, Vesely, & Wingfield, 2006). Related evidence comes from ERP studies showing that the perception of phrase boundaries in garden-path sentences (Steinhauer et al., 1999) as well as in musical pieces (Knösche et al., 2005; Neuhaus et al., 2006) elicits very similar positive-going waveforms with centroparietal scalp distribution, termed *closure positive shift* (CPS). These combined results suggest that phrasing in both domains may rely on similar mechanisms and neural structures, providing one further piece of evidence that music and language may be more similar than initially believed.

3.2.3 Rule-Based Sequencing

Both music and language consist of a limited number of discrete elements (e.g., notes vs. phonemes) that are combined according to specific rules to generate an unlimited number of hierarchically structured signals (e.g., musical phrases vs. sentences). These sets of rules may be denoted as *syntax* (e.g., Koelsch, 2005; Lerdahl & Jackendoff, 1983; Patel, 2003a).

Listeners show implicit knowledge of these syntactic principles, e.g., when detecting agreement errors in previously unheard sentences (e.g., “Daddy *love* his car.”), or “sour” notes in music. Notably, in both domains, this complex structural knowledge is acquired in a seemingly effortless way during early childhood, by mere exposure to the idiom of the respective culture (e.g., Kuhl, 2004; McMullen & Saffran, 2004; Tillmann et al., 2000). Furthermore, it has been proposed that similar (implicit) learning mechanisms like statistical or rule-based learning may operate in the acquisition of both linguistic and musical syntax (McMullen & Saffran, 2004).

Certainly, the details of the syntactic regularities as well as the nature of the single combinatorial items may considerably differ between music and language. For example, while the perception of phonemes very much depends on the ability to decode temporal differences in the order of tens of milliseconds, the perception of tones relies more on the fine-grained analysis of pitch, thought to determine basic processing differences between both domains already at the level of the primary auditory cortices (Belin et al., 1998; Jamison et al., 2006; Zatorre, Belin, & Penhune, 2002). Furthermore, as opposed to language, the rules of musical syntax apply most often to two dimensions: horizontal (melody) and vertical (harmony). In general, music-syntactic rules seem to be far more flexible and open for ambiguity than the rules of linguistic grammar. While the arrangement of words follows quite strict regularities in order to convey a clear semantic message, a violation of music-syntactic conventions is a key element of aesthetics and makes music appealing.

Nevertheless, on a more abstract level, the similarity of music and language is determined by the very fact of their *generative nature*, i.e., the build-up of meaningful structures through the rule-governed combination and permutation of discrete items.

This apparent similarity of syntax processing in music and language and the obvious differences mentioned above have been reconciled in the Shared Syntactic Integration Resource Hypothesis (SSIRH) set up by Patel (2003a). He proposed that the representation of the particular syntactic regularities are domain-specific and reside most presumably in distinct (posterior) brain areas, explaining the occurrence of dissociated deficits in music or language processing (e.g., Luria et al., 1965; Peretz et al., 1994). The resources for computations on these representations, i.e., for generative processes like the integration of incoming and the prediction of upcoming events may, however, be domain-general and reside in overlapping (frontal) brain regions (see below).

Indeed, the cognitive neurosciences provide several lines of evidence for the functional overlap of musical and linguistic syntax processing. First, EEG studies have demonstrated *similar brain signatures* in both domains. Patel, Gibson, et al. (1998) reported statistically indistinguishable late positivities (P600) elicited by syntactically incongruous words in garden-path sentences and harmonically incongruous chords in music. Furthermore, out-of-key chords evoked a right antero-temporal negativity (RATN) that was reminiscent of the left anterior negativity (LAN) typically associated with linguistic grammatical processing (Gunter et al., 2000). Later studies elaborated these findings by describing similar early deviance related negativities elicited either by harmonically irregular Neapolitan sixth chords within chord progressions, or word-category errors in German passive sentences: the Early Right Anterior Negativity in music (ERAN; Koelsch et al., 2000; Koelsch, 2005), and the Early Left Anterior Negativity in language (ELAN; Friederici et al., 1993; Hahne & Friederici, 1999). Both ERPs show correspondence with respect to latency, polarity, and most of their functional characteristics. They both exhibit an anterior scalp distribution, though with slightly different hemispheric weighting: The ELAN is mostly rather left lateralised (but see Eckstein & Friederici, 2006, for bilateral scalp distributions), whereas the ERAN most often exhibits larger amplitudes over right hemisphere leads (but see Loui et al., 2005; Leino et al., 2007; Miranda & Ullman, 2007; Steinbeis et al., 2006, for bilateral scalp distributions). Despite their sometimes different laterality, it has been suggested that these brain potentials may reflect the operation of analogous or shared mechanisms in music and language.

This assumption found strong support in later studies that simultaneously presented music and language to investigate the *interaction* of these ERPs. The LAN elicited by agreement violations in language was indeed reduced if concurrently presented with a syntactic mu-

sis violation (Koelsch, Gunter, et al., 2005; Steinbeis & Koelsch, 2008b). Likewise, the ERAN elicited by harmonic irregularities in music was significantly reduced if syntactic errors occurred simultaneously in the language material (Steinbeis & Koelsch, 2008b). Notably, no such interactions were found if music-syntactic errors and semantic errors were concurrently presented, that means, neither was the N400 (as a marker of semantic processing in language; Kutas & Hillyard, 1980a, 1984) modulated by harmonic violations in music (Koelsch, Gunter, et al., 2005), nor was the ERAN affected by semantic errors in language (Steinbeis & Koelsch, 2008b; see also Fedorenko et al., 2007; Slevc et al., 2007 for converging results in behavioural studies). Therefore, the interactions between ERAN and LAN were taken as evidence for the *competition of musical and linguistic parsing processes for shared syntactic resources* rather than competition for unspecific attention or working memory resources.

Perhaps related to these findings, *domain-general training effects* have been observed in children. For example, musically trained 11-year olds exhibited not only larger ERAN amplitudes than musically untrained children when encountering harmonically irregular chords, but also a greater late sustained negativity (probably a developmental precursor of the ELAN), elicited by word-category errors in language. Furthermore, the musically trained group exhibited an ELAN that was not yet developed in the non-musician group. These findings suggest that musical training may lead to a parallel improvement of musical and linguistic syntax processing (Jentschke et al., 2005).

Conversely, it has been reported that *deficits in the processing of linguistic syntax are associated with parallel deficits in the music domain*. For example, 5-year olds with specific language impairment, a developmental language disorder with pronounced deficits in syntactic processing, exhibited no ERAN when encountering music-syntactic violations, whereas such an ERP was found in 5-year olds with typical language development (Jentschke et al., 2008). Moreover, agrammatic Broca's aphasics with severe deficits in linguistic syntax processing showed similarly impaired explicit and implicit processing of musical syntactic relations (Patel et al., 2008). Taken together, musical and linguistic syntax processing appear to mutually interact with each other leading to the assumption of a functional link between these operations. It remains to be clarified whether this link concerns shared syntactic processes or shared attention or working memory resources.

This consistent *functional* overlap between both domains is thought to rely on an (at least) partial *anatomical* overlap of the underlying neural networks processing syntax in music and language. The SSIRH proposed the frontal lobes as likely candidates for domain-general processing resources (Patel, 2003a). Indeed, fMRI constrained *dipole fitting* procedures applied to the magnetic equivalents of the ERAN and the ELAN revealed similar

sources within left and right inferior frontal brain areas (ERAN: Maess et al., 2001; ELAN: Friederici, Wang, et al., 2000). Further sources were localised within the left and right anterior STG in both domains (ERAN: Koelsch, 2006; ELAN: Friederici, Wang, et al., 2000; Gross et al., 1998).

These results are supported by *similar brain activation patterns* observed in music and language fMRI studies: The perception of music-syntactically irregular chords/notes was found to enhance the level of activation within bilateral (mostly right-accentuated) inferior frontal and superior temporal brain areas (Koelsch, Gunter, et al., 2002; Koelsch, Fritz, et al., 2005; Krumhansl, 2004; Tillmann, Janata, & Bharucha, 2003; Tillmann, Koelsch, et al., 2006). Similar brain activations (mostly left-dominant) have been observed during the processing of syntactically incorrect sentences (e.g., Brauer & Friederici, 2007; Friederici, Rüschemeyer, et al., 2003; Rüschemeyer et al., 2005).

Although these fMRI and MEG/EEG source modelling results appear to be consistent and nicely fit into the framework of domain-general frontal brain areas, caution must be still exercised when interpreting these data in terms of a co-localisation of musical and linguistic syntax processing: First, to date, localisations have been always compared between studies. Slight differences between peak coordinates were commonly attributed to a normal variability between samples and studies. But what if these differences were meaningful? As described in Chapter 1, the IFG is highly heterogeneous in terms of microarchitecture and function, and might easily support both musical and linguistic syntax processing in close neighbourhood without any overlap. Within-subjects investigations are required to answer this question. Second, to date, localisations have been always compared based on group averages. This is problematic for the co-localisation of functions because averaging blurs brain activations due to the natural interindividual anatomical and functional variability, thus, perhaps artificially creating an overlap (Cohen, Jobert, Bihan, & Dehaene, 2004; G. A. Ojemann & Mateer, 1979). Examinations at single subject level would help to clarify this issue. Third, these studies measure activation instead of disruption (see Chapter 4). Hence, they are not able to clarify whether the observed brain areas are *essentially* involved in musical and linguistic syntax processing. This information appears, however, crucial to savely conclude that a given brain region support both functions in a domain-general way.

In sum, the IFG as well as the anterior STG are conceivable candidates for domain-general syntactic operations that may underlie the functional overlap of musical and linguistic syntax processing. However, this assumption requires further evidence, as will be collected in the present dissertation.

3.3 Summary

Music and language appear to be very different to the listener. However, there are considerable structural similarities that were summarised in the present chapter. Keeping differences like discreteness of pitch, isochrony and semanticity in mind, it was shown that phrasing in music and language as well as the processing of speech intonation and melodic contour probably rely on shared cognitive and neural resources. The functional link between musical and linguistic syntax processing was particularly emphasised, presenting data on resource competition, domain-general training effects, or parallel music-syntactic deficits in individuals with developmental or acquired agrammatism. The IFG as well as the anterior STG of both hemispheres were identified as likely candidates for a neuroanatomical co-localisation of syntax processing in both domains, possibly accounting for these functional interactions. The verification of this assumption will be the purpose of the present thesis.

Chapter 4

Electrophysiological Methods Applied in Human Brain Mapping

Localising the neural structures that underlie human cognitive functions is the principle aim of functional neuroimaging studies. A large body of research has been devoted to this aim, using, e.g., positron emission tomography (PET) and functional magnetic resonance imaging (fMRI; e.g., Cabeza & Nyberg, 2000). However, due to their coarse temporal resolution these methods are not well suited to investigate the precise time course of different cognitive functions. Yet, this information appears pertinent for the understanding on how the human brain processes auditory signals like music and language that evolve and decay extraordinarily quickly over time. In this regard, electro- and magnetoencephalography (EEG, MEG) offer a solution by recording the neuronal activity in a submillisecond range. These methods, however, face the problem that brain activity measured at the scalp is poorly localised, i.e., does not indicate where in the brain these potentials are generated. There are several attempts to tackle this trade-off between spatial and temporal resolution, e.g., by using sparse temporal sampling designs with shifted stimulus presentation in fMRI (e.g., Gaab et al., 2003), or by applying source localisation algorithms to EEG and MEG data (see, e.g., Michel et al., 2004, for an overview of actual methods). The following sections will focus on two alternative approaches to infer the localisation of brain functions from EEG data: The analysis of intracranially recorded potentials and the lesion method. Before discussing the advantages and disadvantages of these approaches, the neurophysiological and technical background of EEG measurements will be described.

4.1 Neurophysiological Bases of the EEG

The *electroencephalogram* (EEG) as primarily described by Hans Berger in 1929 (Berger, 1929) is the derivation and recording of time-varying voltages on the human scalp that are mainly generated by the electrical activity of the neocortex.¹ The human neocortex, i.e. the grey matter of the brain, is organised in six layers containing different types of nerve cells. These neurons can be divided into 2 categories: 80% of them are *pyramidal cells*, that is excitatory neurons projecting to other areas of the brain and the spinal cord. The other 20% are diverse *nonpyramidal cells*, mostly interneurons projecting to nearby nerve cells (see Kandell, Schwartz, & Jessell, 1991, for more details). The activity picked up by the EEG stems mostly from the pyramidal cells, more precisely, from a large number of closely interconnected, synchronously active pyramidal cells. Due to the parallel alignment of their apical dendrites perpendicular with respect to the cortex surface, the electric currents of these neurons effectively summate generating field potentials strong enough to be measured by surface electrodes.

The apical dendrites of pyramidal cells reach out until the cortical layers I and II where they build synapses with primarily excitatory afferent fibres from the thalamus as well as from association and commissural fibres (Birbaumer & Schmidt, 2006). The ionic fluctuations at these synapses, especially the excitatory postsynaptic potentials (EPSP) lead to the generation of a current flow alongside the axis of the neurons which makes them electric dipoles (see Figure 4.1). Interestingly, action potentials only minimally contribute to the scalp recorded potentials because they hardly summate due to their very short duration (see Kandell et al., 1991, for a detailed description).

Notably, not all electric activity of the brain can be detected by scalp EEG. Some neuronal populations may be too small or the activity may be insufficiently synchronous to create measurable electric fields. In a number of brain structures like the thalamus or other subcortical nuclei – so called *closed field* structures (Rugg & Coles, 1995) – the pyramidal cells are not arranged parallel to one another precluding the detection of their activity with distant scalp electrodes. These potentials can be only invasively measured by inserting depth electrodes, as sometimes done in clinical applications (see section 4.4).

The human EEG is composed of several superimposed frequency bands ranging between DC potentials below 1 Hz up to 100 Hz and more (see, e.g., Curio, 2000, for a summary on scalp recorded frequencies up to 1000 Hz). In surface recordings, the voltage ampli-

¹Although this seems trivial, it has to be kept in mind that the brain generated EEG may be contaminated by various kinds of artefacts due to, e.g., eye blinks or movements, muscle activity, impedance fluctuations or technical interference.

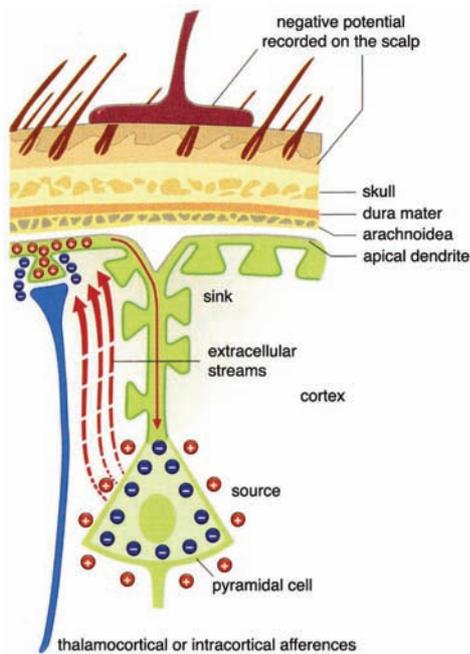


Figure 4.1: Dipole characteristics of a pyramidal cell. EPSPs at synapses evoke extracellular streams alongside the axis of the apical dendrite that can be recorded with scalp electrodes (illustration adapted from Birbaumer and Schmidt, 2006).

tudes normally vary between 1 and 200 μV (Birbaumer & Schmidt, 2006). The temporal resolution of the EEG lies within the millisecond range; the spatial resolution of the scalp recorded EEG is comparably rough, lying between 1 and 5 cm. This is markedly lower than the resolution obtained when directly recording from the cortex (see section 4.4) due to the low conductivity of the skull. That means, when passing through the meninges, skull and skin, the EEG signal is strongly attenuated and blurred in terms of its spatial distribution (Nunez, 1981).

Importantly, depending on the orientation of the cortical dipoles with respect to the scalp (determined by the folding of the cortex) and due to the volume conducting properties of brain and skull, EEG signals recorded at a particular active electrode are not necessarily attributable to the brain regions underneath this channel, but may have been generated by more distant brain structures. For instance, the bilateral activation of the auditory cortex in the supratemporal plane generates strongest potentials not at temporal but at central electrodes on top of the head. These spatial properties of the EEG render it difficult to directly infer the localisation of neural generators of scalp recorded potentials from their topography. However, by means of source modelling it is partly possible to reconstruct the cerebral current sources underlying the scalp recorded EEG pattern (see Michel et al., 2004, for an overview over the different approaches).

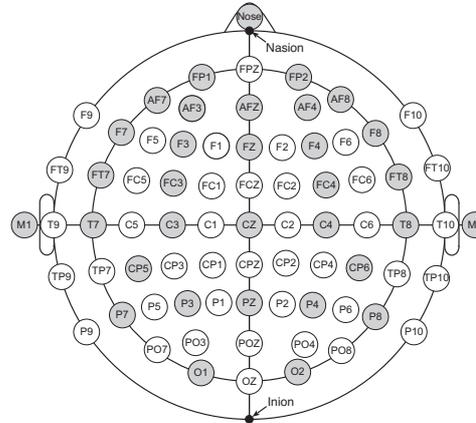


Figure 4.2: Electrode positions according to the extended 10-20 system (Sharbrough et al., 1991). Channels employed in the present dissertation are shaded in grey.

4.2 Recording of an EEG

The EEG measures voltages within pairs of electrodes, most often in monopolar derivations, that is, the difference potential between several *active electrodes* placed at sites of neuronal activity and one common *inactive electrode* placed at a site with no or only little brain activity, serving as a reference.² The ongoing voltage changes captured by the electrodes are amplified, sampled (at 250 to 1000 Hz and higher), digitised (up to 32 bits, in units of about 0.1 μV), and stored on a computer for further processing. It has to be kept in mind that certain characteristics of the amplifiers as well as the sampling rate act like filters determining the frequency range of the EEG recording.³

An important issue in EEG recordings is the kind of reference used, since the choice of the reference application substantially influences the shape and distribution of the signal. In auditory experiments, mostly a *linked mastoids reference* is used, that is, the algebraic mean between the two electrodes placed on the mastoid bones behind the left and the right ear (M1 and M2 in Figure 4.2). Since this reference is mathematically centred between both hemispheres, a lateralised EEG effect can be taken as evidence for the hemispheric lateralisation of the underlying neural generators. If the sources of the EEG signal are located in the supratemporal plane (e.g., the auditory cortex) and are, thus, oriented vertically so that the negative polarity projects to electrodes above, the positive polarity to electrodes below the level of the Sylvian fissure, it is useful to place the *reference electrode on the nose tip* (i.e., within the plane drawing through the Sylvian fissure; see, e.g., Näätänen, 1992) to ob-

²In order to accentuate regional differences in electric fields, the EEG may also be recorded as potential difference between two active electrodes, termed bipolar derivation.

³The *Nyquist-Shannon sampling theorem* states that the sampling frequency must be strictly greater than twice the signal bandwidth to achieve an unambiguous representation of the signal (Shannon, 1998).

serve this *polarity inversion*. Predominantly experiments with high density arrays (i.e., with 128 electrodes or more) compute an *average reference* to separate out the activity of the reference site. That is, in order to circumvent that amplitudes of recordings are attenuated according to their proximity to the reference site (the closer, the more attenuated), the mean of all electrodes is subtracted from each channel (see Dien, 1998, for a review on different reference montages).

For the recording of an EEG, mostly Ag/AgCl electrodes fixed in an elastic cap are placed on the subject's head. The site of each single electrode is predefined according to the *International 10-20 system* which originally defines the placement of 19 electrodes (Jasper, 1958). The positions of the principle electrodes are determined relative to anatomical landmarks like the nasion, the inion, the left and right postauricular point and situated in relative distances between these reference points (originally 10% and 20%). The electrodes are named using a combination of letters and numbers to indicate their proximity to underlying brain regions (F: frontal, C: central, T: temporal, P: parietal, O: occipital), and their laterality (odd numbers: left hemisphere, even numbers: right hemisphere, subscript z: anterior-posterior midline). That is, T8 is placed over the right temporal lobe, whereas O1 is situated over the left occipital lobe. Due to the need of larger electrode arrays, an extended version of the system has been established by the American Electroencephalographic Society (Sharbrough et al., 1991, see Figure 4.2).

4.3 From EEG to ERPs

An *event-related potential* (ERP) is the set of voltage changes within an epoch of the EEG that is time-locked to some event (Rugg & Coles, 1995). It is generally assumed that ERPs reflect cognitive processes related to the event, from the strictly sensory processing to higher order integrative levels. This makes ERPs a highly suitable tool for the investigation of neural mechanisms within different cognitive domains.

Generally, the amplitudes of ERPs are very small, ranging between 1 and 30 μV (Birbaumer & Schmidt, 2006), which makes them hardly distinguishable from the “background” EEG reflecting the vast number of operations permanently performed by a living brain. Therefore, signal processing procedures have to be applied in order to extract the event-related *signal* from the uncorrelated *noise*. This is ideally done by averaging, thus, increasing the *signal-to-noise-ratio* (SNR; see Figure 4.3).

During an ERP experiment, the same stimulus (e.g., a tonic chord), or stimuli belonging to one category (e.g., different sentences all containing the same type of syntactic violation)

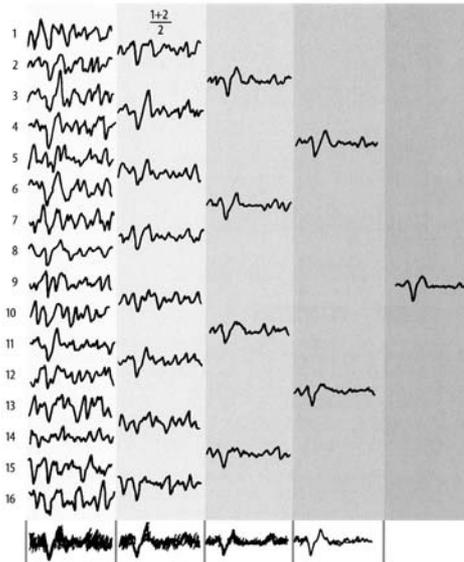


Figure 4.3: From single trials to ERPs. In single epochs, the event-related signal is still indistinguishable from the background activity (total left). The more epochs that enter the average the more noise is eliminated and the clearer the event-related activity becomes (illustration adapted from Birbaumer & Schmidt, 2006).

are repeatedly presented. When analysing the data, epochs around the stimuli (e.g., starting 200 ms prior to and ending 1000 ms after the onset of the event) are cut, and all trials of one condition are averaged for each corresponding sampling point. Assuming that EEG activity not time-locked to the stimulus varies randomly across epochs, this uncorrelated noise tends to cancel out, and the remaining signal reflects activity tightly connected to the processing of the stimulus (see Figure 4.3). The ideal number of trials within one experiment depends on the amplitude of the ERPs. Note that ERP amplitudes are measured in relation to a (mostly pre-stimulus) baseline time window, in which the average voltage is zero per definition. The baseline is chosen so as to comprise equal or at least similar cognitive processes in both experimental conditions.

The positive and negative deflections of an ERP are referred to as *ERP components* and are associated with different cognitive functions. Most often, they are described in terms of polarity, scalp distribution, and peak latency: For example, the Early Right Anterior Negativity (ERAN) has a negative polarity, is frontally distributed with a slight right hemispheric preponderance and peaks early (around 200 ms) after stimulus onset. More generally, a nomenclature using letters and numbers is employed to characterise the components' main properties. Thus, an N100 is a negativity peaking at 100 ms after stimulus onset, whereas a P600 is a positivity usually peaking at a latency of 600 ms. Commonly, there is a rough distinction between *exogenous components* which are mainly determined by stimulus properties, i.e., reflect bottom-up processes, and *endogenous components* which are associated with higher order cognitive functions, i.e., top-down processes. The exact functional mean-

ing of a given component has to be inferred from its sensitivity to specific experimental manipulations (Rugg & Coles, 1995).

It is not trivial to determine ERP components, especially their onsets and offsets (due to overlapping mental processes). There are some attempts to distinguish single components by analysing the changing topography of the EEG signal following the assumption that a different scalp distribution reflects the involvement of different neural generators, and thus, different cognitive processes (Michel et al., 2004; Skrandies, 2003). It is important to note, that one ERP component as measured on the scalp may be generated by multiple cortical sources. That is, the recorded signal reflects the linear superposition of the activity of all generators. To which extent one electrode measures the activity of each source depends on the distance and the orientation of the dipoles with respect to the electrode (see section 4.1).

4.4 Intracranial EEG Recordings

In human brain research, the EEG is mostly applied as a noninvasive method to gain insights into brain functions. However, in some clinical populations, the EEG is collected from electrodes that are implanted directly inside the skull for diagnostic or therapeutic reasons (Nair, Burgess, McIntyre, & Lüders, 2008). Such recordings are mostly obtained from patients suffering from medically untreatable epilepsy. Less frequently, intracranial EEG (iEEG) is also applied in patients with brain tumours for the mapping of eloquent areas. In some cases it is possible to present these patients with experimental paradigms while they have electrodes implanted, opening a unique window to human brain functions.

In the field of epileptology, iEEG has been in use since the late 1940s (see A. K. Engel, Moll, Fried, & Ojemann, 2005, for the milestones of the history of invasive recordings in humans) and is nowadays applied in roughly 25-50% of the adult patients at centres doing epilepsy surgery (Spencer, Sperling, & Shewmon, 1997). The implantation of electrodes is (if necessary) the final step in an extensive and differentiated diagnostic evaluation process including the exact description and classification of the seizures,⁴ laboratory tests, neuropsychological investigations, scalp recorded EEG, computer tomography (CT), anatomical and functional magnetic resonance imaging (MRI), single photon emission computed tomography (SPECT), intra-arterial Amobarbital procedures (known as “Wada test”) etc.

⁴In 1981, a commonly used classification of epileptic seizures was introduced by the International League Against Epilepsy (ILAE, 1981; Dreifuss, 1997). In short, this classification distinguishes *partial (focal, local) seizures* starting in a system of neurons limited to part of one cerebral hemisphere from *generalised seizures (convulsive or nonconvulsive)* in which initially both hemispheres are involved (see Part III of J. J. Engel & Pedley, 1997, for a detailed description).

(see section IV in J. J. Engel & Pedley, 1997, for a detailed description of each diagnostic tool).

Intracranial EEG recordings are used to precisely localise the *epileptogenic zone* (i.e., the brain area necessary and sufficient to cause spontaneous seizures; see Spencer et al., 1997) as well as to delineate functionally relevant brain structures, like motor cortex or language areas, in order to plan precise surgical resection of epileptogenic tissue while sparing eloquent areas. Based on the noninvasively obtained data, that might have been insufficient to precisely define the epileptic seizure onset zone, electrodes (see section 4.4.3) are implanted in/on “suspicious” brain areas for seizure onset. Mostly, patients keep those implants for up to a couple of weeks, during which iEEG data are continuously collected and behavioural manifestations of spontaneously occurring seizures are simultaneously videotaped. During this long-term monitoring, the patients, waiting for seizures, may agree to perform cognitive tasks for research projects while their iEEG is continuously recorded. Needless to say, that the site of electrode implantation as well as the duration of the monitoring phase depend solely on clinical aspects.

4.4.1 Benefits of iEEG

The human iEEG usually measures local field potentials (LFP; A. K. Engel et al., 2005),⁵ that is the summation of EPSPs (like in scalp EEG) of small cell assemblies. The temporal resolution of iEEG is that of surface recorded EEG (i.e., milliseconds), the amplitudes of intracranially recorded signals are naturally larger – in the region of 2 to 60 times (Chatrian & Quesney, 1997) – than scalp recorded potentials, because they are not attenuated by the meninges, liquor, skull, and skin (Figure 4.4 A).

The major benefit of iEEG is its favourable spatial resolution approaching that of fMRI (functional Magnetic Resonance Imaging) or PET (Positron Emission Tomography), thus, coming close to the “gold-standard” of human brain imaging, the millimetre/millisecond resolution. Indeed, it has been repeatedly shown that cortical grid electrodes (see section 4.4.3) assess the LFPs generated within a 10 mm radius, and that signals generated more than 1 cm apart contribute only minimally to the recording (see Figure 4.4 B; Bullock et al., 1995; Menon et al., 1996; Lachaux et al., 2003). Even if the exact spatial resolution may vary slightly depending on the electrode impedances, the diameter of the electrical

⁵With special extracellular microelectrodes and a high sampling rate (up to 30 kHz) also single and multi-unit activity may be recorded, that is, the spike activity of individual neurons or circumscribed cell assemblies (see, e.g. Bechtereva & Abdullaev, 2000). This is rarely done, e.g., during neurosurgery in Parkinsonian patients. In order to focally lesion or stimulate parts of the basal ganglia, the neurosurgeon moves an electrode through these deep brain structures and analyses the spike signature characteristic for the different nuclei (e.g. Lachaux, Rudrauf, & Kahane, 2003).

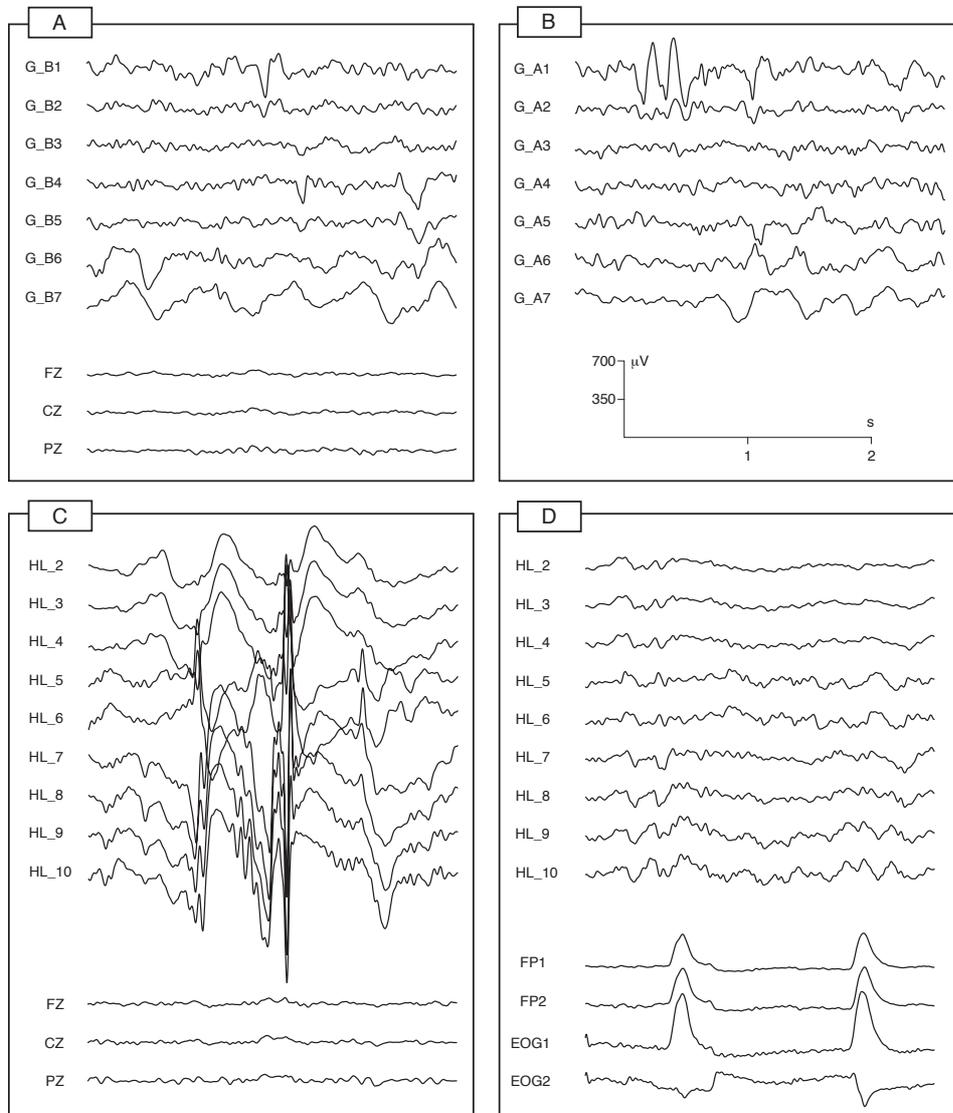


Figure 4.4: (A) The amplitudes of iEEG potentials (top) are significantly larger than simultaneously recorded surface activity (bottom). (B) The spatial resolution of iEEG is far better than the one obtained with scalp recordings. The electrodes G_A1 and G_A2 as well as G_A6 and G_A7 placed on the left temporal cortex show distinct EEG patterns, even though they are spaced only 1 cm apart from one another. (C) Intracranial electrodes allow the investigation of brain activity from closed field structures. Electrodes HL_2 to HL_10 (top) situated in the left hippocampus of a patient show clear inter-ictal activity, whereas surface electrodes (bottom) remain silent. (D) Finally, iEEG (top, showing electrodes in the left hippocampus) is less vulnerable to eye movement or muscle artefacts (not shown) than surface EEG (bottom).

contacts and their spacing, as well as the volume conduction properties of the underlying tissue (Lachaux et al., 2003), the topography of iEEG data is far less blurred than scalp recorded potentials, making a localisation of transient brain activity possible.

Another great advantage of iEEG is its ability to assess activity from closed field structures that are inaccessible for distant recordings (Figure 4.4 C). By inserting depth electrodes, e.g., in the hippocampus or basal ganglia, valuable insights into memory functions (e.g. Fernández et al., 1999) or language processing (e.g., Fried, Ojemann, & Fetz, 1981; P. Meyer et al., 2005) can be gained, providing a bridge between imaging and scalp EEG data.

Finally, iEEG is less vulnerable to eye movements or muscle artefacts (Figure 4.4 D) than surface recordings, rendering it possible to investigate questions related to the temporal dynamics of oculomotor control or the processing of complex motor tasks that otherwise would produce considerable noise in scalp EEG.

4.4.2 Limitations of iEEG

Apart from these great advantages, iEEG has a number of limitations. One major constraint is that, for obvious reasons, the recordings are exclusively acquired from patients with *neurological disorders*. This raises the concern whether their cognitive processes are a good model for normal human brain functions. It might be that the brain tissue that is recorded from is organised differently than that in healthy subjects. Generally, electrodes recording from macrostructurally abnormal or lesioned brain tissue (e.g., dysplastic or sclerotic areas), as far as visible with MRI, should be excluded from the data analysis, while still being aware that this does not prevent from recording from possibly microscopically malformed tissue.

Many epilepsies are symptomatic,⁶ that is, are elicited by brain pathologies like gliomas, cortical dysplasia or hippocampal atrophy. Furthermore, the neurosurgical treatment of epilepsy is mostly the last step in a long history of disease, sometimes already beginning in childhood. Thus, significant *reorganisational processes* may have taken place caused by the pathology, so that brain functions may be localised differently than in healthy subjects. Therefore, it must be well documented, at which age the seizures started. Additionally, the

⁶In 1989, the ILAE classification of epileptic seizures was revised by introducing a second order categorisation related to the aetiology (ILAE, 1989). Apart from the partial vs. generalised distinction, one additionally distinguishes idiopathic (genetic causes), symptomatic (in relation with a brain lesion), and cryptogenic epilepsies (unknown aetiology).

results of the cortical mapping by means of electrical stimulation⁷ may give a rough idea on the functional organisation of the patient's cortex.

Another concern is the possibility that the performance and neurophysiological response of the patients may be altered due to the *anticonvulsant medication*. It is desirable to keep this factor constant across subjects, which is, however, difficult to achieve for medical reasons. Therefore, the medication of each patient has to be precisely documented and (if necessary) considered when interpreting the data. On the other hand, a major benefit of the medication is that it reduces inter-ictal activity, thus, allowing to record an iEEG less afflicted with *activity related to the epilepsy* (such as low amplitude fast waves or interictal spikes as shown at electrodes HL_3 to HL_10 in Figure 4.4 C). Periods contaminated with these artefacts have to be carefully eliminated.

For obvious reasons, the location where electrodes are implanted is chosen merely on medical grounds. This has two implications for intracranial ERP research: First, contrary to scalp EEG, the electrode positions differ significantly between patients, hindering the straightforward calculation of a grand average across subjects as commonly done in ERP research. In order to make assumptions across patients, the *individual electrode positions* have to be precisely localised with respect to the individual brain anatomy, which can be reconciled with a standard norm brain later on for all patients.⁸

Second, the *electrodes cover only limited parts of the brain*, leaving most of the brain volume unexplored. Therefore, it is desirable to make assumptions on where a specific ERP effect might be generated and to choose patients with corresponding electrode placements for the study. Since the position of the electrodes is determined on the basis of clinical considerations, fairly often electrodes do not optimally cover the area of interest of a study so that experimental effects may emerge at border electrodes of the grid (see section 4.4.3), yielding a localisation of this effect but leaving open, whether it would have been even larger in regions closely beyond the electrode grid. At this point it is important to mention that, dependent on the prevalence of different types of epilepsy and the feasibility of a

⁷In order to identify functionally relevant brain structures, e.g., language areas, weak currents are delivered between two electrodes while the patient is performing different tasks, e.g., counting, naming, reading aloud, or repeating words. If the stimulation disrupts the patient's behaviour this is taken as evidence that the relevant function is located underneath these electrodes. On the other hand, electric stimulation may also induce muscle twitches, bodily sensations, or visual phosphenes, helping to identify motor, sensorimotor or visual brain areas. The strength of the applied currents depends on the individual after-discharge threshold (after-discharges are taken as precursors of seizures).

⁸Software packages (e.g., Kovalev et al., 2005) have been developed to help extracting the electrode positions from an anatomical MRI scan recorded after implantation by analysing the imaging artefacts induced by the electrodes (see Figure 4.5), and match these coordinates with a co-registered non-artefacted pre-implant MRI scan of the patient. Note that despite the precise matching of both datasets, the spatial precision of the mapping is still determined by possible tissue deformations caused by the electrode implantation (Lachaux et al., 2003).

neurosurgical treatment, some electrode placements are more frequent than others. This determines the brain areas and, thus, research questions which may be investigated with iEEG. For instance, the implantation of medial temporal depth electrodes are quite common due to the high prevalence and typically good surgical outcome of temporal lobe epilepsies (very often caused by hippocampal sclerosis), enabling the investigation of questions related to memory formation or emotional processing. Similarly, the frequent implantation of left fronto-temporo-lateral electrode grids for electric stimulation and identification of language relevant areas prior to neurosurgery yields a good starting point for language studies. On the other hand, implantations in homotope right hemispheric areas are done far less frequently, because right hemisphere surgeries rarely require language mapping, making the investigation of functions thought to be achieved by this region more difficult.

Finally, the population receiving such a neurosurgical treatment and being, moreover, suited to participate in the study, is extremely small. Therefore, a study with intracranial recordings will mostly have to deal with *small and heterogeneous samples* (in terms of disease history and pathogenesis, electrode location, medication etc.). However, if experimental effects are traceable across these heterogeneous cases, this at least rebuts the argument that certain pathologies or medications would have causally influenced the effect.

4.4.3 Facilities for iEEG Recordings

The most commonly used invasive electrodes are stereotactically implanted depth electrodes (Figure 4.5 left), and subdural strip or grid electrodes (Figure 4.5 middle and right) described in more detail in the following paragraphs. Less frequently, epidural electrodes placed between skull and dura mater, or foramen-ovale electrodes especially suited for mesial temporal lobe recordings are implanted, being less invasive, though, also less sensitive (see Noachtar & Arnold, 2003; Wieser & Morris, 1997). Mostly, different types of electrodes are inserted in combination to make use of the complimentary information provided by each single electrode type for precise localisation of the epileptogenic zone. The choice of electrodes depends on the hypothesised localisation of the epileptogenic area, so as to best cover this region while keeping the number of implanted electrodes as low as possible to avoid potential risks.

Depth electrodes (Figure 4.5 left) penetrate brain tissue directly making it, thus, possible to record from deep brain structures that are otherwise inaccessible like the hippocampus or the amygdala. These are multicontact electrodes (carrying 4 to 12 contacts along their length, spaced 5 to 10 mm apart from one another) which are inserted through bur holes

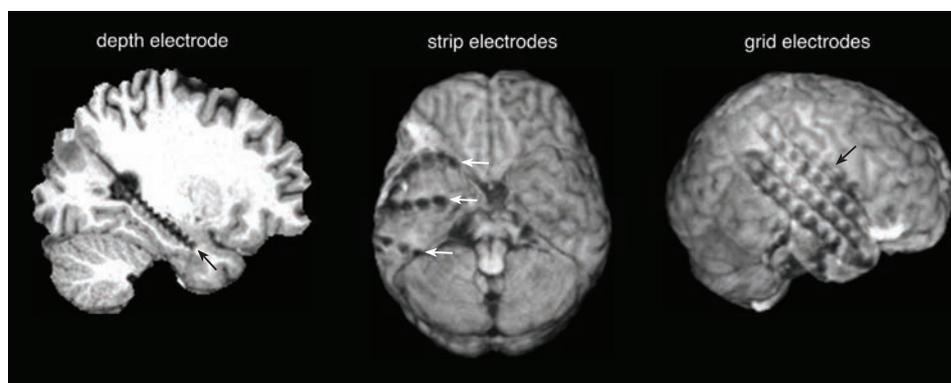


Figure 4.5: MRI scans after the implantation of a medial temporal depth electrode (left), three temporo-basal strip electrodes (middle), and a temporo-lateral 4×8 electrode grid.

with stereotactic MR or CT guidance so that the location of each contact can be exactly predetermined.

Subdural strip electrodes (Figure 4.5 middle) are 2 to 12 platinum or stainless steel contact disks embedded in a flexible strip of Silastic or Teflon. Interelectrode (centre-contact to centre-contact) spacing varies between 5 and 10 mm, depending on the individual requirements; overall contact diameter is most often 4 mm, only the inner 2.3 mm are exposed to the cortex surface. Strip electrodes are especially suited to record from medial inferior temporal and interhemispheric cortical areas hardly accessible with large grid electrodes, but also lateral neocortical areas may be targeted with strip electrodes. They are inserted through bur holes into the subdural space and manually manipulated to the desired area, yielding a less precise positioning than depth or grid electrodes.

Subdural grid electrodes (Figure 4.5 right) have similar technical properties as strip electrodes, solely providing larger configurations, like 4×8 or 8×8 contacts arranged within sheets of Silastic or Teflon. Due to their size, the insertion and removal of electrode grids requires a craniotomy which makes an accurate placement of the contacts on the target area possible. Grid electrodes provide optimal coverage of the relevant cortical region and allow the detailed functional mapping of eloquent areas with electric stimulation.

4.4.4 Source Reconstruction from Intracranial EEG

Under certain circumstances, it is possible to make assumptions on the localisation of the neural sources underlying the iEEG signal from the spatial distribution of the electric potentials. Considering for example subdural grid electrodes, a negative potential with no

neighbouring positivity indicates most likely a source which is radially (i.e., orthogonally) oriented with respect to the brain surface. Furthermore, deep radial sources normally produce more broadly distributed potentials than superficial sources. On the other hand, if an iEEG signal inverts polarity at neighbouring contacts, i.e., displays a bipolar potential structure, a tangential source situated in a plane orthogonal to the line joining the negative and the positive pole is very likely (e.g., Lachaux et al., 2003; Rosburg, Trautner, Dietl, Korzyukov, et al., 2005). Note, however, that this approach gives only a rough approximation of the exact source localisations and most often the intricate potential distribution precludes the unequivocal identification of the underlying source configuration: First, very often more than one negativity and one positivity are observed within a time step, rendering it difficult to decide which poles belong together, if at all they do so. Second, the electrode grid samples only a restricted portion of the brain and is blind (due to its good spatial resolution) to activity beyond its borders. Potentials at bordering electrodes could therefore reflect either the activity of a radial source or of one pole of a tangential source (the other being located outside the covered area).

To improve the precision of source localisations in iEEG data, first attempts have been made to apply source modelling techniques to intracranial recordings similar to the methods used to reconstruct neural generators from scalp EEG (Baumgartner, Barth, Levesque, & Sutherling, 1991; Korzyukov et al., 2007). Results look promising, however, several critical questions need to be answered to proof the reliability of these approaches, among them: (a) how many intracranial electrodes (and in which configuration) are at least needed to yield stable solutions (i.e., are 32 subdural electrodes as analysed in the present dissertation sufficient to obtain reliable results), or (b) what are the volume conduction properties of the underlying brain tissue and cerebrospinal fluid (see Lachaux et al., 2003, for a discussion of these and other points). Nevertheless, the approximation of the sources as possible by means of intracranial EEG recordings clearly exceeds the explanatory power of scalp EEG.

4.5 The Lesion Method

The *lesion method* is essentially the establishment of associations between cognitive functions and brain anatomy by investigating the changes of behaviour after circumscribed brain lesions (Damasio & Damasio, 1989). This research tradition has been mainly founded by Pierre Paul Broca in 1861 when he assigned the functions underlying speech production to the third convolution of the inferior frontal gyrus (IFG; Broca, 1861). For a long time, the lesion approach has been the only method to infer functions of brain areas, and has enormously contributed to our present knowledge on the human brain (Rorden & Karnath,

2004). However, a number of fundamental criticisms have been levelled against the lesion method, and the rise of new imaging techniques like PET, SPECT, and fMRI (that measure brain activations directly in healthy subjects and circumvent the difficulties that occur when making inferences on intact brain functions based on deficient processing) have challenged the value of the lesion method. The following sections will focus on the strengths and weaknesses of the lesion approach compared to imaging techniques, arguing that lesion studies in combination with imaging methods provide a unique window to the anatomical foundation of human brain functions (Damasio & Damasio, 1989).

4.5.1 Limitations of the Lesion Method and Ways to Address Them

Historically, the lesion method follows the *locality* or *modularity assumption* (Fodor, 1983), saying that single encapsulated cognitive functions may be investigated by virtue of focal brain lesions, assuming at the same time that after a focal lesion the nondamaged modules continue to work as they did before the damage (see Farah, 1994, for a critical discussion). However, for several reasons, *a lesion is almost never that local*. Firstly, brain injuries are largely determined by the brain's design, its blood supply, and the surrounding skull (Kretschmann & Weinrich, 2003), and are rarely restricted to one anatomical structure or one cognitive module (Caviness et al., 2002; Heinsius, Bogousslavsky, & Melle, 1998), obscuring the relation between function and anatomy. With this respect, group studies are important: Comparing the behaviour of patients with lesions covering different areas makes it possible to untangle which region is supporting a particular cognitive function (Rorden & Karnath, 2004).

Secondly, the brain is a highly dynamic organ. Damage to part of it initiates a number of surprisingly quick and complex *reorganisation processes* which may considerably change the involvement of the perilesional and otherwise interconnected brain regions responsible for a given function (e.g., Marsh & Hillis, 2006; Saur et al., 2006). In a strict sense, lesion studies investigate the function of the tissue that has been damaged as much as the function of the tissue that has been spared (and is involved in neural compensation; Walsh & Pascual-Leone, 2003). Unfortunately, data obtained shortly after brain injury, attempting to avoid compensatory plasticity, are largely confounded by the temporary disconnection (diaschisis) of apparently intact brain areas due to the disrupted perfusion after the noxious event (Marsh & Hillis, 2006; Rorden & Karnath, 2004). This makes acute and subacute data even more difficult to interpret than data obtained with chronic lesions. These allow at least unidirectional interpretations: The disruption of a behaviour in a chronically brain lesioned patient can be taken as evidence that the damaged structure is (at least somehow)

involved in the task. On the other hand, an intact behaviour does not necessarily mean that this area does not support the function because its deficiency may have been compensated by other brain areas.

Finally, the locality assumption – regardless of whether an experiment is conducted with brain lesioned or healthy participants – neglects that the majority of functions is processed in *distributed neural networks* (Farah, 1994). From this perspective, behavioural deficits are not due to the damage of one single brain area or encapsulated functional module, but rather emerge from disconnections within a network: (A) *anatomically*, caused by white matter ablations and damage to fibre tracts, or (B) *functionally*, caused by the disruption of earlier processing steps required by apparently intact brain regions or modules to accomplish the task. These challenges can be partly faced by a well controlled choice of the patients with regard to location and extent of the lesion and potentially damaged fibre tracts (which sometimes makes lesion studies a long term project). Imaging techniques like MRI and diffusion tensor imaging (DTI; Mori, 2006)⁹ are excellent tools for the exact description of the total extent of the disruption after brain injury remarkably increasing the precision and validity of the lesion method (Damasio & Damasio, 1989; Rorden & Karnath, 2004). Functional disconnections are perhaps the greatest intrinsic limitation of lesion studies. However, the systematic investigation of how damage of single network constituents (as identified by imaging techniques) influences behaviour, has the potential to even refine our understanding of the relationship between the units of a hypothesised functional network (Damasio & Damasio, 1989).

4.5.2 Benefits of the Lesion Method

Imaging (fMRI, PET) and brain activation methods (EEG, MEG) are able to easily overcome the majority of the criticisms raised above by associating cognitive functions with brain activations in healthy subjects. Furthermore, they offer a better spatial (fMRI, PET, MEG) and temporal (EEG, MEG) resolution than the lesion method. Still, despite these advantages, the explanatory power of those techniques is limited in one respect: They measure activation instead of disruption.¹⁰ That means, these methods describe correlations

⁹DTI noninvasively traces fibre tracts making it possible to visualise white matter lesions and to estimate the extent of disconnections.

¹⁰Other methods measuring disruption are Transcranial Magnetic Stimulation (TMS; Walsh & Pascual-Leone, 2003) and Transcranial Direct Current Stimulation (tDCS; Nitsche & Paulus, 2000; Priori, 2003). By means of rapidly changing magnetic fields (TMS) or the application of a direct current flow (tDCS), these methods induce temporary *virtual lesions* in healthy subjects, thus, being able to overcome the problems related to neuronal plasticity. Furthermore, lesion site and extent may be well controlled. Even if the neurophysiological effects of both techniques are still not fully understood they represent promising tools in neuroscientific research. On the other hand, they are in some respect not able to replace the classical lesion method: So, nei-

between a cognitive function and brain activations, but are not able to clarify whether a given structure is necessary for performing a task. In principle, it may be possible that brain areas activated in an fMRI study have no direct role in information processing but may depend on the choice of the baseline condition or may be solely co-activations due to their strong neural connections with eloquent brain areas (e.g., the homotope area of the contralateral hemisphere). To give an example: Although a number of brain imaging studies reported bilateral activations in language tasks (e.g., Friederici & Alter, 2004; M. Meyer et al., 2000, 2004; Price et al., 2005), the temporary disruption of right hemisphere functions by injecting Amobarbital into the right carotid artery (termed “Wada” test) rarely causes severe language deficits (Rasmussen & Milner, 1975; Wada & Rasmussen, 1960/2007). So, although lesion data do not provide the spatial precision of imaging or activation data, they enable us to infer whether a cerebral region is *necessary* for a given cognitive process or not.

To conclude, both lesion method and imaging techniques have limitations, but several of their strengths and weaknesses are complimentary, so that a combined use of both approaches has the potential to provide new insights into the functional organisation of the human brain. Furthermore, it can be argued that a deliberate experimental design as well as new techniques for precisely imaging the extent of disruption can effectively address some of the limitations of the lesion method, leaving it a valid means of neuroscientific research.

4.6 Summary

Language comprehension as well as music processing are characterised by their remarkable speed adjusted to the fast decay of the auditory signal. To study the underlying neural processes, methods with a temporal resolution in the milliseconds range are needed. The present chapter focussed on the neurophysiological, technical and methodological background of the EEG which fulfils these requirements. Furthermore, the special case of intracranially recorded EEG signals was introduced and compared to conventional scalp EEG, highlighting its favourable spatial resolution and special value in estimating the generators of neuronal activity. In the last section, the lesion method was introduced as another approach to localise cognitive functions. It was particularly stressed that, as opposed to correlative approaches like PET or fMRI, this method is able to determine whether a given brain region is *essentially* involved in a given task or not. The present dissertation will apply

ther TMS nor tDCS are able to access deep brain structures. Additionally, TMS is hardly applicable on brain areas underneath large face muscles (e.g., Broca’s area or the anterior temporal lobe underneath the temporalis muscle) because the magnetic stimulation leads to distracting twitches and possibly painful cramps of the face muscles.

these methods to investigate whether the neural networks supporting language comprehension and music processing overlap.

Part II

Experiments

Chapter 5

Experiment 1: The Brain Basis of Music-Syntactic Processing - A Lesion Approach

A longstanding debate in neuropsychology is centred on the domain-specificity or domain-generality of music and language processing (e.g., von Frankl-Hochwart, 1891; Marin & Perry, 1999).

Specificity of language and music processing. On the one hand, the functional autonomy of both domains is defended by a certain tradition of case studies reporting on brain lesioned patients who suffered from *aphasia without amusia* (e.g., Amaducci et al., 2002; Assal, 1973; Basso & Capitani, 1985; von Frankl-Hochwart, 1891; Luria et al., 1965; Signoret, Eeckhout, Poncet, & Castaigne, 1987; Tzortzis, Goldblum, Dang, Forette, & Boller, 2000) or from *amusia without aphasia* (e.g., Griffiths et al., 1997; Johannes, Jöbges, Dengler, & Münte, 1998; Mavlov, 1980; Peretz et al., 1994; Peretz, Belleville, & Fontaine, 1997; Piccirilli, Sciarna, & Luzzi, 2000).

For example, the famous Russian composer Vissarion Shebalin (1902-1963) suffered from severe aphasia after a stroke that largely lesioned his left temporo-parietal brain. Despite his language impairment he continued writing a number of influential musical pieces - with unchanged quality compared to previous works. Contemporaries like Shostakovich stated: "Shebalin's Fifth Symphony is a brilliant creative work, [...]. This symphony composed during his illness is a creation of a great master." (Luria et al., 1965, p. 292). Similarly, the outstanding French composer Maurice Ravel (1875-1937) developed a severe ideomo-

tor apraxia of unknown aetiology accompanied by a (nonfluent) aphasia, but “his ability to recognise and remember a very minute change in the interpretation of his works was preserved up to a few weeks before his death.” (Amaducci et al., 2002).

Conversely, Peretz et al. (1994, 1997) reported on three patients exhibiting manifest impairments of music perception (e.g., the recognition of familiar and unfamiliar tunes, or the detection of scale, interval, or contour differences between two melodies) in the absence of language comprehension deficits after bilateral lesions of the temporal lobes encompassing portions of the left and right auditory cortex (but see Tillmann, Peretz, Bigand, & Goselin, 2007, for evidence for spared musical abilities if applying an implicit experimental paradigm).

These combined findings represent a double dissociation of selective impairments in the music or the language domain and have been taken as evidence for the functional autonomy of these mental processes.

Overlap of language and music processing. On the other hand, an increasing number of recent neuroimaging and EEG studies challenge the strict dissociation of music and language processing. Investigating the question of overlapping or specialised mechanisms separately for distinct components of music and language processing (since neither music nor language are monolithic phenomena but comprise a set of isolable functions; see Chapters 1 and 2), these studies consistently demonstrated that several of these subprocesses share more resources than previously believed,¹ e.g., the neural correlates of singing and speaking (e.g., S. Brown et al., 2006; Callan et al., 2006; Ozdemir, Norton, & Schlaug, 2006), the processing of melody in music and pitch contour, i.e., prosody in language (Besson et al., 2007; Magne et al., 2006; Moreno & Besson, 2006; Patel, Foxton, & Griffiths, 2005; Patel & Iversen, 2007; Schön et al., 2004), the processing of rhythm in both domains (Patel, 2003b; Patel & Daniele, 2003; Patel, Iversen, & Rosenberg, 2006), as well as the perception of meaning in music and language (Koelsch, Kasper, et al., 2004; Steinbeis & Koelsch, 2008a, 2008b).

Another line of evidence for shared resources comes from studies on syntax processing. As described in Chapter 3.2.3, studies in this field yielded very similar brain signatures during the processing of syntactically inappropriate words or chords (the ELAN in language: Friederici et al., 1993; Hahne & Friederici, 1999; the ERAN in music: Koelsch et al., 2000; Koelsch, 2005; see also the similarity of the P600 in music and language reported by Patel, Gibson, et al., 1998). Furthermore, it has been illustrated that musical training may enhance

¹Note, however, that none of the studies claims a complete overlap of music and language processing in the studied function.

syntactic processing in language (Jentschke et al., 2005), and conversely, that deficient language processing coincides with an impaired processing of music-syntactic irregularities (Jentschke et al., 2005, 2008; Patel et al., 2008). Finally, behavioural (Fedorenko et al., 2007; Slevc et al., 2007) and ERP experiments (Koelsch, Gunter, et al., 2005; Steinbeis & Koelsch, 2008b) have shown that both domains compete for resources as soon as syntactic errors occur simultaneously in music and language.

Taken together, these combined data suggest (partially) overlapping functions for several aspects of music and language processing, thus, obviously conflicting with the lesion literature that strongly argues for a double dissociation of both domains.

Shared Syntactic Integration Resource Hypothesis (SSIRH). Patel (2003a) recently introduced a theoretical framework that reconciles the apparent contradiction between neuropsychology and neuroimaging for the domain of syntax processing: The Shared Syntactic Integration Resource Hypothesis (SSIRH). This model proposes that the neural resources underlying the procedural aspects of structural integration are domain-general, whereas the actual mental representations of the corresponding syntactic rule system are domain-specific. In other words, the computational units of syntax processing are shared by both domains, whereas the underlying principles of word or chord arrangement are distinct between music and language. Referring to the prevailing literature in the language (e.g., Kaan & Swaab, 2002) and the music domain (e.g., Peretz & Kolinsky, 1993; Griffiths et al., 1997; Ayotte, Peretz, & Hyde, 2002), the SSIRH allocates these separate “representation units” to rather posterior brain areas, whereas the neural location of the hypothesised overlapping “processing units” for language and music are proposed to reside in frontal brain regions.

The assumed domain-general role of frontal brain areas in the analysis of sequential (auditory) information is supported by a number of fMRI and MEG source localisation studies showing that the inferior frontal gyrus (IFG), as well as the adjacent anterior superior temporal gyrus (aSTG) are activated when encountering syntactic errors in both language (e.g., Friederici, Wang, et al., 2000; Friederici, Rüschemeyer, et al., 2003; Rüschemeyer et al., 2005) and music (e.g., Koelsch, Gunter, et al., 2002; Koelsch, Fritz, et al., 2005; Maess et al., 2001; Tillmann, Janata, & Bharucha, 2003; Tillmann, Koelsch, et al., 2006).

However, the mere similarity of brain activations is not sufficient to make a claim on overlapping brain functions. As pointed out in Chapter 4, brain activation (e.g., EEG and MEG) and neuroimaging methods (e.g., fMRI and PET) describe correlations between activated brain areas and a cognitive function, but are not able to clarify whether these structures are crucial for the investigated mental process. Thus, it is possible that brain areas are found to be activated even if they are not directly related to the task, e.g., due to the choice of the

baseline or to co-activations of brain areas belonging to a larger processing network. It is, for example, conceivable that, e.g., the left IFG is crucial for the processing of syntax in language, but not necessary (even if activated) for the processing of harmonic structure in music.

The present study. One way to substantiate the hypothesis of shared resources within the IFG, and possibly aSTG, is to demonstrate that lesions within these brain areas lead to parallel deficits in linguistic and musical syntax processing.

In the language domain, approving evidence for the functional role of left fronto-temporal brain areas in syntax processing has been gathered by numerous studies and case reports (for a review see, e.g., Grodzinsky, 2000; Stowe et al., 2005). The necessity of the left inferior frontal lobe was first demonstrated by the deficits in Broca's aphasics to comprehend semantically reversible passives such as "*The cat was chased by the mouse.*" which can only be correctly understood when relying on syntactic information (e.g., Caplan & Futter, 1986; Caplan, Hildebrandt, & Makris, 1996; Caramazza & Zurif, 1976; Schwartz et al., 1980). These findings have been recently replicated in a patient with temporal hypoperfusion of Broca's area (encompassing BA 44 and BA 45 of the left IFG; Amunts et al., 1999; Amunts & Zilles, 2006) who showed (amongst others) acutely impaired comprehension of semantically reversible sentences, but immediate recovery as soon as the blood flow was restored (Davis et al., 2008). Likewise, patients with left anterior temporal brain lesions have been shown to exhibit marked deficits in comprehending complex morphosyntactic structures (e.g., Dronkers et al., 1994; Grossman et al., 1998). Particular evidence for the essential role of fronto-temporal brain areas in syntax processing in language comes from EEG studies showing that the Early Left Anterior Negativity (ELAN) - a marker of phrase-structure building processes during speech perception - is abolished if left fronto-lateral or anterior temporal brain areas are damaged (Friederici et al., 1998, 1999; Friederici & Kotz, 2003; Kotz, von Cramon, & Friederici, 2003).

Conversely, in the music domain, the processing of syntax has been addressed by only three clinical studies that, however, offer no insight concerning the exact localisation of this function. First, Peretz and Kolinsky (1993) and Peretz et al. (1994) described a patient with left temporal and right fronto-opercular brain lesions exhibiting marked deficits in perceiving scale violations or tonal closure. Yet, the bilateral lesion configuration prevents to conclude on the anatomical substrate of this deficit. Second, by demonstrating that bilateral primary auditory cortex lesions did not disrupt harmonic priming, the study of Tramo, Bharucha, and Musiek (1990) though *excluded* these areas as neural substrate of music-syntactic processing, but did otherwise not clarify which brain regions are *included* in this task. Finally,

Tramo and Bharucha (1991) observed impaired harmonic priming in the right but not the left hemisphere of two split-brain patients, offering tentative evidence for a right hemisphere specialisation for harmony perception in music. Note, however, that this study neither precisely localised the function within the right hemisphere, nor fully excluded the involvement of the left hemisphere in harmonic priming due to the specific task requirements. Taken together, the clinical literature on music-syntactic processing is sparse and does not yield a spatial localisation of the perturbed functions. Therefore, it remains unresolved whether left inferior frontal and left anterior temporal brain structures are particularly relevant for the processing of musical structure.

The present lesion study (Experiment 1B) was designed to fill this gap. Aiming to investigate whether harmonic structure building as part of musical-syntax processing essentially depends on left inferior frontal and/or left anterior temporal brain structures, an EEG music experiment was conducted in patients with circumscribed lesions in the left IFG or the left aSTG. The ERAN elicited by chord sequences with harmonically irregular endings was analysed as an index of intact or disrupted music-syntactic processing (see Friederici et al., 1999; Kotz, von Cramon, & Friederici, 2003, for a parallel approach in the language domain). The reduction or even absence of the ERAN would provide direct evidence for the necessity of the respective brain area in music-syntactic processing. Referring to the well-established fact that the studied brain areas are essentially implicated in linguistic syntax processing, such a finding would additionally specify the neural substrate of overlapping syntax processing in music and language.

Before turning to this study (Experiment 1B), Experiment 1A describes the creation and evaluation of stimulus material particularly suited for this project. The crucial point in this experiment was to eliminate sensory confounds within the chord sequences that could potentially elicit a Mismatch Negativity (MMN; for a review see Näätänen et al., 2007; for a distinction between sensory and cognitive priming see, e.g., Bigand et al., 2003; Koelsch et al., 2007). This is specifically relevant, because the MMN (reflecting the detection of physical deviance; e.g., Winkler, 2007) and the ERAN (reflecting the detection of higher-order music-syntactic irregularities; e.g., Koelsch, in press) emerge in similar time windows, thus, potentially adding up if sensory and music-syntactic errors co-occur (see Hahne, Schröger, & Friederici, 2002, for corresponding results in the language domain). Furthermore, there is evidence for inferior frontal as well as temporal generators of the MMN (e.g., Alho, 1995; Doeller et al., 2003; Opitz, Rinne, Mecklinger, Cramon, & Schröger, 2002; Rinne et al., 2000; Rosburg, Trautner, Dietl, Korzyukov, et al., 2005), i.e., in the brain areas that will be lesioned in Experiment 1B. Hence, the exclusion of any cues triggering processes of sensory deviance detection is vital for the unmistakable attribution of a potential decrease

of the ERAN amplitude to the disruption of music-syntactic (and not sensory deviance) processing.

Chapter 6

Experiment 1A: Pilot Study

Since the seminal work of Bharucha and Krumhansl (1983) on the cognitive representation of harmonic structure in music (see also Chapter 2.1.2), one major branch of research in the field of neurocognition of music has aimed at deciphering the mental representations of music-syntactic regularities in musicians and in non-musicians. The presentation of chord sequences and the comparison of behavioural, electrophysiological, or haemodynamic responses to harmonically related or less related elements has been proven to be a fruitful approach (e.g., Janata, 1995; Koelsch et al., 2000; Patel, Gibson, et al., 1998; Tillmann, Janata, & Bharucha, 2003).

Studies applying chord sequence paradigms are, however, confronted with the problem that music-syntactic regularity is rooted in psychoacoustic similarity of sounds, that is, syntactically related events are also related at a sensory level (see, e.g., Bigand et al., 2003; Bigand, Tillmann, & Poulin-Charronnat, 2006; Koelsch et al., 2007; Leman, 2000; Parncutt, 1989; Tekman & Bharucha, 1998). For example, a tonic chord (e.g., C-E-G) presented at the end of a harmonic sequence in C major is music-syntactically strongly related but also acoustically very similar to the preceding harmonic context, because it contains overlapping frequencies (i.e., overlapping component tones) with the previously presented C major chords. On the other hand, a *Neapolitan chord* (e.g., F-A^b-D^b) as frequently employed by previous studies (e.g., Koelsch et al., 2000; Koelsch, Schmidt, & Kansok, 2002; Koelsch, Gunter, et al., 2005; Loui et al., 2005; Maess et al., 2001; Steinbeis & Koelsch, 2008b) has less pitches in common with its predecessors, representing, thus, not only a music-syntactic irregularity but also a sensory deviant. In other words, changes in behavioural, electrophysiological and haemodynamic measures elicited by these irregular chords cannot simply be attributed to music-syntactic processing, but could be merely grounded on acoustic dissimilarity.

These considerations are specifically relevant for Experiment 1B aiming to investigate whether the integrity of the left inferior frontal (IFG) and the left anterior superior temporal gyrus (STG) is necessary for harmonic structure building in music, taking the ERAN as an index for intact music-syntactic processing. However, as long as the stimuli employed to elicit an ERAN may trigger “cognitive” mechanisms (related to music-syntactic processing) as well as “sensory” mechanisms (related to the processing of the acoustic deviance), it is impossible to determine whether a potential reduction of the ERAN amplitude in brain lesioned patients reflects a deficient processing of harmonic regularities or of acoustic deviance. To even complicate the endeavour, the IFG as well as the STG have been associated with the processing of sensory deviance (see the numerous studies investigating the Mismatch Negativity (MMN), e.g., Doeller et al., 2003; Opitz et al., 2002; Rinne et al., 2000; Rosburg, Trautner, Dietl, Korzyukov, et al., 2005) and musical syntax (e.g., Koelsch, Gunter, et al., 2002; Koelsch, Fritz, et al., 2005; Krumhansl, 2003; Maess et al., 2001; Tillmann, Janata, & Bharucha, 2003; Tillmann, Koelsch, et al., 2006) once more calling for unfounded stimulus material to conclude on the functional significance of these brain areas.

Several approaches have been proposed to untangle sensory and cognitive aspects of harmonic priming (e.g., Bharucha & Stoeckig, 1987; Bigand et al., 2003; Tekman & Bharucha, 1992). In a recent study intending to prove the cognitive rather than sensory origin of the ERAN, Koelsch et al. (2007) constructed chord sequences (containing five chords each) minimising acoustic differences between music-syntactically irregular (*double dominants*, V/V) and regular final chords (tonics, I; see Figure 6.1 A). The stimuli were thoroughly controlled for roughness, pitch repetition, and pitch commonality (Parncutt, 1989) such that the pitches of irregular V/Vs (compared to the tonic chords) were acoustically even more similar to the pitches of the previous harmonic context stored in sensory memory, as supported by the modelling of the short-term memory traces of the stimuli (Leman, 2000; Leman, Lesaffre, & Tanghe, 2005). Notably, these acoustically well balanced chord sequences elicited an ERAN, providing strong evidence that this ERP is not merely a reflection of sensory deviance but is in large parts driven by cognitive processes (for further evidence on a music-syntactic rather than sensory background of the ERAN see the studies comparing ERAN and MMN by, e.g., Koelsch, Gunter, et al., 2001, 2005; see also the review by Koelsch, in press).

The present study is a continuation of this work, excluding further acoustic cues within the sequences of Koelsch et al. (2007) that could still have partly elicited a deviance-related negativity. Special emphasis is placed on the parameter of pitch class repetition. As explained by the authors, regular tonic chords introduced two new pitches with respect to the previous chords (i.e., the C and the E in the base and the top voice, see arrows in the upper

panel of Figure 6.1 A), whereas the irregular V/Vs contained only one new pitch (the F \sharp in the top voice, see arrow in the lower panel of Figure 6.1 A). However, in contrast to tonic chords, this single note in V/Vs represented a new pitch class,¹ i.e., an out-of-key note that had never been presented in the previous context, neither one octave higher nor lower. Given that the V/Vs, thus, introduced a frequency deviant, it is conceivable that the ERAN observed with these stimuli has been at least partly driven by this new pitch class and not exclusively by the music-syntactic irregularity of the V/Vs (but see Koelsch et al., 2007, Experiment 2, for an ERAN elicited by sequences without out-of-key notes).

Addressing this issue, the following chapter presents new chord sequences in which the out-of-key notes of the V/Vs are contained in the harmonic context. The acoustic properties of these stimuli are analysed, and the behavioural and electrophysiological effects elicited by these stimuli and by the sequences of Koelsch et al. (2007, Experiment 1) are compared.

6.1 Acoustic Properties of the New Chord Sequences

The stimuli employed by Koelsch et al. (2007, Experiment 1; termed *Set A* in the remainder of the chapter, see Figure 6.1 A) were modulated to obtain new chord sequences (termed *Set B*, see Figure 6.1 B). Like in previous studies (e.g., Koelsch et al., 2000, 2007), the initial chords, i.e., the harmonic context, was identical in regular and irregular sequences: Dominant [V] - tonic [I] - subdominant [IV] - supertonic [II] - dominant [V]. Regular sequences ended on a tonic chord [T], whereas irregular sequences ended on a *double dominant* [V/V]. Contrary to the sequences of Koelsch et al. (2007), all pitch classes of the final chords (including the new pitch class of the V/Vs, e.g., the F \sharp in C major, see arrow in the lower panels of Figure 6.1) were incorporated into the preceding harmonic context by means of auxiliary and passing notes (see 8th notes in Figure 6.1 B). Apart from balancing the acoustic similarity between final chords and harmonic context, these 8th notes made the sequences more polyphonic resulting in more naturally sounding musical stimuli. Finally, all new sequences started with a dominant upbeat, not with a tonic chord as in previous studies (e.g., Koelsch et al., 2000, 2007), to avoid that final regular chords sounded more similar simply because they repeated the chord function of the first chord.

To test the newly created sequences for their acoustic properties, the roughness of the final chords and the pitch commonality between the final and penultimate chord were calculated according to Parncutt (1989). These analyses showed that roughness values did neither differ between regular ($M = 0.035$) and irregular chords ($M = 0.030$; *t*-test for independent

¹A pitch class contains all pitches that are separated by octaves, e.g., the pitch class C comprises C1, C2, C3, C4 etc.

The figure displays four musical staves in a 2x2 grid. The columns are labeled 'A' and 'B' at the top. The rows are labeled 'regular' and 'irregular' on the left. Each staff shows a piano accompaniment in C major with a sequence of chords. Arrows point to specific notes in the final chord of each sequence that were not present in the previous chords.

- Set A (regular):** Chord sequence I IV II V I. The final I chord has an arrow pointing to the G5 note.
- Set A (irregular):** Chord sequence I IV II V V/V. The final V/V chord has an arrow pointing to the F#5 note.
- Set B (regular):** Chord sequence V I IV II V I. The final I chord has an arrow pointing to the G5 note.
- Set B (irregular):** Chord sequence V I IV II V V/V. The final V/V chord has an arrow pointing to the F#5 note.

Figure 6.1: **A:** Examples of the chord sequences employed by Koelsch et al. (2007, termed “Set A” in the remainder of the chapter). Chord sequences ended either on a regular tonic chord [I] or on a slightly irregular double dominant [V/V]. Arrows mark pitches that were not contained in the previous harmonic context. Note that, even if V/Vs introduced less new pitches than tonic chords, these notes in V/Vs represented a new pitch class (see text for further details). **B:** Examples of the new chord sequences created for the present study (termed “Set B” in the remainder of the chapter). Like in Set A, the final regular chord was a tonic [I], the final irregular chord a double dominant [V/V]. Arrows indicate the pitches that were not contained in the previous chords. Contrary to Set A, however, all of these pitches, including the out-of-key note of the V/Vs (see arrow in the lower panel), were presented one octave higher or lower in the preceding harmonic context using auxiliary and passing notes (see, e.g., the 8th note in the base voice of the supertonic [II] introducing the F# of the V/Vs).

samples: $t(22) = 1.367, p > .185$) nor between sequences of Set A and Set B (as the final chords in both sequences were identical).

As intended, the pitch commonality between the final and the preceding chord was significantly higher in irregular ($M = 0.843$) than in regular sequences ($M = 0.580$; t -test for independent samples: $t(22) = -79.00, p < .0001$), like in the stimuli of Koelsch et al. (2007, irregular: 0.769, regular: 0.563), demonstrating the negative relation between music-syntactic irregularity and acoustic dissimilarity in the new stimuli. A univariate ANOVA with the factors Regularity (I vs. V/V) and Set (A vs. B) revealed a main effect of Regularity ($F(1, 44) = 16350.73, p < .0001$; indicating that, compared to tonic chords, V/Vs had more pitches in common with the preceding dominant chord), a main effect of Set ($F(1, 44) = 621.96, p < .0001$; indicating that the new chord sequences of Set B had higher pitch commonality values than the old sequences of Set A), as well as an interaction of Regularity \times Set ($F(1, 44) = 237.68, p < .0001$) indicating that the pitch commonality difference between irregular and regular sequences was even higher in the new (Set B) compared to the old stimuli (Set A).

Furthermore, auditory modelling was performed using the Contextuality Module of the IPEM-Toolbox (Leman, 2000; Leman et al., 2005). This module estimates the pitch commonality between the actual musical event and the sensory traces of the musical context accumulated in sensory memory and decaying over time. Hence, for each sequence type and for each of the twelve keys, correlations were calculated between a gliding local integration window of 100 ms (pitch image of the current chord) and a global context integration window of 1500 ms duration (echoic memory representation as established by the previously heard context). The results are depicted in Figure 6.2 B. Like in the study of Koelsch et al. (2007, see Figure 6.2 A), the pitch images of the final V/Vs were more congruent with the sensory trace of the preceding context in echoic memory compared to final tonic chords.

Taken together, the results show that the new chord sequences are acoustically well balanced and successfully disentangle cognitive and sensory relatedness. In particular the pitch commonality values (Parncutt, 1989) demonstrate the acoustic improvement of the new sequences (Set B) compared to the stimuli of Set A, due to the incorporation of the new pitch class of the V/Vs into the context. Within the next paragraphs, behavioural and electrophysiological effects of the new and the old sequences will be compared.

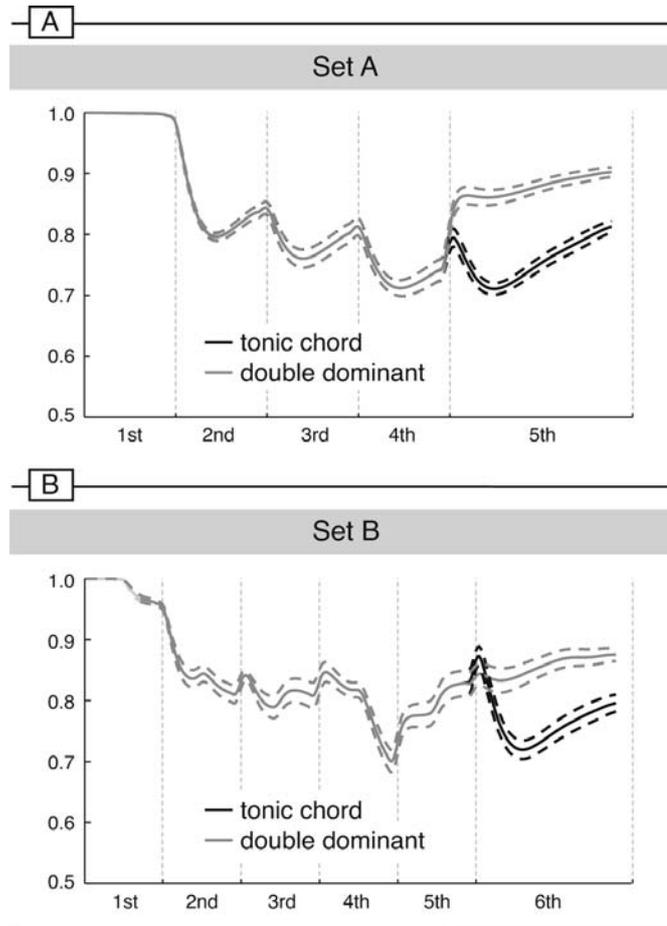


Figure 6.2: Mean correlation of the local pitch image with the global echoic memory representation established during listening, separately for the sequences of Set A (top; adapted from Koelsch et al., 2007) and the new sequences (Set B, bottom). The abscissa depicts the time line (all chords had a duration of 500 ms except the final chords that were presented with a duration of 1000 ms). The ordinate indicates correlation values. The graphs show that the irregular VIVs (grey solid line) were acoustically more congruent with the preceding harmonic context than regular tonic chords (black solid line). Dashed lines indicate the standard error of mean (SEM). Modelling was performed using the Contextuality Module of the IPeM-Toolbox (Leman, 2000, see text for further details).

6.2 Behavioural Experiment

6.2.1 Methods

Participants. To estimate the detectability of the irregular sequence endings, 16 right-handed students (mean handedness according to the Edinburgh Handedness Inventory (Oldfield, 1971): 89.62%, 10 women, mean age: 23.31 years, age range: 18-27 years) participated in a behavioural experiment. None of them had ever learned to play a musical instrument, and musical education did not exceed music classes at school. None of the participants reported hearing difficulties or neurological and psychiatric disorders.

Stimuli. Participants were presented with the new sequences introduced in the previous section (see Section 6.1). Hence, the stimulus material consisted of the two sequences (regular and irregular) shown in Figure 6.1 B transposed to all twelve major keys resulting in 24 different stimuli. Sound files of the sequences were generated using Cubase SX 2.0 (Steinberg Media Technologies, Hamburg, Germany) with a grand piano sound (Steinberg, The Grand). The presentation time of all chords was 500 ms, except the critical final chords which lasted 1000 ms and were followed by a 1500 ms pause. Compared to the study of Koelsch et al. (2007), stimuli were slightly speeded up to allow the acquisition of more trials within a shorter experimental time. Having forethought to the work with brain lesioned patients unable to attend to long lasting experiments (see Experiment 1B in Chapter 7) this is a way to keep an appropriate signal-to-noise ratio (SNR) in short sessions. Across the experiment, participants listened to 96 (pseudo-)randomly presented chord sequences. Consecutive sequences always had a different tonal key and not more than 3 sequences of the same type followed each other. Regular and irregular sequences occurred equiprobably ($p = .5$).

Procedure. During the experiment, listeners were seated in a sound shielded room. Stimuli were presented via Headphones (Sennheiser HD 202) with PRESENTATION 0.53 (Neurobehavioral Systems, Inc., Albany, Canada). Participants were asked to indicate as quickly and accurately as possible via button press whether the final chord was a regular or an irregular ending of the harmonic progression, i.e., whether the composer intended to close or to continue the sequence. Key assignment was counterbalanced across subjects. The experiment had a duration of approximately 10 minutes.

6.2.2 Results

Participants had on average 66.21% correct responses ($SD = 13.11\%$), that is, they performed significantly above chance level (one sample t -test with test-value 50: $t(15) = 4.95, p < .001$). The overall performance in the present experiment was tendentially lower ($p < .054$) and reaction times were significantly longer ($p < .011$) than in the study of Koelsch et al. (2007, see Table 6.1 for detailed statistical values).

	Set A	Set B	$t(30)$	p -value
Hits (%)	75.86	66.21	2.02	< .054
RT (ms)	732.72	970.06	-2.74	< .011

Table 6.1: Hit rates and reaction times (RT) observed in non-musicians by Koelsch et al. (2007, Set A) and in the present experiment with the newly created stimulus material (Set B). Hit rates were tendentially lower and reaction times significantly longer during the new sequences of Set B as assessed with two-sample t -tests (see t - and p -values).

6.2.3 Discussion

Participants were able to detect the irregular chords in the new sequences, even if the out-of-key note of the V/Vs was contained in the preceding context. The data, thus, replicate the results of Koelsch et al. (2007, Experiment 3), and demonstrate that the detection of the music-syntactic irregularities reported by the authors was unlikely to be caused only by the new pitch class introduced by the V/Vs. Furthermore, the data show that the irregularity of the final V/Vs can be also detected at an increased tempo of presentation (500/1000 ms in the present compared to 600/1200 ms in previous studies), however, apparently at the expense of performance accuracy and speed of response, which is in keeping with the data of Bigand et al. (2003) and Tekman and Bharucha (1992) describing a systematic decrease of response accuracy and speed with increasing tempo of the chord sequences.

Alternatively, the lower performance in the present experiment compared to Koelsch et al. (2007) may be explained in terms of *sensory similarity*. The lower outcome may, thus, be associated with the higher acoustic overlap between V/Vs and the harmonic context in the present sequences (Set B) compared to the sequences of Koelsch et al. (2007, but see the Results of Experiment 2A for an alternative view). Hence, this account would suggest that the new pitch class of the V/Vs in Set A actually impacts on the detection of the irregularities (even if only minimally) and, thus, justifies the attempt of the present study to exclude this potentially confounding factor.

On the other hand, the lower outcome may also be interpreted with respect to *cognitive* mechanisms: The incorporation of the out-of-key note in the harmonic context as well as the presentation of a dominant instead of the tonic at the first position of the chord sequences, may have resulted in a less strong representation of the actual key and, consequently, less specific harmonic expectations of the listeners. Final V/Vs of Set B were, thus, perceived as less unexpected than the V/Vs of Set A accounting for the reduced performance. Similar results on the impact of key representation have been reported by a previous study observing significantly lower hit rates and nominally longer reaction times for irregular Neapolitan chords presented at the third compared to the fifth position of chord sequences (58% and 584 ms vs. 79% and 559 ms Koelsch et al., 2000, Experiment 3). Like in the present study, these results were taken to reflect the differential strength of key representation and the differential specificity of the listeners' expectations on upcoming events at different stages of context build-up (third vs. fifth position). Further studies are needed to clarify whether the sensory or the cognitive interpretation, or possibly both, apply to the present results (see, e.g., Experiment 2A for strong evidence for the cognitive account).

Finally, the data demonstrate the sophisticated ability of non-musicians to process musical structure without explicit musical training, providing further evidence for the apparently incidental acquisition of an implicit representation of the harmonic hierarchy of the Western tonal idiom during every day listening (see, e.g., Bigand et al., 2003; Bigand & Poulin-Charronnat, 2006; Koelsch et al., 2000; Tillmann et al., 2000).

Taken together, the ability of the participants to identify music-syntactic irregularities that were reassessed with respect to pitch class repetition, indicates that the detection of the irregular chords in the study of Koelsch et al. (2007) was not only driven by the new pitch class of the V/Vs, but strongly relied on the (implicit) music-syntactic knowledge of the listeners. Hence, these results support the prevalence of cognitive over sensory mechanisms in the processing of harmonic structure (see also Bharucha & Stoeckig, 1987; Bigand et al., 2003; Tekman & Bharucha, 1998). In this context, assuming a mainly cognitive rather than sensory origin of the ERAN, it is hypothesised that the present stimulus material (like the stimuli of Koelsch et al., 2007) will elicit an Early Right Anterior Negativity (ERAN). The slightly lower performance observed for the new (Set B) compared to the old sequences (Set A) predicts, however, a potentially smaller ERAN amplitude during the presentation of the sequences of Set B than of Set A.

6.3 EEG Experiment

To test these predictions, an EEG experiment was conducted comparing the ERPs elicited by the new sequences (Set B) and by the stimuli of Koelsch et al. (2007, Set A) within subjects. As an aside, the study was conducted with musicians and non-musicians to test whether musical novices and participants with extensive musical practise rely to different degrees on sensory cues or cognitive mechanisms respectively. Such a difference would be well conceivable because trained musicians have a more sophisticated cognitive representation of the regularities of the Western harmonic system than non-musicians (even if those have a profound implicit knowledge on the regularities; Koelsch, Schmidt, & Kansok, 2002; Koelsch, Fritz, et al., 2005). Accordingly, it was predicted that the ERAN amplitude may be diminished in non-musicians when listening to the acoustically adjusted sequences compared to the sequences of Koelsch et al. (2007), because they possibly rely more strongly on sensory cues than musicians. The ERAN amplitude in musicians, however, should remain unaffected by the acoustic manipulation assuming that musically trained subjects would rely predominantly on their cognitive representation of harmonic structure.

6.3.1 Methods

Participants. Data were collected from 12 musicians (age range: 23-28, mean age: 25.58 years, 6 men) and 12 non-musicians (age range: 19-27, mean age: 23.42 years, 6 men). Musicians had learned at least one instrument for on average 14.25 years (age range: 8-20 years) and were still actively playing at the time of the experiment. Non-musicians did not have any formal musical training besides typical school education and had never learned to play a musical instrument. All participants were right handed (mean LQ = 93.79%) according to the Edinburgh Handedness Inventory (Oldfield, 1971), and reported to have normal hearing and no neurological disease. None of the participants had participated in the behavioural experiment.

Stimulus Material. Participants were presented with the two different sets of chord sequences. *Set A* (see Figure 6.1 A) comprised the sequences employed by Koelsch et al. (2007, Experiment 1) presented at a faster rate (500/1000 ms instead of 600/1200ms, see below) for a better comparability with the new sequences (Set B). Each sequence consisted of five chords, the chord functions of the first four chords were identical in regular and irregular sequences: Tonic [I] - subdominant [IV] - supertonic [III] - dominant [V]. The fifth

chord was a tonic chord [I] in regular sequences (Figure 6.1 A, top), and a *double dominant* [V/V] in the irregular sequences (Figure 6.1 A, bottom).

Set B (see Figure 6.1 B) consisted of the newly created sequences described above (see Section 6.1). Like in Set A, both sequence types differed only with respect to the final chord, the other chords were identical: Sequences began with a dominant [V] upbeat, followed by a tonic [I] - subdominant [IV] - supertonic [II] - dominant [V]. Regular sequences ended on a tonic chord [I] (Figure 6.1 B, top), whereas irregular sequences ended on a V/V as in Set A (Figure 6.1 B, bottom). Additionally, 8th notes (auxiliary and passing notes) were inserted in a polyphonic fashion, incorporating the out-of-key note of the V/V (F \sharp in C-major) into the context.

Both sequence types (regular and irregular) of both sets (A and B) were transposed to all twelve major keys and generated using Cubase SX 2.0 (Steinberg Media Technologies, Hamburg, Germany) with a grand piano sound (Steinberg, The Grand), resulting in 48 different stimuli. In addition, a second sound file of each of the 48 sequences was generated with one chord being played by a deviant instrument (bells, VST-sound a1) to provide the participants with an easy detection task (see below). Such timbre deviants occurred with equal probability at any of the chord positions. The presentation time of all chords was 500 ms, except of the critical final chords which lasted 1000 ms and were followed by a 500 ms pause. Across the experiment, each piano sequence was presented 16 times (plus 88 sequences which contained a chord played by a deviant instrument) resulting in 856 sequences presented in total. Regular and irregular sequences occurred equiprobably ($p = .5$), consecutive sequences always had a different tonal key and not more than 3 sequences of the same type (regular or irregular) followed each other.

Procedure. Stimuli of Set A and Set B were presented in different blocks, counterbalanced across subjects. Each block was further subdivided into two sub-blocks. In the first sub-block, participants looked at a fixation cross while listening to the stimuli; in the second sub-block, they watched a silent movie (without subtitles, reduced to 1/4th of its original size in order to avoid eye movement artefacts). This “entertainment” was chosen to allow the acquisition of more trials to increase the SNR. The duration of the experiment was approximately 60 minutes.

Participants sat in a comfortable chair in a sound proof cabin. Stimuli were presented via loudspeakers at a comfortable volume using PRESENTATION 0.53 (Neurobehavioral Systems, Inc., Albany, Canada). Participants were not informed about the regular and irregular sequence endings, but were asked to press a button whenever they detected a deviant instrument. This task has already been employed in a number of previous studies (e.g., Koelsch et

al., 2000, 2007; Koelsch & Jentschke, 2008; Miranda & Ullman, 2007; Poulin-Charronnat et al., 2006) and allowed to control that listeners attended to the stimuli. Furthermore, it prevented ERPs like the N2b or P300 that would have been elicited during an overt discrimination task, and overlap with the ERAN and the N5, thus, obscuring brain potentials of music-syntactic processing (see, e.g., Experiment 1 in Koelsch et al., 2007).

Data Recording and Analysis. The EEG was recorded with 30 Ag/AgCl cap-mounted electrodes (Electrocap International) according to the extended 10–20 system (cf., Sharbrough et al., 1991). The electrode positions were: FP1/2, AF7/8, AF3/4, AFZ, F7/8, F3/4, FZ, FT7/8, FC3/4, T7/8, C3/4, CZ, CP5/6, P7/8, P3/4, PZ, O1/2). Left mastoid (M1) served as reference; an additional electrode was placed on the nose-tip and the right mastoid bone (M2) for off-line re-referencing. The ground electrode was located on the sternum. To monitor eye movements and blinks, horizontal and vertical electrooculograms (EOG) were bipolarly recorded from electrodes placed on the outer canthus of each eye (horizontal EOG), as well as above and below the right eye (vertical EOG). Impedances were kept below 5 k Ω . Signals were amplified with two synchronised PORTI-32/MREFA amplifiers (Twente Medical Systems International B.V., Enschede, NL) and digitised with a sampling rate of 250 Hz.

After the measurement, data were re-referenced to linked mastoids and filtered using a 0.5–20-Hz bandpass filter (finite impulse response (fir), 1001 points, hamming window). For artefact reduction, EEG data were rejected whenever the standard deviation of the signal recorded at any electrode exceeded 25 μ V within a 200-ms or 800-ms gliding window. Additionally, trials with typical eye blinks were marked and corrected by applying an electrooculogram correction tool (xeog, EEP software 3.2 for Unix; Nowagk & Pfeifer, Leipzig, Germany; see Friederici et al., 1999, for a detailed description of the tool). Finally, ERPs were calculated separately for the regular and irregular final chords of each set using a 200-ms prestimulus baseline and a 1000-ms poststimulus window. Sequences containing deviant instruments were excluded from the analysis because being targets they triggered cognitive mechanisms other than mere music-syntactic processing.

For statistical analysis, mean amplitude values within a time window from 160 to 200 ms (centred around the ERAN peak) were calculated for 4 Regions of Interest (ROIs; see also Figure 6.3 B): Left anterior (AF3, F7, F3, FT7, FC3), right anterior (AF4, F8, F4, FT8, FC4), left posterior (T7, C3, CP5, P7, P3), and right posterior (T8, C4, CP6, P8, P4). An ANOVA for repeated measures with the within-subjects factors Chord (regular [I] vs. irregular [V/V]), Hemisphere (left vs. right), AntPost (anterior vs. posterior), Set (A vs. B), VisStim (fixation cross vs. movie), and the group factor Expertise (musicians vs. non-

musicians) was calculated. Since no interaction involving VisStim and Chord ($p > .135$) was found (indicating that the ERAN was not affected by the visual stimulation), data of the blocks with fixation cross and silent film were pooled (separately for Set A and B) to enhance the statistical power, resulting in a 5-way ANOVA with the factors Chord, Hemisphere, AntPost, Set, and Expertise. Whenever an interaction was observed at a significance level of $p \leq .05$, subsequent analyses were conducted by splitting up the general linear model (GLM). The same analysis was computed for a later time window from 450 to 700 ms covering the N5.

6.3.2 Results

Behavioural Data. Participants detected on average 99.48% of the deviant instruments and had only about 0.58% false alarms, showing that they attended to the musical stimuli and reliably identified the deviant instruments. Hit rates did not differ between sets ($p > .08$) or groups ($p > .1$).

ERAN time window (160..200 ms). Figure 6.3 A shows the ERPs elicited by regular and irregular sequence endings separately for Set A and Set B, and separately for musicians and non-musicians. V/Vs of both stimulus sets elicited an ERAN (see also Table 6.3) with a mean peak latency of 180 ms. As can be best seen in Figure 6.3 B, the effect was maximal at fronto-central electrodes and was larger at right than left frontal leads. At frontal electrodes, sequences of Set A evoked larger ERAN amplitudes than stimuli of Set B. Finally, the ERAN tended to be larger and more strongly right lateralised in musicians than in non-musicians (Figure 6.3 B). If re-referenced to the nose electrode, the ERAN inverted polarity at mastoidal leads (see Figure 6.3 C) excluding that this negativity represents an N2b (the N2b has a central maximum, is not lateralised, and does not invert polarity).

A global ANOVA for repeated measures with the within-subjects factors Chord, Hemisphere, AntPost, Set, and the between-subjects factor Expertise (see Chapter 6.3.1) revealed a main effect of Chord ($p < .0001$) indicating that irregular chords elicited an ERAN, an interaction of Chord \times Hemisphere ($p < .007$) indicating that the ERAN was right-lateralised, as well as an interaction of Chord \times AntPost ($p < .0001$) reflecting the frontal scalp distribution of the ERAN (see Table 6.3 for detailed statistical values). Furthermore, a significant three-way interaction of Chord \times Set \times AntPost ($p < .033$) was found, indicating that the ERAN elicited by the two sequence types differed at anterior leads. Follow-up ANOVAs with factors Chord, Hemisphere, Set, and Expertise computed separately for anterior and posterior ROIs showed a significant interaction of Chord \times Set at anterior

ROI	Musicians		Non-musicians	
	Set A	Set B	Set A	Set B
<i>ERAN time window: 160..200 ms</i>				
left anterior	-2.02 (\pm 0.87)	-1.59 (\pm 1.02)	-1.70 (\pm 1.07)	-1.31 (\pm 0.91)
right anterior	-2.58 (\pm 0.71)	-1.86 (\pm 0.92)	-1.99 (\pm 1.08)	-1.29 (\pm 1.14)
left posterior	-1.14 (\pm 0.70)	-1.13 (\pm 0.87)	-0.97 (\pm 1.12)	-0.84 (\pm 0.72)
right posterior	-1.61 (\pm 0.80)	-1.30 (\pm 0.74)	-1.17 (\pm 1.27)	-0.73 (\pm 0.83)
<i>N5 time window: 450..700 ms</i>				
left anterior	-0.51 (\pm 0.72)	-0.31 (\pm 0.55)	-0.42 (\pm 0.53)	-0.26 (\pm 0.37)
right anterior	-0.71 (\pm 0.87)	-0.29 (\pm 0.58)	-0.49 (\pm 0.68)	-0.40 (\pm 0.38)
left posterior	-0.17 (\pm 0.39)	-0.09 (\pm 0.63)	-0.35 (\pm 0.47)	0.00 (\pm 0.39)
right posterior	-0.35 (\pm 0.50)	-0.10 (\pm 0.45)	-0.55 (\pm 0.79)	-0.14 (\pm 0.30)

Table 6.2: Mean ERAN and N5 amplitudes (μ V; \pm SD) elicited in musicians and non-musicians by the old sequences of Set A and the new sequences of Set B in anterior and posterior ROIs.

($F(1, 22) = 4.79, p < .039$) but not posterior electrodes ($F(1, 22) < 1, p > .341$), demonstrating that at frontal sites the sequences of Set A elicited a larger ERAN than the sequences of Set B. The interaction of Chord \times Expertise missed the level of significance in the global ANOVA ($p > .104$), even if musicians had a nominally larger ERAN than non-musicians (see Table 6.2). Finally, the interaction of Chord \times Set \times Expertise was far away from being significant ($p > .92$) indicating that non-musicians did not rely more strongly on sensory cues than musicians, even if their cognitive representations of the Western harmonic system may be less explicit than in musically trained subjects.

N5 time window (450..700 ms). In both stimulus sets, the ERAN was followed by a later anterior negativity (see Figure 6.3 B) peaking around 500 ms after onset of the irregular V/Vs, the N5 (Koelsch et al., 2000). The N5 was slightly right-lateralised, and was larger in Set A than in Set B, but did not differ between musicians and non-musicians.

A global ANOVA analogous to the one carried out for the ERAN computed for a time window from 450 to 700 ms revealed a significant main effect of Chord ($p < .001$) indicating that irregular V/Vs elicited an N5, an interaction of Chord \times AntPost ($p < .014$) reflecting the frontal scalp distribution of the N5, and an interaction of Chord \times Hemisphere ($p < .027$), demonstrating the right-lateralisation of the N5 (see Table 6.3 for detailed statistical values). Moreover, a significant interaction of Chord \times Set was observed ($p < .050$), showing that stimuli of Set A evoked a larger N5 than sequences of Set B. Follow-up ANOVAs with the factors Chord, Hemisphere, AntPost, and Expertise calculated

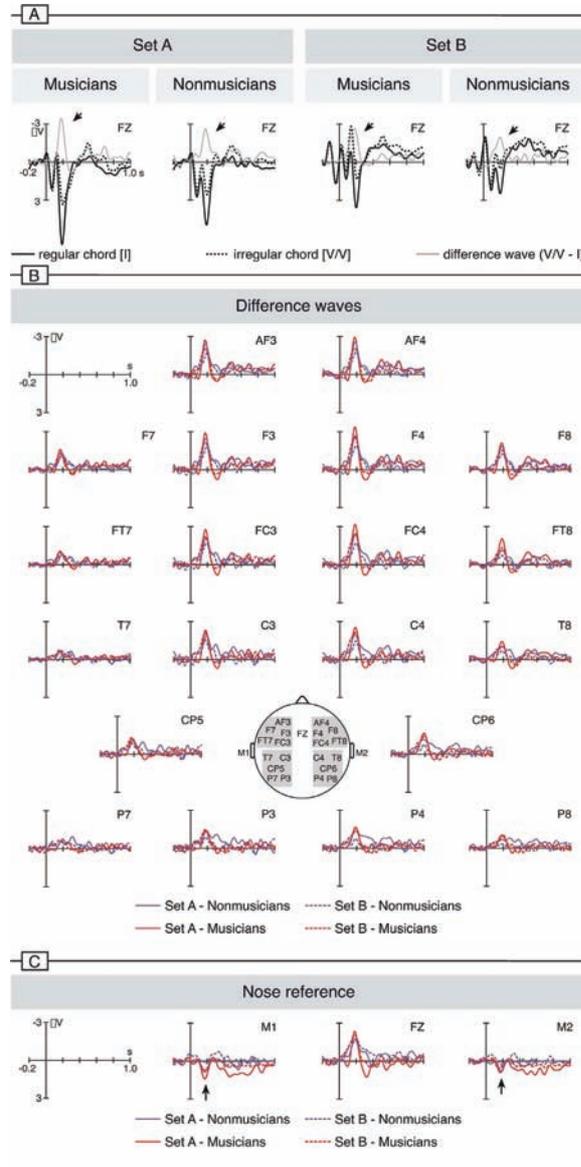


Figure 6.3: **A:** ERPs elicited by the regular (thick solid line) and irregular chords (dotted line) at electrode FZ (referenced to linked mastoids). Stimuli of both sets (A and B) elicited an ERAN in both groups (musicians and non-musicians; see arrows). **B:** Difference waves (I subtracted from V/Vs) depicted for Set A (solid lines) and Set B (dashed lines) in musicians (red lines) and non-musicians (blue lines). All electrodes entering the statistical analysis are shown, regions of interest (ROIs) are shaded in grey in the head schema. At frontal sites, stimuli of Set A elicited a larger ERAN than sequences of Set B. Musicians showed a nominally higher ERAN amplitude than non-musicians. **C:** The ERAN inverted polarity at mastoid leads (M1, M2; see arrows) when potentials were referenced to nose electrode, differentiating the ERAN from an N2b.

Factors	ERAN (160..200 ms)		N5 (450..700 ms)	
	<i>F</i> (1, 22)	<i>p</i> -value	<i>F</i> (1, 22)	<i>p</i> -value
Chord	148.48	< .0001	21.54	< .001
Chord × Expertise	2.88	> .104	0.01	> .940
Chord × Hemisphere	8.88	< .007	5.67	< .027
Chord × AntPost	29.87	< .0001	7.28	< .014
Chord × Set	2.87	> .104	4.32	< .050
Chord × Hem. × Exp.	3.32	< .082	0.23	> .636
Chord × Hem. × AntPost	1.52	> .230	0.49	> .492
Chord × Hem. × Set	3.53	< .074	0.72	> .404
Chord × AntPost × Exp.	0.08	> .781	0.91	> .350
Chord × AntPost × Set	5.22	< .033	0.11	> .748
Chord × Set × Exp.	0.01	> .920	0.00	> .953
Chord × Hem. × AntPost × Exp.	0.00	> .997	0.40	> .531
Chord × Hem. × AntPost × Set	0.00	> .963	0.15	> .706
Chord × Hem. × Set × Exp.	0.00	> .982	0.91	> .350
Chord × AntPost × Set × Exp.	0.24	> .628	1.65	> .212
Chord × Hem. × AP. × Set × Exp.	0.00	> .951	0.62	> .438

Table 6.3: Summary of the global ANOVAs with the factors Chord × Hemisphere × AntPost × Set × Expertise for the ERAN and the N5. Only main effects and interactions involving the factor Chord are depicted. Bold font indicates significant effects ($p < .05$). Hem. = Hemisphere, Exp. = Expertise, AP. = AntPost.

separately for Set A and Set B showed that stimuli of both sets elicited a significant N5 (main effect of Chord for Set A: $F(1, 22) = 19.58, p < .001$; Set B: $F(1, 22) = 5.88, p < .025$).

6.3.3 Discussion

The present data replicate the findings of Koelsch et al. (2007) on the predominant role of implicit music-syntactic knowledge (opposed to the role of psychoacoustic similarity) during the processing of harmonic progressions. Irregular V/Vs of both sets of stimuli elicited an ERAN (and an N5), even though the irregular V/Vs had more pitches in common with the previous context than regular tonic chords (Set A and B), and the V/Vs' out-of-key note was incorporated into the harmonic context (Set B). These data, thus, confirm that the ERAN is rather unlikely to be caused only by the occurrence of sensory dissimilarities,²

²It remains to be tested in future studies in how far the ERAN is influenced by the fact that the pitches of the final tonic chord are repeated more often in the previous context than the pitches of the V/Vs.

and more specifically that the ERAN reported by Koelsch et al. (2007) was not (or only minimally) grounded on the new pitch class occurring in the irregular V/Vs. Hence, the present findings assent to the notion of a prevalence of cognitive over sensory mechanisms at the origin of the ERAN (see also Bharucha & Stoeckig, 1987; Bigand et al., 2003; Tekman & Bharucha, 1998, for similar conclusions in behavioural studies on harmonic priming).

The ERAN was larger when elicited by sequences of Set A than by those of Set B, mirroring the higher detection rate of V/Vs in sequences of Set A than Set B observed in the behavioural experiment (see Section 6.2). This finding may be explained in favour of sensory as well as of cognitive theories, and, clearly, future studies are necessary to untangle these conflicting views:

According to a *sensory account*, the amplitude reduction may be due to the higher similarity between final irregular chords and the harmonic context in Set B. This interpretation implicates that the ERAN elicited by the stimuli of Set A (even though largely determined by cognitive processes) has been still partly driven by sensory mechanisms owing to the new pitch class introduced by V/Vs, justifying the aim of the present study to exclude this confounding factor (but see Chapter 9 for results showing that stimuli that are acoustically less well controlled elicit a smaller ERAN than the present stimuli, arguing strongly against a sensory account).

According to a *cognitive account*, the occurrence of the out-of-key notes in the context of Set B as well as the presentation of a dominant instead of a tonic chord at the first position may have made the extraction of the tonal centre more difficult, resulting in a less stable key representation at the time of the final chord, making V/Vs in Set B perhaps more acceptable than V/Vs in Set A. Correspondingly, the impact of the degree of key establishment has been demonstrated in previous studies (e.g., Koelsch et al., 2000; Koelsch, Gunter, et al., 2001; Maess et al., 2001) comparing the ERPs elicited by irregular Neapolitan chords presented at the third or at the fifth position of a harmonic progression, i.e., at different stages of context build-up. In support of our interpretation, Neapolitan chords at the third position evoked a smaller ERAN than those at the fifth position most presumably based on a less distinct key representation and less specific expectations on upcoming events at the time of the third compared to the fifth chord. Consequently, the integration of irregular Neapolitan chords at the third position required less processing resources than those at the fifth position. The V/Vs of Set B presented in a harmonically less clear context than V/Vs of Set A possibly tapped into a similar mechanism.

Finally, even if the ERAN tended to be larger in musicians than in non-musicians, demonstrating that music-syntactic processing is enhanced by long-term musical training (e.g., Jentschke et al., 2005; Koelsch, Schmidt, & Kansok, 2002; Koelsch et al., 2007; Koelsch, in press), no difference of listening behaviours in terms of a preference for sensory or cognitive cues was found between musical novices and musically highly trained participants (no interaction of Chord \times Set \times Expertise). The present findings, thus, converge with a number of studies showing that non-musicians' brains process Western musical harmonies after the same principles as musicians do (e.g., Bigand & Poulin-Charronnat, 2006; Koelsch et al., 2000).

6.4 Conclusion

In summary, the present study successfully created new chord sequences that were carefully controlled for a number of sensory confounds like roughness, pitch (class) repetition, and pitch commonality. The combined findings illustrate that the ERAN elicited by these stimuli reflects mainly cognitive music-syntactic processing. Hence, the present chord sequences are particularly suited as stimulus material in a lesion study aiming to investigate the necessity of circumscribed brain areas (e.g., the left IFG and aSTG) in the processing of musical syntax. On part of the stimuli, a potential reduction of the ERAN amplitude in these patients can be confidently attributed to a disruption of the underlying cognitive rather than sensory mechanisms.

Chapter 7

Experiment 1B: Music-syntactic processing in patients with lesions in left fronto-temporal ‘language areas’

As lined out in Chapters 3.2.3 and 5, an increasing number of behavioural (Fedorenko et al., 2007; Slevc et al., 2007; Patel et al., 2008) and EEG studies (Jentschke et al., 2005, 2008; Koelsch, Gunter, et al., 2005; Steinbeis & Koelsch, 2008b) point to a functional overlap of syntax processing in language and music. These findings lend support for the Shared Syntactic Integration Resource Hypothesis (SSIRH) set up by Patel (2003a), proposing domain-general procedural components of musical and linguistic syntax processing that act on domain-specific representations of music and language. The model suggests that these overlapping processing units are located in frontal brain areas that have been previously associated with the analysis of sequential information across different domains, e.g., language (e.g., Friederici, 2002; Grodzinsky, 2000), and music (e.g., Janata & Grafton, 2003; Koelsch & Siebel, 2005; Krumhansl, 2004; Tillmann, Koelsch, et al., 2006).

The present experiment tested the hypothesis of domain-general anterior brain regions by examining whether patients with lesions in the left IFG or the left aSTG, i.e., in brain regions known to be essential for syntax processing in language (see Chapters 1 and 5), exhibit deficits in the processing of musical structure. The amplitude and scalp distribution of the ERAN (an electrophysiological marker of musical syntax processing) were investigated as

a function of lesion site and lesion onset in 13 brain damaged patients and matched healthy controls. It was hypothesised that:

1. The patients would exhibit a significantly smaller ERAN amplitude than the controls, but that the ERAN would not be completely abolished due to still functional generators within the right hemisphere.
2. The scalp topography of the ERAN would differ between patients and controls due to the breakdown of the left hemispheric generators.
3. The amplitude reduction and topography shift would be less pronounced in patients with chronic compared to more recent lesions due to the influence of neuronal reorganisation processes.

7.1 Methods

7.1.1 Patients

Lesion site. The present study investigated musical structure building in two patient groups and two matched groups of healthy controls. Patients were chosen according to their lesion site and not according to functional deficits, because the focus of the present study was the anatomical, not the functional overlap of musical and linguistic syntax processing (see Patel et al., 2008, for the inverse approach, focusing on functional deficits independent of lesion site).

The first lesion group comprised six patients (one woman) with lesions encompassing the left inferior frontal gyrus (IFG) including the pars opercularis and the pars triangularis, encroaching upon the deep frontal operculum and the anterior insula in most of the cases. The temporal lobe was spared in all patients (see Table 7.1 and Figure 7.1). The lesions had different aetiologies, e.g., ischemic stroke ($N = 4$), cerebral haemorrhage ($N = 1$), or tumour resection ($N = 1$; see Table 7.1). Five patients were right-handers, one patient was ambidexter according to the Edinburgh Handedness Inventory (Oldfield, 1971). They had a mean age of 52.50 years (age range: 22-67 years) and had suffered their lesion on average 7 years and 1 month before they participated in the present study (range: 7 months - 10 years 5 months). Education varied from 8 to 12 years ($M = 10$), accumulated musical practise over life time ranged from 0 to 4 years ($M = 1.67$; see Table 7.2 for detailed information).

The second lesion group comprised seven patients (two women) with lesions in the left anterior temporal lobe including the anterior superior temporal gyrus (aSTG) and the planum

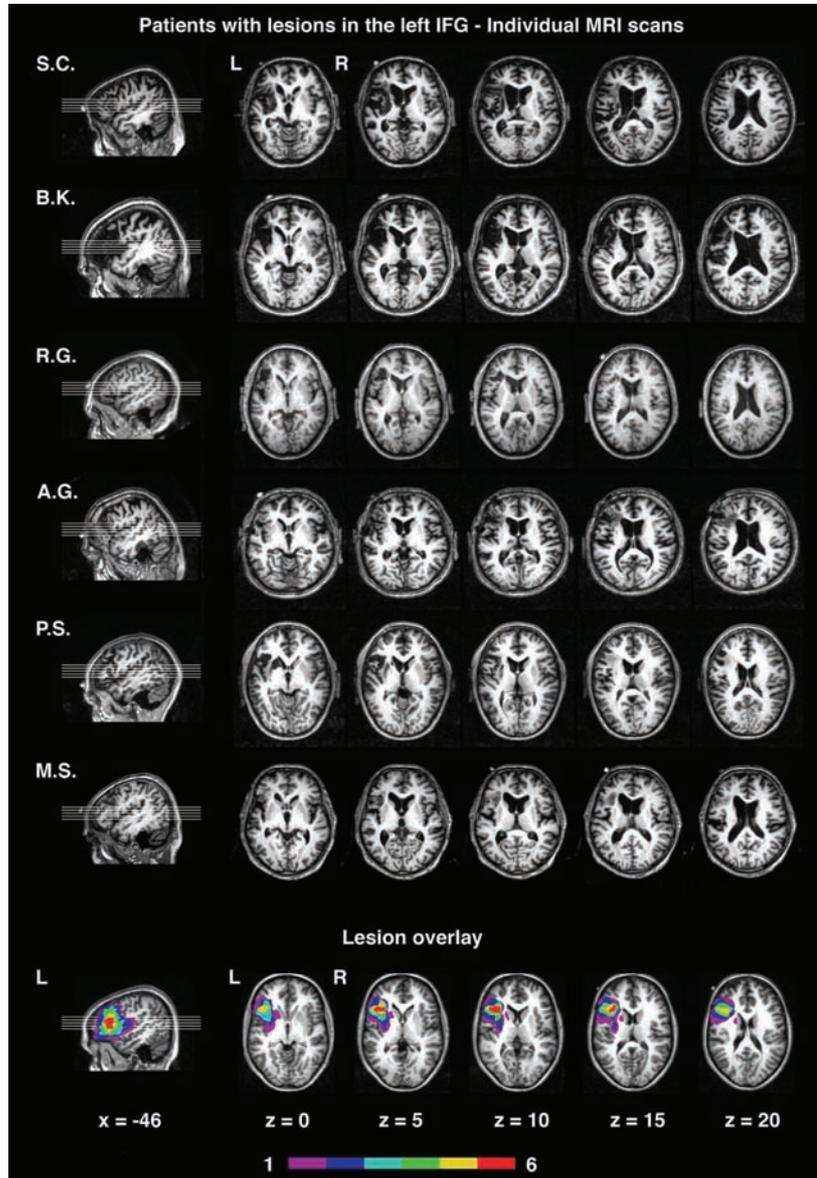


Figure 7.1: MRI scans of the left IFG lesion group. Each row depicts five slices (Talairach z 's = 0, 5, 10, 15, and 20) of one individual suffering from a lesion within the left IFG. Notably, the left aSTG region is unaffected in all patients. The lowest panel shows an overlay of the lesions of all patients. The colour code indicates the number of patients having a lesion in the given area (purple = 1 patient, red = all 6 patients).

polare (PP). Heschl's gyrus and the frontal lobe were spared in all patients (see Table 7.1 and Figure 7.2). Lesion aetiology differed between patients, e.g., ischemic stroke ($N = 1$), tumour resections ($N = 2$), traumatic brain injuries ($N = 2$), or herpes encephalitis ($N = 2$; see Table 7.1). Six patients were right-handers, one was ambidexter. They had a mean age of 54.71 years (age range: 49-62 years) and had suffered their lesion on average 7 years before they participated in the present study (range: 4 years 2 months - 8 years 11 months). Education varied from 10 to 12 years ($M = 11.43$), the accumulated musical practise over life ranged from 0 to 12 years ($M = 2$; see Table 7.2 for detailed information).

Language comprehension. Patients showed only very mild or no language comprehension deficits at the time of testing as assessed by the Token Test, a subtest of the Aachen Aphasia Test (Huber, Poeck, Weniger, & Willmes, 1993, see Table 7.2). Note, however, that all patients had been diagnosed with aphasic deficits at lesion onset, demonstrating the impact of neuronal reorganisation that has acted during the on average 7 years since brain injury (Marsh & Hillis, 2006). Yet, an above-cut-off performance in language tests does not necessarily indicate unimpaired language processing as in non-brain-damaged individuals. In spite of an apparent recovery as assessed by off-line methods (i.e., behavioural measures), the enduring impairment of language processing can be demonstrated by on-line measures, like EEG. To give an example, patients S.C. and B.K. (corresponding to patients 009 and 102 in Friederici et al., 1999), readily detected word-category errors in sentences (96% and 100%) but did not display an ELAN as healthy controls, indicating persistent deficits in the processing of linguistic syntax. For these reasons, the presence of only minimal behavioural language deficits did not deter from investigating musical syntax processing in these patients by means of EEG.

Cognitive abilities. To rule out severe cognitive impairments caused by the lesion, abstract reasoning (taken as an index for nonverbal intelligence), as well as short term (STM) and working memory (WM) capacities were assessed in all patients. Therefore, the third subtest of the L-P-S (Leistungsprüfsystem; Horn, 1983) or L-P-S 50+ (if the patient was older than 50 years; Sturm, Willmes, & Horn, 1993)¹ was applied as intelligence measure. The blockspan test forward and backward (part of the Wechsler Memory Scale, WMS; Wechsler, 1987)² was conducted to assess STM and WM functions.

¹In the third subtest of the L-P-S and L-P-S 50+, candidates are asked to identify the erroneous elements within 40 rulebased sequences each consisting of 8 geometric figures. The test is timed to 5 minutes. L-P-S and L-P-S 50+ differ solely in font size.

²In the blockspan test, the candidate is required to reproduce the trajectory between an increasing number of little cubes, either forward to test the STM, or backward to test the WM.

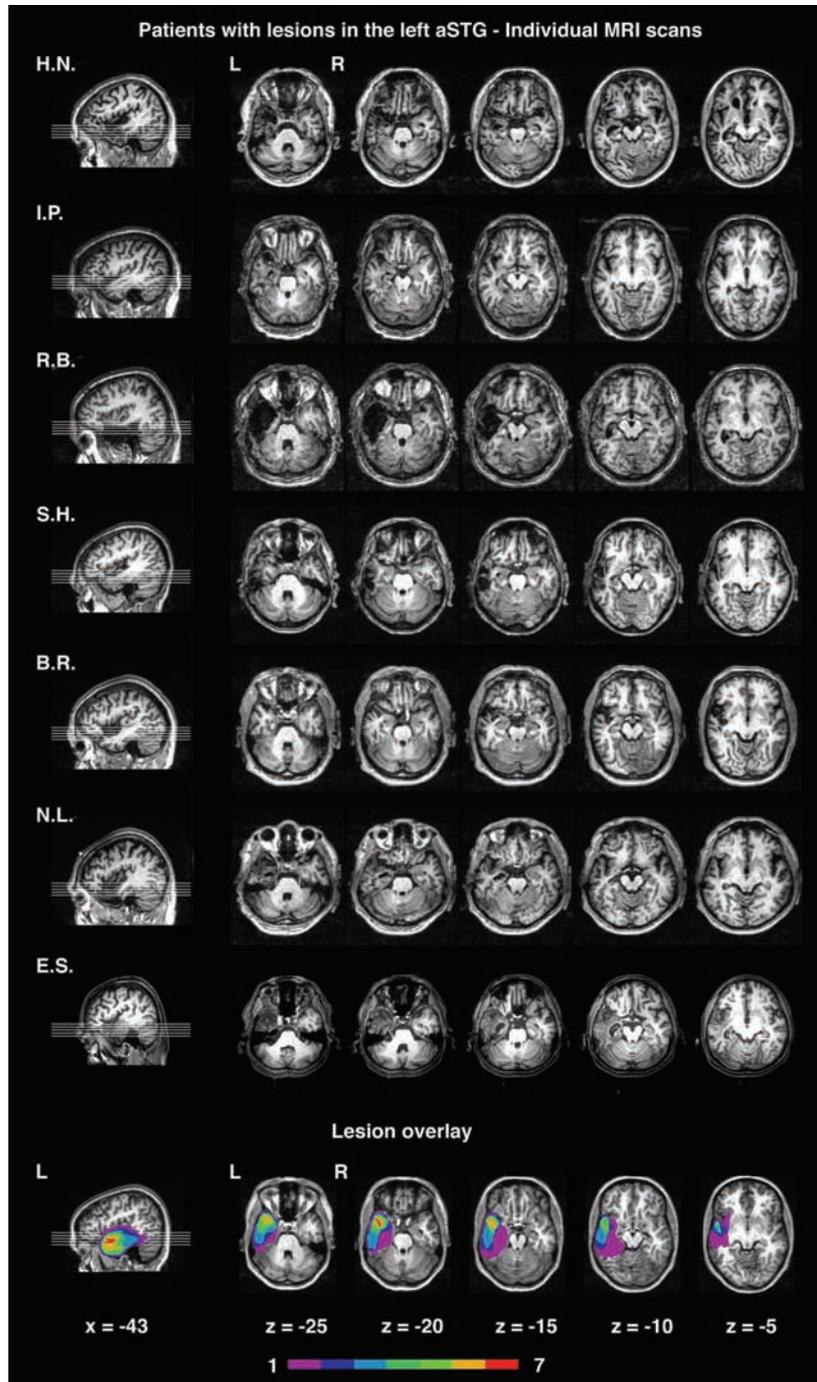


Figure 7.2: MRI scans of the left aSTG lesion group. Each row depicts five slices (Talairach z 's = 0, 5, 10, 15, and 20) of one individual suffering from a lesion within the left aSTG. Notably, the left IFG region is unaffected in all patients. The lowest panel shows an overlay of the lesions of all patients. The colour code indicates the number of patients having a lesion in the given area (purple = 1 patient, red = all 7 patients).

Lesion sites	Left IFG patients					Left aSTG patients							
	S.C.	B.K.	R.G.	A.G.	P.S.	M.S.	H.N.	I.P.	R.B.	S.H.	B.R.	N.L.	E.S.
Aetiology	IS	IS	CH	T	IS	IS	TBI	HE	T	TBI	IS	T	HE
Lesion onset (yrs.:mon.)	10;5	9;9	8;0	7;11	5;9	0;7	8;7	8;6	6;2	8;11	5;2	7;8	4;2
IFG, pars opercul.	+	+	+	+	+	+	(+)	-	-	(+)	-	-	-
IFG, pars triangul.	(+)	+	+	+	+	+	-	-	-	-	-	-	-
IFG, pars orbitalis	(+)	+	+	-	+	+	-	-	-	-	-	-	-
Inf. precentr. gyr.	-	+	-	-	-	+	-	-	-	-	-	-	-
Anterior insula	+	+	-	(+)	+	+	-	-	-	-	-	-	-
STG, anterior part	-	-	-	(+)	-	-	+	+	+	+	+	+	+
STG, middle part	-	-	-	-	-	-	+	-	+	+	-	+	+
Heschl's gyrus	-	-	-	-	-	-	-	-	-	-	-	-	-
MTG, anterior part	-	-	-	-	-	-	+	-	+	+	-	+	+
MTG, middle part	-	-	-	-	-	-	+	-	+	+	-	+	+
Temporal pole	-	-	-	-	-	-	(+)	+	+	+	-	+	+

Table 7.1: Description of the lesions for each individual patient in the left IFG and left aSTG group. Aetiology: IS = ischemic stroke, CH = cerebral haemorrhage, T = tumour resection, TBI = traumatic brain injury, HE = herpes encephalitis. The average time between lesion onset and the experimental sessions is indicated in years:months. The extent of the lesion was determined by MRI scans. Note that anterior temporal structures were intact in patients with lesions in the left IFG. By contrast, frontal areas were spared in patients with lesions in the left aSTG (see also Figures 7.1 and 7.2). In all patients, Heschl's gyrus was intact. + = unequivocal lesion; (+) = likely lesion; - = no lesion.

Lesion sites	Left IFG patients					Left aSTG patients							
	S.C.	B.K.	R.G.	A.G.	P.S.	M.S.	H.N.	I.P.	R.B.	S.H.	B.R.	N.L.	E.S.
Age	63	56	63	45	22	67	57	57	50	62	52	57	49
Gender	F	M	M	M	M	M	M	M	M	F	M	M	F
Handedness	R	R	R	R	A	R	R	R	A	R	R	R	R
School education	8	10	12	8	10	12	12	12	12	10	12	12	10
Musical training	0	0	4	4	0	2	2	0	0	0	12	0	0
Token Test	2	0	0	0	2	3	0	0	-	0	0	0	3
L-P-S 3	35	52	54	48	55	46	44	59	-	38	44	59	55
Blockspan	27/5	27/92	58/10	50/2	95/93	88/67	98/70	27/70	-	27/22	71/55	85/70	71/92
Pitch test	95.83	95.83	96.88	93.75	89.58	90.63	100	100	-	98.96	89.58	97.92	93.75
MBEA Scale	23	28	26	24	27	18	30	25	-	26	24	23	16
MBEA Contour	19	27	23	26	22	25	26	27	-	22	18	22	17
MBEA Interval	22	29	22	16	23	21	29	26	-	26	19	21	15
MBEA Rhythm	24	25	26	24	22	24	28	26	-	20	22	24	27
MBEA Metre	22	20	25	19	17	22	26	19	-	26	24	23	30
MBEA Memory	22	18	21	23	23	14	19	15	-	19	18	20	15
MBEA Total	22.00	24.50	23.83	22.00	22.17	20.67	26.33	23.00	-	23.17	20.83	22.17	20.00

Table 7.2: Personal and neuropsychological data of the patients with left hemisphere lesions. Gender: F = female, M = male. Handedness is indicated according to the Edinburgh Handedness Inventory (Oldfield, 1971): R = right handed, A = ambidexter. School education is depicted in years. Musical training indicates the accumulated years of playing an instrument. The severity of language comprehension deficits is indicated by the number of mistakes (age corrected) in the Token Test: no/very mild disorder (0-6); mild (7-21); medium (22-40); severe (>40). The nonverbal intelligence was assessed using the third subtest of the Leistungsprüfungsystem (L-P-S, or L-P-S 50+ if the patient was older than 50 years). T-values below 40 (bold font) indicate a nonverbal intelligence inferior of the norm range. Nonverbal STM and WM were tested with the blockspan test forward and backward. Results are indicated as percentages (blockspan forward/backward). Values below 16 (bold font) indicate a deficient memory performance. The performance of the patients in a pitch discrimination test is indicated in %correct responses. The scores achieved in the MBEA are depicted as number of correct responses. Bold font indicates scores more than 3 SD's under the mean value of the MBEA control group (Ayotte et al., 2002), i.e., marks a deficient performance. Behavioural data of patient R.B. could not be assessed due to serious illness.

The results of the tests are depicted in Table 7.2: All (but two) patients obtained normal nonverbal intelligence scores in the L-P-S: Patients S.C. and S.H. closely missed the norm range³ with T-scores of 35 and 38. STM and WM was normal to superior in all patients with aSTG lesions. Similarly, STM was intact in all patients with lesions in the left IFG, even though three of these patients showed deficits in the WM task (S.C., R.G., and A.G.; see Table 7.2).

Pitch discrimination. Furthermore, the patients' ability to detect pitch changes was tested. Therefore, candidates were presented with 96 tone sequences, each consisting of 6 piano tones generated with Cubase SX 2.0 (Steinberg Media Technologies, Hamburg, Germany). In half of the sequences ($N = 48$), all six tones had the same pitch. In the other half of the stimuli, a pitch change occurred between the 5th and the 6th tone. The pitch distance was either one, two or three semitones, rising or falling, resulting in 6 different pitch changes (+3, +2, +1, -1, -2, -3 semitones) each of them presented 8 times in random order (see Peretz et al., 2002, for a similar paradigm). The test covered a frequency range from A2 (110 Hz) to F#4 (370 Hz). The initial five tones of each sequence had a duration of 500 ms, the critical final tone was presented with a duration of 1000 ms. After each sequence a 1000 ms pause was inserted for the participant's response. The stimuli were presented via headphones (Sennheiser HD 202) at a comfortable volume using PRESENTATION 0.53 (Neurobehavioral Systems, Inc., Albany, Canada). The participants were instructed to decide as quickly as possible whether the final tone was the same or differed from the preceding tones.

Patients with left IFG lesions achieved a mean performance of 93.75% (range: 89.58-96.88%; SD : 3.02%), patients with left aSTG lesions achieved 96.70% correct responses (range: 89.58-100%; SD : 4.19%). Both groups performed well above chance level as revealed by one-sample t -tests with the test value 50 (left IFG: $t(5) = 35.50, p < .0001$; left aSTG: $t(5) = 27.31, p < .0001$). This demonstrates the unimpaired ability of both patient groups to detect pitch changes in the given frequency range.

Music perception - MBEA. To characterise the patient samples in terms of music perception abilities, the Montreal Battery of Evaluation of Amusia (MBEA; Peretz, Champod, & Hyde, 2003) was carried out. The MBEA is a model-based (Peretz & Coltheart, 2003) battery of 6 musical tests assessing the ability of the normal, musically untrained adult listener to perceive (1) scale, (2) contour, (3) interval, (4) rhythm, (5) metre, and (6) to incidentally

³T-values between 40 and 60 (i.e., the range of one standard deviation) are considered as normal.

learn new melodies. While the first three subtests (scale, contour, and interval) predominantly address the perception of spectral (i.e., pitch-related) cues of music, subtests 4 and 5 (rhythm and metre) focus on the perception of temporal (i.e., time-related) features of music. In tests 1-4, the candidates are required to perform a “same-different” classification task. Therefore, they are presented with pairs of short melodies: In half of the trials both melodies are identical, in the other half one tone in the second melody has been changed. (1) In the scale test, this tone violates the tonal key (while retaining the original melodic contour). (2) In the contour test, the pitch direction of one interval has been reversed (e.g., the interval is rising instead of falling) while maintaining the original key. (3) In the interval test, one interval within the melody has been changed (e.g., a third is played instead of a fifth) while pertaining the pitch direction. (4) In the rhythmic test, the duration values of two adjacent tones have been manipulated while retaining the melodic contour and metre. (5) In the metric test, participants are presented with single melodies written in duple or triple metre. Listeners are required to categorise these sequences as either a march or a waltz. (6) In the incidental memory test, listeners are asked to discriminate melodies that have already been presented earlier during the session from new melodies that are presented for the first time. Participants are not informed in advance that their memorisation of the tunes would be tested at the end. The MBEA provides test results of 160 normal participants of variable age and education serving as reference sample (i.e., scores more than 3 *SD*'s below the mean of this group indicate a deficiency; Ayotte et al., 2002).

In subtests 1-5 of the MBEA, both patient groups performed on average within a 3 *SD*'s range compared to the MBEA reference sample, indicating a more or less intact perception of scale, contour, interval, rhythm, and metre in patients with lesions in the left IFG or aSTG (see Table 7.2 for the individual data). However, the group of left aSTG patients showed deficient incidental memory abilities, as indicated by scores more than 3 *SD*'s below the mean of the MBEA control group. In the left IFG group a similar trend was observed but less pronounced than in the aSTG group (i.e., about 2 *SD*'s below the mean of the reference sample).

7.1.2 Matched Controls

For each patient, one healthy control subject matched in gender, age (± 2 years), handedness, and school education was recruited for the study (see Table 7.3). On average, they have had the same amount of musical training as the patient groups (as revealed by *t*-tests for independent samples; left IFG: $t(10) = 0.38, p > .712$; left aSTG: $t(12) = 0.22, p > .828$).

Cognitive abilities. As for the patients, the nonverbal intelligence, as well as the STM and WM performance was tested using the L-P-S (Horn, 1983) or the L-P-S 50+ (Sturm et al., 1993), and the blockspan forward and backward. All participants performed within the norm range or above (see Table 7.3).

To compare the memory performance and intelligence between the patients and the controls, two-sample *t*-tests were calculated. Neither STM nor WM nor intelligence of the patients with left IFG lesions differed significantly from the performance of the controls (see Table 7.4). Similarly, the intelligence level and STM performance of the patients with left aSTG lesions did not significantly differ from the performance of the controls. Accordingly, differences in behavioural performance or electrophysiological effects cannot be attributed to a different intelligence level or STM (WM) capacity of patients and controls. However, the WM performance of the left aSTG patients was significantly lower than the performance of the matched controls which has to be taken into account when interpreting the data.

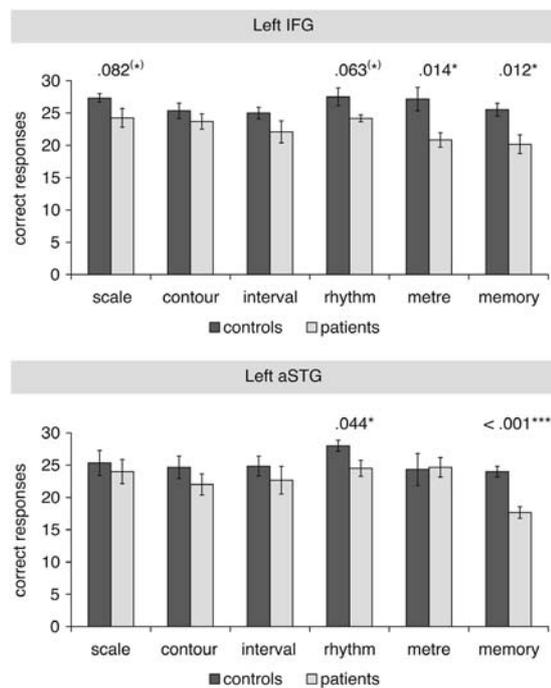


Figure 7.3: MBEA performance of patients and controls.

Pitch discrimination. In the pitch discrimination test, controls of the left IFG patients had on average 98.44% correct responses (range: 96.88-100%; *SD*: 1.44%); controls of the left aSTG patients gave on average 98.61% correct responses (range: 97.92-100%; *SD*:

Lesion sites	Left IFG controls					Left aSTG controls						
	G.M.	H.L.	V.G.	M.F.	L.G.	K.G.	T.W.	L.R.	V.M.	F.T.	H.A.	G.P.
Age	63	55	61	44	22	66	55	51	64	54	56	49
Gender	F	M	M	M	M	M	M	M	F	M	M	F
Handedness	R	R	R	R	R	R	R	R	R	R	R	R
School education	8	10	10	10	10	12	12	12	10	12	12	10
Musical training	6	0	3	0	0	4	0	1	4	0	0	0
Token Test	0	0	0	0	0	0	0	0	0	0	0	0
L-P-S	47	48	55	60	55	52	59	59	50	58	58	57
Blockspan	27/45	71/55	98/97	93/92	76/75	77/67	90/97	90/55	95/85	90/92	85/92	50/92
Pitch test	100	97.92	96.88	98.96	96.88	100	97.92	97.92	100	97.92	97.92	100
MBEA Scale	29	26	25	27	29	28	20	26	31	20	25	30
MBEA Contour	27	27	21	24	29	24	21	23	27	22	22	29
MBEA Interval	29	23	25	25	25	23	20	24	27	28	21	29
MBEA Rhythm	30	30	23	31	27	24	29	29	31	27	25	29
MBEA Metre	30	19	30	30	29	25	13	24	30	24	26	29
MBEA Memory	25	21	26	26	28	27	24	23	24	25	21	27
MBEA Total	28.33	24.33	25.00	27.17	27.83	25.17	21.17	24.50	29.00	24.33	23.33	28.83

Table 7.3: Personal and neuropsychological data of the healthy controls. Participants are arranged in the same order as the patients in Table 7.2. Gender: F = female, M = male. Handedness is indicated according to the Edinburgh Handedness Inventory (Oldfield, 1971): R = right handed. School education is depicted in years. Musical training indicates the accumulated years of playing an instrument. The nonverbal intelligence test (L-P-S, or L-P-S 50+ if the participant was older than 50 years) showed that all participants performed within the norm range (i.e., had T-values between 40 and 60). The blockspan test forward and backward revealed that nonverbal STM and WM was normal (i.e., percentages between 16 and 84) or superior to normal (i.e., percentages above 84) in all participants. The performance of the participants in a pitch discrimination test is indicated in %correct responses. The scores achieved in the MBEA are indicated as number of correct responses. Bold font indicates scores more than 3 SD's under the mean value of the MBEA control group (Ayotte et al., 2002), i.e., marks a deficient performance.

1.08%). Both groups performed highly above chance level as shown by one-sample t -tests with the test value 50 (left IFG: $t(5) = 82.63, p < .0001$; left aSTG: $t(5) = 110.68, p < .0001$), demonstrating the ability of both control groups to detect simple changes in pitch. The statistical comparison of patients and controls showed that the performance of the left IFG patients was significantly lower than the performance of the controls. The performance of left aSTG patients and their controls did not significantly differ (see Table 7.4).

Musical abilities - MBEA. In all MBEA subtests, both control groups performed on average normally within the 3 SD 's range indicating an unimpaired musical processing in both groups. To statistically compare the performance of patients and controls, two-sample t -tests were calculated for each subtest (see Table 7.4). These analyses showed that both patient groups had significantly lower incidental memory scores than their controls (left IFG: $p < .012$; left aSTG: $p < .0004$). Furthermore, the left aSTG patients scored significantly lower in the rhythmic test than their controls ($p < .045$). Likewise, the left IFG group obtained (marginally) significantly lower results in the rhythmic test ($p < .064$) and the metric test ($p < .015$) than the controls.

Test	left IFG		left aSTG	
	$t(10)$	p -value	$t(10)$	p -value
L-P-S	1.27	> .234	1.47	> .187
Blockspan forward	1.03	> .328	1.39	> .193
Blockspan backward	1.36	> .214	2.95	< .031
Pitch Test	3.44	< .007	1.08	> .323
MBEA Scale	1.94	> .082	0.50	> .631
MBEA Contour	0.99	> .345	1.12	> .291
MBEA Interval	1.52	> .159	0.82	> .430
MBEA Rhythm	2.24	> .063	2.30	< .045
MBEA Metre	2.96	< .015	0.12	> .911
MBEA Memory	3.04	< .012	5.27	< .0004
MBEA Total	4.24	< .003	1.67	> .125

Table 7.4: Results of the two sample t -tests comparing the cognitive abilities and music perception between patients and controls. The L-P-S estimates nonverbal intelligence, the blockspan forward and backward assess STM and WM functions. Note that the performance of patients and controls did not differ in these basic tests, apart from the left aSTG patients showing significantly lower WM scores than their controls (who scored mostly even above the norm range). In the pitch test, left IFG patients performed significantly lower than their controls, even though the patients performed well above chance level, indicating that their pitch discrimination ability was unimpaired. In the MBEA, the scores of the incidental memory test as well as of subtests 4 and 5 assessing the perception of temporal features of music were significantly lower in left aSTG and left IFG patients than in controls.

7.1.3 Stimulus Material and Procedure

During the EEG experiment, participants were presented with the chord sequences of Set B as described in Experiment 1A (see section 6.1 for a detailed description). Briefly, as in previous experiments (e.g., Koelsch et al., 2000, 2007; Koelsch & Sammler, 2008), the initial five chords were identical in both sequence types (regular and irregular): Dominant [V] - tonic [I] - subdominant [IV] - supertonic [II] - dominant [V]. In regular sequences, the final chord was a Tonic [I] (e.g., C-E-G in a C major sequence), irregular sequences ended on the *double dominant* [V/V] (e.g., D \flat -F-A \flat in C major).

Like in Experiment 1A, chord sequences were presented with a grand piano sound. Infrequently one sequence contained a chord played by a deviant instrument. The presentation time of all chords was 500 ms, except the critical final chords which lasted 1000 ms and were followed by a 500 ms pause. Across the experiment, participants listened to 192 regular and 192 irregular sequences as well as 48 sequences containing a deviant instrument resulting in 432 sequences in total. Regular and irregular sequences were pseudorandomly intermixed. Consecutive sequences always had a different tonal key and not more than 3 sequences of the same type followed each other. Like in Experiment 1A, the EEG session was divided into two blocks. In the first block, participants looked at a fixation cross while listening to the stimuli; in the second block, they watched a silent film (without subtitles, reduced to 1/4th of its original size in order to avoid eye movement artefacts). This “entertainment” was chosen to increase the patience of the participants, to relax the eyes and to decrease the tension of the face muscles allowing to record less noisy data and more trials. Every 5 minutes participants had the opportunity to take a short break. The experiment had a duration of approximately 30 minutes.

Participants sat in a comfortable chair in a sound proof cabin. Stimuli were presented via loudspeakers at a comfortable volume using PRESENTATION 0.53 (Neurobehavioral Systems, Inc., Albany, Canada). Participants were not informed about the regular and irregular sequence endings to avoid electric brain responses that would be elicited in a conscious discrimination task (e.g., the N2b or P300) and obscure the brain responses related to the musical structure building (i.e., the ERAN and N5; Koelsch et al., 2000). Instead, participants were informed about infrequently occurring deviant instruments and instructed to respond to them by pressing a button.

To test, whether participants were able to perceive the slight harmonic violation at the end of the irregular sequences, all participants were invited a second time at least 2 days after the EEG measurement and again presented with the chord sequences. This time, they were informed about the regular and irregular sequence endings. After a short training (10-30

sequences, depending on the need of practise), candidates were asked to discriminate the two sequence endings, and to indicate their decision by pressing a button - right for regular, left for irregular. The button press was not timed, each sequence start was self-paced. Altogether, 48 regular and 48 irregular sequences were presented in random order via headphones (Sennheiser HD 202) in a silent room using PRESENTATION 0.53 (Neurobehavioral Systems, Inc., Albany, Canada). In the middle of the test, participants had the opportunity to take a short break. The test had a duration of approximately 10 minutes. In the same session, the cognitive abilities and music perception (described above) of the patients were tested.

7.1.4 Data Acquisition and Analysis

EEG experiment. The EEG was recorded with 30 Ag/AgCl electrodes placed according to the extended international 10–20 system (cf., Sharbrough et al., 1991). The electrode positions were: FP1/2, AF7/8, AF3/4, AFZ, F7/8, F3/4, FZ, FT7/8, FC3/4, T7/8, C3/4, CZ, CP5/6, P7/8, P3/4, PZ, O1/2. Left mastoid (M1) served as reference; an additional electrode was placed on the right mastoid bone (M2) and the nose-tip for off-line re-referencing. The ground electrode was located on the sternum. To monitor eye movements and blinks, horizontal and vertical electrooculograms (EOG) were bipolarly recorded from electrodes placed on the outer canthus of each eye (horizontal EOG), as well as above and below the right eye (vertical EOG). Impedances were kept below 5 k Ω . Signals were amplified with two synchronised PORTI-32/MREFA amplifiers (Twente Medical Systems International B.V., Enschede, NL) and digitised with a sampling rate of 250 Hz.

After recording, the software package EEP 3.2 (ANT-software) was used to re-reference the data to linked mastoids (i.e., to the algebraic mean of M1 and M2) and to filter the data using a 0.4-Hz highpass filter (fir, 3465 points; to eliminate drifts). Further processing steps were accomplished using EEGLAB 5.03 (Delorme & Makeig, 2004) in MATLAB 7.1.0. In a first step, data were cut into epochs of -2700 to 1000 ms relative to the onset of the final chord, i.e., covering the whole chord sequence and part of the preceding pause. Epochs containing strong muscle artefacts, electrode drifts, or technical artefacts were rejected manually. Non-rejected epochs were subjected to an Independent Component Analysis (ICA). The resulting component structure of the data was used to reject eye movement and eye blink artefacts, muscle artefacts and extensive alpha activity. Then the data were filtered with a 25-Hz lowpass filter (fir, 277 points) to eliminate muscle artefacts and 50 Hz line noise. Afterwards, data were rejected [1] for threshold (whenever the amplitude value of one channel exceeded $\pm 55 \mu\text{V}$), [2] for linear trends (whenever the linear trend of one channel exceeded

$\pm 50 \mu\text{V}$ in a 400 ms gliding window), [3] for improbable data (if the trial lay outside a $\pm 5 SD$ range (for a single channel) or $\pm 3 SD$ range (for all channels) of the mean probability distribution), [4] for abnormally distributed data (if the data lay outside a $\pm 6 SD$ range (for a single channel) or $\pm 3 SD$ range (for all channels) of the mean distribution of kurtosis values), and [5] by visual inspection. Finally, non-rejected epochs were averaged in a time window from 0 to 1000 ms relative to the onset of the final chord with a -200 to 0 ms baseline. On average 246 trials were averaged for each participant (range: 143-346, $SD = 63$). Trial numbers did not differ significantly between patients and controls (two-sample t -tests; left IFG group: $t(10) = 0.056, p > .957$; left aSTG group: $t(12) = 1.13, p > .282$).

For the statistical analysis of the ERP data, mean amplitudes were calculated for each condition in a time window from 150 to 250 ms after onset of the final chord (centred around the peak of the ERAN) for four Regions of Interest (ROIs): Left anterior (AF3, F3, F7, FC3, FT7), right anterior (AF4, F4, F8, FC4, FT8), left posterior (C3, T7, CP5, P3, P7), and right posterior (C4, T8, CP6, P4, P8). To test whether the irregular chords elicited an ERAN in the patients and controls, an ANOVA for repeated measures with the within-subjects factors Chord (regular [I] vs. irregular [V/V]), Hemisphere (left vs. right), and AntPost (anterior vs. posterior) was calculated on these mean amplitude values for both patient and control groups.⁴ To test group differences, an ANOVA for repeated measures with the within-subjects factors Chord, Hemisphere, AntPost and the between-subjects factors Group (patients vs. controls), and LesionSite (left IFG vs. left aSTG) was computed. Whenever an interaction with the factor Chord was observed at a significance level of $p \leq .05$, subsequent analyses were conducted by splitting up the general linear model (GLM). Komolgorov-Smirnov tests calculated beforehand for each patient and control group separately for each condition and ROI confirmed the normal distribution of the data (p 's $> .455$), thus, allowing the application of an ANOVA. An analogue analysis was run for a later time window from 400 to 600 ms covering the N5.

Behavioural discrimination test. The hit rates in the explicit discrimination test were extracted and subjected to one-sample t -tests with the test value 50 in each patient and control group in order to evaluate whether the participants performed above or below chance. To statistically compare the performance of the patients and the controls, t -tests for independent samples were calculated. Beforehand, the normal distribution of the data was verified by computing Komolgorov-Smirnov tests for each of the four experimental groups (p 's $> .272$).

⁴The data of the two blocks (fixation cross vs. silent film) were pooled since ANOVAs with the factors Chord, Hemisphere, AntPost and Block did not reveal a significant interaction of Chord \times Block (p 's $> .225$) in any of the four groups.

7.2 Results

7.2.1 EEG Experiment

Behavioural performance. Participants detected on average 99.28% of the deviant instruments and had only about 0.24% false alarms, showing that they attended to the musical stimuli and reliably identified the deviant timbre. An ANOVA with the between-subjects factors Group (patients vs. controls) and LesionSite (IFG vs. aSTG) on the hit rates showed that patients and controls performed similarly (no main effect of Group: $F(1, 22) = 1.02, p > .751$, no interaction of Group \times LesionSite: $F(1, 22) = 1.02, p > .753$)

ERAN time window (150..250 ms). In both patient and control groups, the irregular chords elicited a significant ERAN peaking around 200 ms with a frontal scalp distribution and a slight right hemispheric preponderance (see Table 7.5 and long arrows in Figure 7.4). If re-referenced to the nose electrode, the potentials at mastoidal leads showed a positive polarity (“polarity inversion”) in the same time window (see short arrows in Figure 7.4), indicating that this effect is not an N2b (an N2b has a central scalp distribution, is not lateralised, and does not invert polarity).

ROI	Left IFG		Left aSTG	
	Controls	Patients	Controls	Patients
left anterior	-0.93 (± 0.54)	-0.77 (± 0.51)	-0.97 (± 0.37)	-0.95 (± 0.35)
right anterior	-1.10 (± 0.61)	-1.05 (± 0.62)	-0.86 (± 0.45)	-0.69 (± 0.25)
left posterior	-0.69 (± 0.21)	-0.04 (± 0.41)	-0.47 (± 0.49)	-0.64 (± 0.37)
right posterior	-0.77 (± 0.57)	-0.38 (± 0.50)	-0.38 (± 0.55)	-0.41 (± 0.17)

Table 7.5: Mean ERAN amplitudes (μV ; $\pm SD$) elicited in healthy controls and patients with lesions in the left IFG or left aSTG in anterior and posterior ROIs.

The ERAN was nominally smaller in patients with brain lesions than in healthy controls. This difference was stronger between left IFG patients and their controls than between the left aSTG groups. Notably, in left IFG patients the ERAN was more frontally distributed and appeared to be more strongly right lateralised compared to the ERAN in the matched healthy controls as well as compared to the patients with left aSTG lesions (see Figure 7.5).

To test the ERAN amplitudes statistically, a three-way ANOVA for repeated measures with the within-subjects factors Chord, Hemisphere, and AntPost (see Section 7.1.4) was calculated separately for each of the four experimental groups (left IFG patients, left aSTG patients, left IFG controls, left aSTG controls). In all patient and control groups, a main

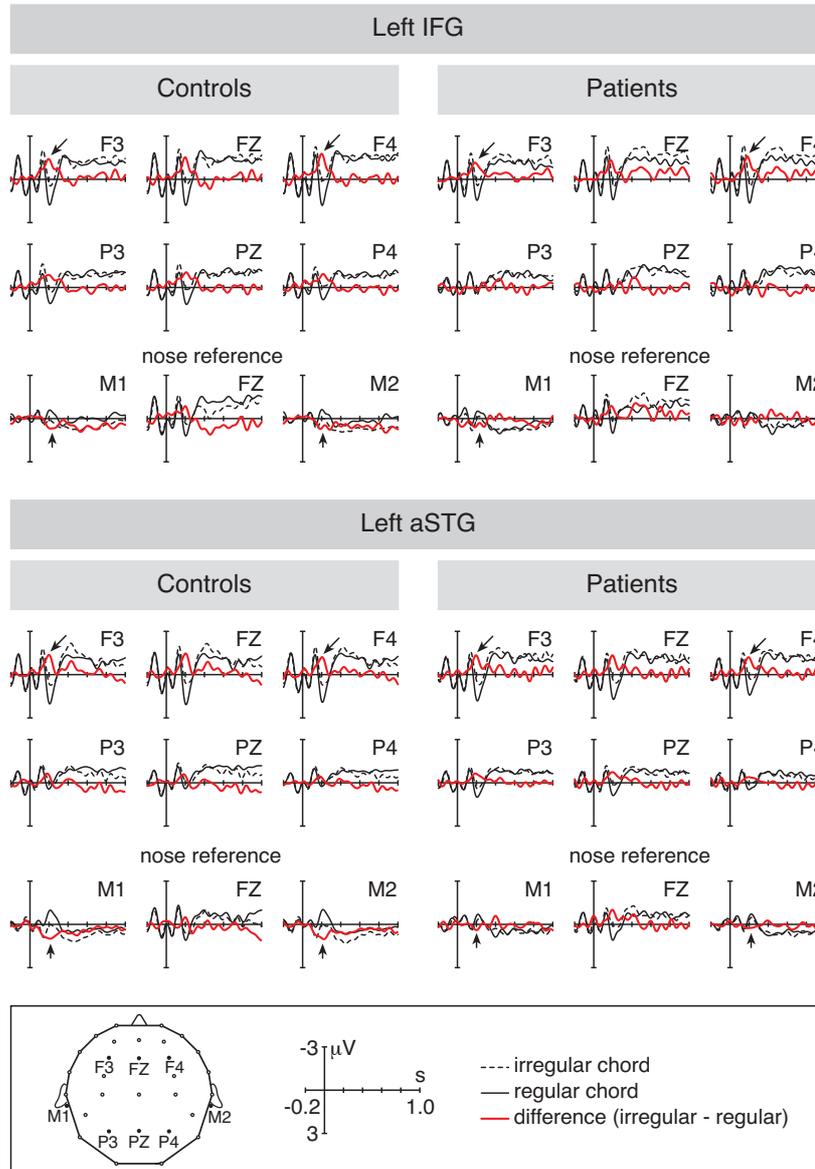


Figure 7.4: ERAN plotted for patients with left IFG or left aSTG lesions and their matched controls. Irregular chords elicited an ERAN (see long arrows) in patients with lesions in the left IFG (upper right), in patients with lesions in the left aSTG (lower right), as well as in the matched controls (upper and lower left). In all groups, a polarity inversion was observed at mastoidal leads if the data were re-referenced to the nose electrode (see short arrows pointing to electrodes M1 and M2 in each group).

effect of Chord was found, indicating that irregular chords elicited a significant ERAN. Furthermore, in all groups a significant interaction of Chord \times AntPost was found, demonstrating the anterior scalp distribution of the effect. The interaction of Chord \times Hemisphere missed the level of significance in all groups indicating a more bilateral scalp distribution of the ERAN (see Table 7.6 for statistical values).

Effect	Left IFG			
	Controls		Patients	
	$F(1, 5)$	p -value	$F(1, 5)$	p -value
Chord	22.21	< .006	9.38	< .029
Chord \times Hemisphere	0.83	> .405	5.47	> .067
Chord \times AntPost	6.28	> .054	32.06	< .003
Effect	Left aSTG			
	Controls		Patients	
	$F(1, 6)$	p -value	$F(1, 6)$	p -value
Chord	15.71	< .008	65.70	< .0001
Chord \times Hemisphere	2.79	> .146	3.15	> .126
Chord \times AntPost	38.88	< .001	17.37	< .007

Table 7.6: ANOVAs of Chord \times Hemisphere \times AntPost for each patient and control group. The main effect of Chord shows that irregular chords elicited a negativity. The interaction of Chord \times Hemisphere indicates the lateralisation of the effect. The interaction of Chord \times AntPost represents the anterior scalp distribution of the ERAN.

To statistically test possible amplitude differences of the ERAN between patients and controls, a five-way ANOVA for repeated measures with the within-subjects factors Chord, Hemisphere, AntPost, and the between-subjects factors Group and LesionSite was computed (see Section 7.1.4). The analysis revealed a main effect of Chord ($F(1, 22) = 77.75, p < .0001$) demonstrating that irregular chords elicited an ERAN. Furthermore, the ANOVA showed an interaction of Chord \times AntPost ($F(1, 22) = 85.24, p < .0001$) describing the anterior scalp distribution of the ERAN, as well as a marginally significant interaction of Chord \times Hemisphere ($F(1, 22) = 5.47, p < .068$) indicating the slight right lateralisation of the ERAN. Moreover, a significant three-way interaction of Chord \times Hemisphere \times LesionSite ($F(1, 22) = 10.66, p < .005$) was observed, indicating that the ERAN was differently lateralised in patients than in controls.

No interactions of Chord \times Group ($F(1, 22) = 0.98, p > .333$) or Chord \times Group \times LesionSite were found ($F(1, 22) = 1.02, p > .324$), which would have indicated a reduced ERAN amplitude in the patients compared to the controls. However, a highly significant

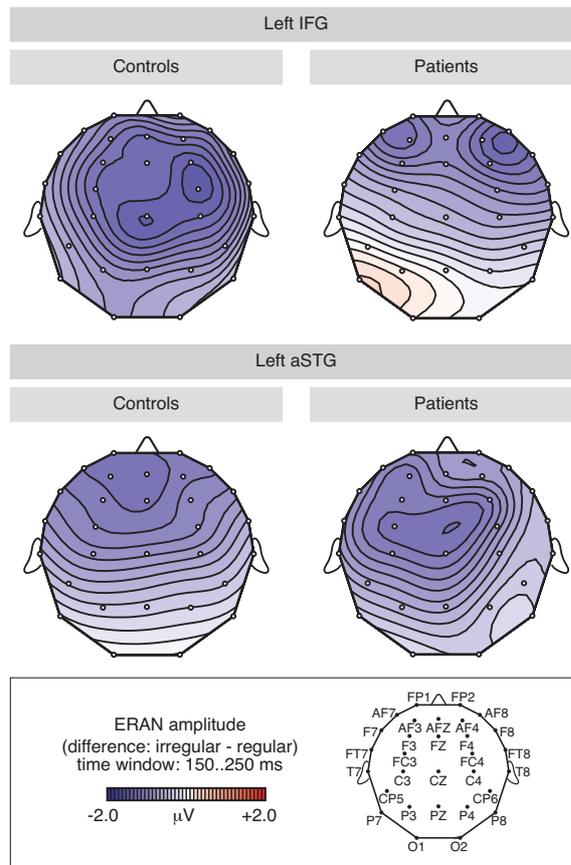


Figure 7.5: Scalp distribution of the ERAN (150-250 ms) plotted for patients with left IFG or left aSTG lesions and their matched controls. In patients with left IFG lesions (upper right), the ERAN was distributed significantly more anteriorly than in the matched controls (upper left) or in the patients with left aSTG lesions (lower right). The scalp distribution of the other groups did not significantly differ from one another.

four-way interaction of Chord \times AntPost \times Group \times LesionSite ($F(1, 22) = 10.40, p < .005$) was observed, demonstrating that the ERAN was distributed more anteriorly in patients with left IFG lesions than in the other experimental groups (see Figure 7.5). To further elucidate this interaction, ANOVAs with the factors Chord, AntPost, Hemisphere, and Group were calculated for each lesion site (i.e., IFG patients vs. IFG controls; aSTG patients vs. aSTG controls), and ANOVAs with the factors Chord, AntPost, Hemisphere, and LesionSite were calculated separately for each group (i.e., IFG patients vs. aSTG patients; IFG controls vs. aSTG controls; see Table 7.7 for statistical values).

These analyses showed that the ERAN was more anteriorly distributed in patients with IFG lesions compared to their controls (interaction of Chord \times AntPost \times Group: $p < .030$), and compared to the aSTG patient group (interaction of Chord \times AntPost \times LesionSite: $p < .015$). This different scalp distribution was specific for the IFG patients. Analogous ANOVAs revealed no significant differences, neither between aSTG patients and aSTG controls (interaction of Chord \times AntPost \times Group: $p > .091$), nor between both control groups (IFG controls vs. aSTG controls; interaction of Chord \times AntPost \times LesionSite: $p > .134$). These findings emphasise that the scalp topography of the ERAN was particularly different only in the IFG patients, providing some evidence for the importance of the left IFG in the processing of harmonic irregularities.

However, despite this different topography, the ERAN amplitude in the IFG patients was not significantly reduced compared to the IFG controls (i.e., no significant interaction of Chord \times Group: $p > .255$; see Table 7.7) as one would have expected if the IFG was involved in the processing of harmonic structure. Also in the aSTG patients, no significant reduction of the ERAN amplitude was observed compared to the aSTG controls ($p > .988$). At this point, the question arises, whether a potential reduction of the ERAN amplitude might have been obscured by neuronal reorganisation processes. As pointed out earlier, the patients had suffered their lesion on average 7 years before they participated in the present study, leaving enough time for the recovery of an initial deficit. If this assumption holds, the ERAN amplitude should be smaller in patients with recent brain injury compared to patients with chronic lesions.

To address this question, one-sided Pearson correlations were calculated between lesion onset and ERAN amplitude for each patient group. As depicted in Figure 7.6, these analyses revealed a very strong correlation in the patients with left IFG lesions ($r = -.747, p < .045$), but not in patients with lesions in the left aSTG ($r = -.063, p > .447$). This demonstrates that lesions in the left IFG with recent onset are more likely to reduce the ERAN amplitude than older lesions, whereas the ERAN amplitude appears to be independent of

Effect	IFG patients vs. IFG controls		aSTG patients vs. aSTG controls		IFG patients vs. aSTG patients		IFG controls vs. aSTG controls	
	$F(1,10)$	p -value	$F(1,12)$	p -value	$F(1,11)$	p -value	$F(1,11)$	p -value
Chord	30.33	<.0001	50.84	<.0001	41.78	<.0001	37.97	<.0001
Chord \times Hemisphere	5.21	<.047	5.31	<.041	0.15	$>.706$	0.03	$>.870$
Chord \times AntPost	34.67	<.0001	55.07	<.0001	52.58	<.0001	33.46	<.0001
Chord \times Group/LesionSite	1.46	$>.255$	0.00	$>.988$	0.35	$>.568$	0.67	$>.430$
Chord \times Hemisphere \times Group/LesSite	0.96	$>.351$	0.87	$>.370$	8.34	<.016	2.53	$>.140$
Chord \times AntPost \times Group/LesSite	6.46	<.030	3.37	$>.091$	8.55	<.015	2.62	$>.134$

Table 7.7: ANOVAs of Chord \times Hemisphere \times AntPost \times Group/LesionSite. The significance values in the lowest row (Chord \times AntPost \times Group/LesionSite) demonstrate that the ERAN was more anteriorly distributed in the IFG patients compared to the IFG controls and compared to the aSTG patients (see bold font), while the ERAN topography did not differ between the other groups. The values for the interaction of Chord \times Group/LesionSite show that the ERAN amplitude did not significantly differ between patients and controls.

the time since brain injury in the aSTG. Consequently, it may be concluded that the left IFG is functionally relevant for the generation of the ERAN, but less so the aSTG.

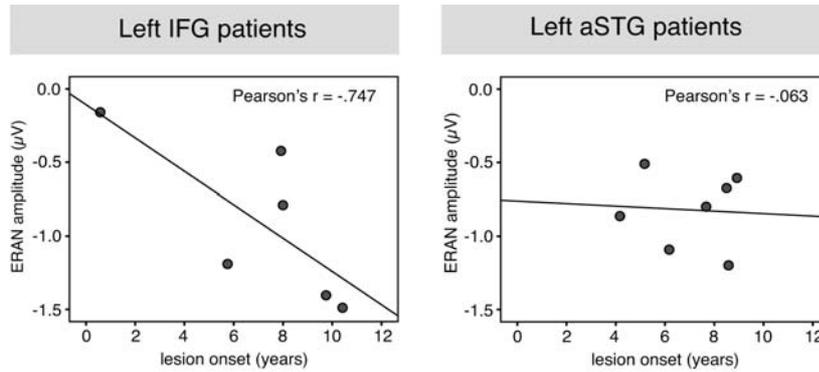


Figure 7.6: Correlation of ERAN amplitude and lesion onset. The ERAN amplitude was significantly related to the lesion onset in patients with left IFG lesions (left panel), that is, the more recently the lesion was acquired (and most presumably the less reorganisation processes have taken place so far), the smaller was the ERAN amplitude. By contrast, in the patients with left aSTG lesions, the ERAN amplitude was not significantly correlated with the time since brain injury (right panel).

N5 time window (400..600 ms). The ERAN was followed by a tendential negativity around 500 ms after onset of the critical chord (i.e., the N5) in left IFG patients, as well as in left aSTG patients and controls. ANOVAs with the factors Chord, Hemisphere, and AntPost calculated separately for each group showed, however, that this effect missed significance in all of the groups (no main effect of Chord, $p > .067$). This finding may be explained by the high variance of the data and the low statistical power due to the small sample size. Therefore, no further statistical analyses were conducted.

ROI	Left IFG		Left aSTG	
	Controls	Patients	Controls	Patients
left anterior	0.03 (\pm 0.47)	-0.39 (\pm 0.71)	-0.36 (\pm 0.39)	-0.28 (\pm 0.67)
right anterior	0.00 (\pm 0.43)	-0.54 (\pm 0.82)	-0.35 (\pm 0.34)	-0.03 (\pm 0.52)
left posterior	0.18 (\pm 0.45)	-0.33 (\pm 0.41)	0.00 (\pm 0.26)	-0.16 (\pm 0.41)
right posterior	0.13 (\pm 0.25)	-0.11 (\pm 0.83)	-0.06 (\pm 0.20)	0.06 (\pm 0.45)

Table 7.8: Mean N5 amplitudes (μ V; \pm SD) elicited in healthy controls and patients with lesions in the left IFG or left aSTG in anterior and posterior ROIs.

7.2.2 Explicit Discrimination Test

All participants expressed their high uncertainty about the distinction between regular and irregular final chords, reflected in relatively low hit rates: IFG controls had 61.81% correct responses ($SD = 9.22\%$), IFG patients achieved an average performance of 54.69% ($SD = 8.66\%$), aSTG controls responded correctly in 60.76% ($SD = 7.62\%$) of the trials, and aSTG patients scored on average 58.16% ($SD = 6.16\%$). Still, both control groups, as well as the aSTG patients performed significantly above the 50% chance level (IFG controls: $t(5) = 3.14, p < .027$; aSTG controls: $t(5) = 3.46, p < .019$; aSTG patients: $t(5) = 3.24, p < .023$). By contrast, patients with lesions in the left IFG performed at chance level ($t(5) = 1.33, p > .242$). In a direct comparison of patients and controls by means of t -tests for independent samples, however, no significant differences were found (IFG: $t(10) = 1.38, p > .198$; aSTG: $t(10) = 0.65, p > .530$).

7.3 Discussion

The present study investigated whether lesions in brain areas that are essentially involved in syntax processing in language, are associated with parallel deficits in the music domain. Therefore, patients with lesions in the left IFG and left aSTG as well as normal controls were tested in a chord sequence paradigm. The ERAN, an ERP typically elicited by harmonically irregular chords, was analysed serving as indicator for intact or disrupted music-syntactic processing in these patients.

Irregular chords elicited an ERAN in both controls and patients, irrespective of lesion site, confirming parts of Hypothesis 1, and replicating the findings of Experiment 1A and of a series of earlier studies using the same or very similar stimulus material (e.g., Koelsch et al., 2000, 2007). Contrary to Hypothesis 1, the average ERAN amplitude was, however, not significantly reduced, neither in left IFG, nor in left aSTG patients, which might indicate that the processing of harmonic progressions does not depend on left fronto-temporal cerebral structures. Alternatively, this finding may perhaps not come as a surprise for two reasons: First, the ERAN is thought to receive contributions from bilateral neural generators. For example, the sources of the magnetic equivalent of the ERAN have been localised in the pars opercularis of the left and right inferior frontal cortex (Maess et al., 2001). Corroboratingly, the majority of fMRI studies using chord sequence paradigms have reported bilateral brain activations, most often even with a right hemisphere weighting (e.g., Koelsch, Gunter, et al., 2002; Koelsch, Fritz, et al., 2005; Tillmann, Janata, & Bharucha, 2003; Tillmann, Koelsch, et al., 2006). Hence, the unilateral left hemisphere lesions in the patients may have been

insufficient to dramatically disrupt the functioning within this (right accentuated) processing network. Second, the study was conducted on average 7 years after brain injury, leaving room for considerable reorganisation processes that possibly promoted a compensation of initial deficits through perilesional left or contralesional right hemisphere brain areas (see below for corresponding evidence; see also Schlaug et al., 2008, for an example of growing contralesional involvement during speech recovery). In fact, it has been shown that amusic deficits after stroke can improve up to normal range within 6 to 12 months after brain damage (Schuppert, Münte, & Altenmüller, 2003). Hence, it is well conceivable that the present data reflect a fully recovered ERAN. Future studies with “younger” or functional lesions as induced by methods like Transcranial Magnetic Stimulation (TMS; e.g., Walsh & Pascual-Leone, 2003) are clearly necessary to clarify this issue.

Nevertheless, the present study yielded several results that indicate the necessity of the left IFG in music-syntactic processing, whereas the role of the left aSTG remains less clear. The results will be discussed in turn, separately for each lesion site.

7.3.1 The Role of the Left IFG in Musical Syntax Processing

The present study yielded 3 main findings in support of the functional role of the left IFG in music-syntactic processing: First, the ERAN in patients with lesions in the left IFG was significantly more frontally distributed and (nominally) more strongly right lateralised than in healthy controls and patients with lesions in the left aSTG. Second, the ERAN amplitude in left IFG patients was significantly correlated with the time since lesion onset. Third, these patients performed below chance level when asked to explicitly discriminate regular and irregular chord functions, whereas controls as well as left aSTG patients performed above chance.

The different scalp topography of the ERAN, being more frontally distributed and nominally more right lateralised in the left IFG patients than in controls, fits well with a modified weighting of the different network constituents in these patients, for instance a greater predominance of the right hemisphere generators than in healthy controls due to the breakdown of the left hemisphere units and/or a shift of the function to the contralesional hemisphere. Notably, the scalp distribution of the ERAN was normal in patients with left aSTG lesions despite equally extended brain damage, similar time since lesion onset, and thus, a comparable degree of ipsilesional noise. This finding renders it highly unlikely that the topography shift observed in the left IFG patients is merely an effect of weaker signal quality over the ipsilesional compared to the contralesional hemisphere.

The finding of a significant correlation between the ERAN amplitude and the time since lesion onset indicates that music-syntactic processing can be shaped by structural and/or functional reorganisation processes that are launched immediately after brain injury and may continue to act over years (see Schuppert et al., 2003, for evidence for recovery from receptive amusia; see also Marsh & Hillis, 2006, for a comprehensive review on the role of reorganisation after brain injury). Consistent with the logic of reorganisation, left IFG patients with more recent lesions, i.e., in an earlier stage of recovery, exhibited smaller ERAN amplitudes than patients with older lesions. In other words, over the years, the ERAN has regained strength, finally even reaching amplitudes equalling those in healthy controls, as observed in the present study conducted on average seven years after lesion onset.

Most importantly, the sensitivity of the ERAN to the time since left IFG injury unequivocally demonstrates that the left IFG is originally an essential neural generator of the ERAN, the dysfunction of which is, however, gradually compensated, most presumably by perilesional left or contralateral right hemisphere structures. Notably, no similar correlation was found in left aSTG patients, demonstrating the predominant role of left inferior frontal compared to left anterior temporal brain areas in early harmonic structure building.

Further support for the functional role of the left IFG in music-syntactic processing comes from the behavioural data: Patients with lesions in the left IFG were found to be impaired in the discrimination of regular and irregular sequence endings, contrary to the patients with left aSTG lesions and healthy controls. It should be mentioned that these deficits could not be attributed to a generally lower cognitive functioning in patients than in controls who scored similar in intelligence, working memory and short-term memory tests.

Taken together, patients with lesions in the left IFG showed an ERAN like healthy controls, that was, however, differently distributed and shaped by neuronal reorganisation processes. Moreover, behaviourally patients failed to perceive harmonic closure. These combined findings suggest that the left IFG plays a seminal role in the processing of musical syntax as part of a larger bilateral processing network. This observation is in keeping with a series of previous MEG (Maess et al., 2001) and fMRI studies (e.g., Koelsch, Gunter, et al., 2002; Koelsch, Fritz, et al., 2005; Tillmann, Janata, & Bharucha, 2003; Tillmann, Koelsch, et al., 2006) reporting bilateral fronto-temporal brain activations related to the processing of harmonic irregularities, consistently encompassing the left IFG.

7.3.2 The Role of the Left aSTG in Musical Syntax Processing

Notably, the ERAN was found to be insensitive to the lesion of the left aSTG, as reflected by its unmodulated amplitude and scalp topography and its independence of time since lesion onset. Furthermore, these patients were able to consciously detect harmonic irregularities. These findings can be interpreted in two ways: Either they demonstrate that the left aSTG is not essentially involved in the processing of musical syntax, or they reflect full recovery in the patients (see above).

The first interpretation apparently conflicts with the neuroimaging literature that consistently reported activations in the left or bilateral aSTG and planum polare (BA 22/38) when comparing the processing of harmonically distantly and closely related items in melodies or chord sequences (e.g., Koelsch, Gunter, et al., 2002; Koelsch, Fritz, et al., 2005; Krumhansl, 2004; Tillmann, Koelsch, et al., 2006). This incongruence may, however, be due to the methodological differences between fMRI experiments and EEG lesion studies: For example, due to the coarse temporal resolution of fMRI, it remains unclear whether the aSTG brain activation really reflects the processes underlying the ERAN. Furthermore, while fMRI identifies the brain structures that *are involved* in a cognitive function, lesion data determine cerebral regions that are *essential* for a given task. Consequently, it may be suggested that the aSTG activations in fMRI studies do not reflect harmonic structure building as indicated by the ERAN per se, but represent related processes in the service of music perception, for instance the computation of pitch patterns at a more perceptual level (e.g., R. D. Patterson et al., 2002, see also Chapter 2.2.1), or the processing of meaning as reflected by the N5 (Steinbeis & Koelsch, 2008b, see also Chapter 2.1.3).

On the other hand, the second interpretation can neither be dismissed. The data were acquired at least four years after lesion onset which may have been sufficient for the full recovery of harmonic structure building (Schuppert et al., 2003). Taken together, based on the present data the function of the left aSTG in music-syntactic processing remains unclear. Future studies with either more recent or functional lesions (as induced, e.g., by TMS) will be necessary to clarify this issue.

As an aside, it should be mentioned that even if the left aSTG may not be involved in the processing of musical syntax, this does not exclude the involvement of other temporal lobe regions in the perception of music-syntactic irregularities, for instance more posterior brain regions as indicated by activations in fMRI studies (e.g., Koelsch, Gunter, et al., 2002; Koelsch, Fritz, et al., 2005; Tillmann, Koelsch, et al., 2006), or the right aSTG as suggested by lesion studies on melody discrimination (Samson & Zatorre, 1988; Zatorre, 1985). Most interestingly, a corresponding (though reversed) asymmetry has been found in the language

domain: While patients with lesions in the left anterior temporal lobe (ATL) showed a dramatic breakdown of the Early Left Anterior Negativity (ELAN), an ERP component indicating the detection of word-category errors in sentences, no such deficits were found in patients with right ATL lesions (Friederici & Kotz, 2003; Kotz, von Cramon, & Friederici, 2003).

7.3.3 Overlap of Musical and Linguistic Syntax Processing

The findings presented so far highlight the particular role of the left IFG in musical syntax processing. This result deserves specific attention, because it provides direct neuroanatomical evidence for the (partial) overlap of musical and linguistic syntax processing frequently claimed in previous works (e.g., Jentschke et al., 2005, 2008; Koelsch, Gunter, et al., 2005; Patel et al., 2008; Steinbeis & Koelsch, 2008b). By showing that harmonic structure building depends on the left IFG, just like the processing of syntax in language (e.g., Caplan et al., 1999, 2000; Davis et al., 2008; Friederici et al., 1999; Friederici, Meyer, & von Cramon, 2000a; Friederici, Bahlmann, et al., 2006, see also Chapter 1), the present study clearly proposes the left IFG as neural substrate underlying the (partial) overlap between musical and linguistic syntax processing.⁵ Notably, this assumption conforms to the proposition of the Shared Syntactic Integration Resource Hypothesis (SSIRH; Patel, 2003a) of domain-general “processing units” within frontal brain areas. This anatomical region might be the relevant interface that at least partly accounts for the influences of musical training on verbal abilities (Chan, Ho, & Cheung, 1998; Ho, Cheung, & Chan, 2003; Jentschke et al., 2005; Schlaug et al., 2008), or conversely, for the impaired musical processing in individuals with language deficits (e.g., Jentschke et al., 2008; Patel et al., 2008; Schuppert et al., 2000).

7.4 Conclusion

The present findings demonstrate that the integrity of the left IFG is essential for the generation of the ERAN, and on a more abstract level, for the processing of rule-based harmonic sequences. This finding is remarkable for two reasons: First, it demonstrates for the first time the particular relevance of the left inferior frontal lobe in higher-order music process-

⁵This finding does however not exclude further anatomical regions of overlap. One likely candidate is, for instance, the right IFG frequently associated with the processing of musical structure (e.g., Koelsch, Gunter, et al., 2002; Koelsch, Fritz, et al., 2005; Krumhansl, 2004; Tillmann, Janata, & Bharucha, 2003; Tillmann, Koelsch, et al., 2006) or pitch working memory (e.g., Zatorre et al., 1994) and the processing of prosody in connected speech (e.g., Friederici & Alter, 2004; M. Meyer et al., 2002, 2004).

ing, complementing the vast literature on the predominance of the right frontal cortex in music perception (e.g., Koelsch, Fritz, et al., 2005; Tillmann, Koelsch, et al., 2006; Zatorre, Evans, Meyer, & Gjedde, 1992; Zatorre et al., 1994). Second, the present data highlight the partial overlap of the neural networks underlying syntax processing in music and language within the left inferior frontal cortex. Hence, the present data substantially contribute to the discussion of overlapping or segregated neural resources of music and language processing, by confirming the existence of (a) shared frontal processing region(s) as proposed by the SSIRH (Patel, 2003a). Furthermore, they add to the growing literature on the left IFG as a brain area that is involved in the processing of sequential rule-based information in a domain-general way.

Chapter 8

Experiment 2 - Syntax Processing in Language and Music - Intracranial Evidence for Shared Neural Resources

The previous experiment proposed a domain-general role of the left IFG in musical and linguistic syntax processing. The exact role of the left anterior STG remained, however, still unclear, calling for further investigations. Likewise, the significance of the domain-general function of the left IFG remains to be validated in two respects: First, although the patients of Experiment 1B had relatively circumscribed frontal lesions, the brain damage mostly exceeded the IFG (extending, e.g., into the insula or the medial frontal gyrus), leaving unclear whether the deficits emerged exactly from the IFG portion of the necrotic region. Furthermore, the IFG is not a unitary structure, but highly heterogeneous in terms of microarchitecture (e.g., Amunts & Zilles, 2006; Anwander et al., 2007) and function (e.g., Bookheimer, 2002; Grodzinsky & Amunts, 2006, see also Chapter 1). Lesions spanning the IFG and beyond may, thus, easily disrupt two closely neighbouring but distinct processing systems, perhaps misleadingly suggesting an anatomical overlap of musical and linguistic syntax processing.

Second, no language data were acquired in Experiment 1B, but the domain-general role of the left IFG was assumed with regard to the prevailing literature on linguistic syntactic processing. In general, to date, the idea of a co-localisation of musical and linguistic syntax processing is exclusively based on comparisons of average peak maxima *between* studies

(e.g., Koelsch, Gunter, et al., 2002; Maess et al., 2001). Slight differences between coordinates are commonly attributed to the normal variance between samples and studies. But what if these differences were meaningful? As described above, it is conceivable that the IFG supports two functions in close neighbourhood without any overlap. Furthermore, the comparison of group average data is only little instructive on the co-localisation of brain functions, because averaging across the anatomical variability of participants can create an artificial overlap between effects that are, actually, anatomically separate in single subjects (e.g., Cohen et al., 2004). Hence, *within-subjects* designs and comparisons at *single subject level* are required to clarify whether musical and linguistic syntax processing are co-localised in inferior frontal and anterior temporal brain areas.

Addressing these criticisms, an intracranial ERP study was conducted (see, e.g., Elger et al., 1997; A. K. Engel et al., 2005; Rosburg, Trautner, Dietl, Korzyukov, et al., 2005), comparing musical and linguistic syntax processing within single subjects. Intracranial recordings were chosen due to their excellent temporal and spatial resolution providing a unique tool to study the localisation of transient ERP effects (see Chapter 4 for a methodological description of intracranial recordings).

Nine patients undergoing invasive EEG monitoring for the presurgical evaluation of pharmacoresistant epilepsy were tested in a language comprehension (Friederici et al., 1993) and a chord sequence paradigm (see Koelsch et al., 2007). The electrocortical equivalents of the ELAN and ERAN were recorded from subdural grid-electrodes placed within perisylvian brain regions, and localised by means of distributed source modelling. The comparison of the generator configurations obtained for the music and the language effect at single subject level ultimately tests the assumption of shared neural substrates of linguistic and musical syntax processing.

Before turning to this study (Experiment 2B), Experiment 2A describes and evaluates the stimulus material developed for the intracranial project. The crucial point of this pilot study was to create chord sequences that contained on the one hand very salient music-syntactic violations to better balance the difficulty level of the music and the language material, but that introduced on the other hand as few physical deviants as possible (see Bigand, 2003; Koelsch et al., 2007, for a discussion on sensory and cognitive components of harmonic priming; see also Chapter 6). This is not an easy task given that harmonic irregularity and sensory deviance are closely intertwined. However, the alignment of the difficulty level of the experimental stimuli appears pertinent to avoid confounds due to the higher expertise of participants in the processing of language compared to music.

Chapter 9

Experiment 2A - Pilot Study

Studies on the specificity or overlap of music and language have a certain tradition in neuropsychological research (see, e.g., Henschen, 1924; Koelsch & Siebel, 2005; Patel, 2003a; Peretz & Coltheart, 2003). Investigations on the similarities and differences of music and language processing, however, are confronted with the problem that, for the most part, the proficiency levels of music and language processing are rarely matched in participants. That is, due to the daily use of language to communicate with others, participants are generally “experts” in understanding and producing speech. In the music domain, this level of expertise is, however, only achieved by professional musicians deliberately practising to sing or to play their instruments over years. In the main part of the population (non-musicians and amateur musicians), the differential quantity and quality¹ of exposure to music and language lead to a differential degree of proficiency in both domains, possibly confounding comparative results. This imbalance does not only result in higher performances (e.g., Koelsch et al., in press; Samson & Zatorre, 1991; Schulze, 2006) and broader brain activations during language than during music tasks (e.g., Koelsch et al., in press; Schön et al., 2008; Schulze, 2006), but inheres the risk to trigger different cognitive processes potentially involving different brain regions like, e.g., additional frontal and parietal areas supporting working memory, attention, or executive functions (e.g., Baddeley, 2003; Collette, Hogge, Salmon, & Van der Linden, 2006; Duncan & Owen, 2000; Wager & Smith, 2003; Zatorre et al., 1994), obscuring similarities and being suggestive of differences between both domains.

¹While language perception and production take place to rather equal extent and both mostly under focused attention, music is more often perceived (mostly incidentally) than produced. Note, however, that also passive exposure, e.g., when incidentally listening to music, leads to a sophisticated implicit knowledge on, e.g., musical structure and emotional content of music, also in non-musicians (e.g., Bigand & Poulin-Charronnat, 2006; Koelsch et al., 2000; Tillmann et al., 2000).

These considerations are most relevant for Experiment 2B aiming to compare the brain potentials elicited by word category violations in language (using the paradigm of Friederici et al., 1993; Hahne & Friederici, 1999) and by harmonically unexpected chords in music (e.g., Koelsch et al., 2000; Koelsch & Sammler, 2008, see also Experiment 1A) to investigate similarities and differences of syntax processing in both domains. As illustrated in Table 9.1, the mean performance to discriminate syntactically correct and incorrect sentences is considerably higher (ceiling effect) than the percent correct responses when asked to discriminate regular and irregular chord sequence endings (close to chance level). It is obvious that a direct comparison of the brain mechanisms elicited by these sets of stimuli would be problematic, because the high performance in the language task suggests a far greater facility to perceive and judge the syntactic errors in the language compared to the music stimuli, possibly involving different degrees of attentional, working memory and executive brain functions.

Group	Language	Music
Healthy young adults	≈ 99 %	66.21 %
Healthy elderly adults	98.83 %	61.28 %
Patients with left frontal lesions	94.33 %	56.42 %

Table 9.1: Illustration of the considerable discrepancy between the mean performances to discriminate syntactically correct/regular and incorrect/irregular sentences or chord sequences in three different subject groups. The largely differing performance levels between domains render a direct comparison of underlying brain mechanisms problematic (see text for more details). Language data are taken from Hahne and Friederici (1999, healthy young adults), and from Friederici et al. (1999). Music data are taken from Experiment 1A (healthy young adults) and 1B (healthy elderly adults and patients).

One way to address this issue is to employ musical stimulus material with more salient harmonic violations, e.g., *Neapolitan sixth chords* that are detected with an accuracy of 79% correct (Koelsch et al., 2000, Experiment 3), to approximate the degree of difficulty of the chord sequences to syntactic violations in language (for studies using strong harmonic violations see also, e.g., Janata, 1995; Koelsch, Fritz, et al., 2005; Loui et al., 2005; Patel, Gibson, et al., 1998; Steinbeis & Koelsch, 2008b). However, as pointed out in Chapter 6, stronger music-syntactic violations (in terms of distance on the circle of fifths; see Chapter 2.1.2) naturally co-occur with a higher acoustic dissimilarity between the chord and its context, leading not only to cognitive but also to sensory differences between the regular and the irregular sequence endings (see, e.g., Bharucha & Stoeckig, 1987; Bigand et al., 2003; Koelsch et al., 2007; Leman, 2000; Parncutt, 1989; Tekman & Bharucha, 1998). That means, the above mentioned Neapolitan chords (e.g., F-A \flat -D \flat in C major) introduce a number of out-of-key notes (namely A \flat and D \flat in a C major chord sequence) that have

never been presented in the previous harmonic context, contrary to the pitches of the regular tonic chords. Therefore, the Neapolitan chords also represent frequency deviants, prone to elicit a mismatch negativity (MMN; Näätänen et al., 2007) overlapping with the ERAN, i.e., to tap into cognitive *and* sensory processes. These confounding sensory mechanisms do not only obscure the actual processing of musical syntax, but, moreover, compromise a direct comparison with (pure) syntax processing in language.

Addressing this problem, Experiment 2A presents newly composed chord sequences aiming to strike a balance between a high salience of the harmonic violations and low acoustic dissimilarity. The following pages will illustrate the careful analysis of these stimuli with respect to their physical properties, as well as their behavioural and electrophysiological effects in healthy young non-musicians.

9.1 Acoustic Properties of the New Chord Sequences

The figure displays two musical staves, each with a treble and bass clef, in common time. The top staff, labeled 'regular', shows a sequence of chords: V (dominant), I (tonic), IV (subdominant), IV (subdominant), V (dominant), and I (tonic). The bottom staff, labeled 'irregular', shows a sequence: V (dominant), I (tonic), IV (subdominant), IV (subdominant), V (dominant), and II↓ (Neapolitan chord). Arrows in both staves point to new pitches introduced in the final chords: C and E in the regular tonic, and D♭ in the irregular Neapolitan chord.

Figure 9.1: Chord sequences presented in Experiment 2A. The first five chord functions of regular (top) and irregular sequences (bottom) did not differ (dominant [V] - tonic [I] - subdominant [IV] - subdominant [IV] - dominant [V]). Regular sequences ended on a highly expected tonic chord [I], whereas the final chord in the irregular sequences was the major chord built on the lowered second degree [II↓]. Note that the tonic chord introduced two new pitches (C and E in C major, see arrows), whereas the II↓ contained only one new pitch (D♭ in C major, see arrow). However, all pitch classes (including the out-of-key pitch classes of the II↓) were introduced in the preceding context (see 8th notes).

To obtain musical stimulus material with a salience approaching as closely as possible the degree of difficulty of the language material, two types of chord sequences (regular and irregular) were composed that contained a more obvious harmonic violation than the se-

quences applied in Experiments 1A and 1B, but were acoustically better controlled than sequences of previous studies using, e.g., Neapolitan chords (e.g., Koelsch et al., 2000; Koelsch, Gunter, et al., 2005; Loui et al., 2005). Both types of chord sequences consisted of six chords (see Figure 9.1). Like in previous studies, the functions of the first five chords of both sequence types were identical: Dominant [V] - tonic [I] - subdominant [IV] - subdominant [IV] - dominant [V]. Regular sequences ended on a Tonic [I] (i.e., C-E-G in C major), whereas irregular sequences ended on the major chord built on the lowered second degree of the scale [II \downarrow] (i.e., D \flat -F-A \flat in C major).

To increase the similarity between final irregular chords and harmonic context and to rebut the argument of frequency deviance, all pitch classes² of the final chords, including the out-of-key pitch classes of the II \downarrow (e.g., A \flat and D \flat in C major) were incorporated into the harmonic context using passing and auxiliary notes (see 8th notes in Figure 9.1). As a result, the pitches of the II \downarrow were even more similar to the previous harmonic context than the pitches of the final tonic chords: While final tonic chords contained two new tones (in both the tenor and the base voice; see the E and the C indicated by the arrows in the upper panel of Figure 9.1), the II \downarrow contained only one new pitch (in the base voice; see the D \flat indicated by the arrow in the lower panel of Figure 9.1). With respect to pitch (class) repetition, the regular tonic chords represented, thus, stronger sensory deviants than the irregular II \downarrow chords.

Like in Experiment 1A (Chapter 6, see also Koelsch et al., 2007; Koelsch & Sammler, 2008), the acoustical properties of the chord sequences were estimated by calculating the roughness of the final chords and the pitch commonality between the penultimate and final chord according to Parncutt (1989). The analyses revealed a similar roughness of final I chords ($M = 0.090$) and final II \downarrow chords ($M = 0.085$; t -test for independent samples: $t(22) = 0.683, p > .502$), whereas the pitch commonality between penultimate (dominant) and final chords was significantly higher in regular than in irregular sequences (t -test for independent samples: $t(22) = 114.039, p < .0001$; see Table 9.2 for pitch commonality values).³

Note, however, that even if the new sequences, thus, did not reach the high acoustic quality of the sequences employed in Experiment 1A, the obtained pitch commonality

²A pitch class contains all pitches that are separated by octaves. For example, the pitch class C contains all Cs across all registers, i.e., C1, C2, C3, etc.

³A similar result was obtained by using the Contextuality Module of the IPEM-Toolbox (Leman, 2000; Leman et al., 2005, see Chapter 6 for methodological information on this approach). The pitch images of the final tonic chords correlated higher than those of final II \downarrow with the echoic memory representation established by the first five chords, most presumably closely linked to the higher pitch commonality between the penultimate dominant and the final tonic chord compared to the II \downarrow , and due to a masking of the initial four chords by the dominant [V].

Source	Chord functions	Pitch commonality	
		regular	irregular
Experiment 1A (Set A)	I vs. V/V	0.563	0.769
Experiment 1A (Set B)	I vs. V/V	0.580	0.843
Jentschke (2007; Experiment I)	I vs. $\flat\text{II}^6$	0.563	0.257
Present experiment	I vs. $\text{II}\downarrow$	0.652	0.439

Table 9.2: Summary of the pitch commonalities observed for the regular and irregular sequences employed in Experiment 1A (see also Koelsch et al., 2007; Koelsch & Sammler, 2008), for sequences comparing final tonic [I] and Neapolitan sixth chords [$\flat\text{II}^6$] (Jentschke, 2007, Experiment I), and for the sequences of the present experiment. Note that the pitch commonalities obtained for the present sequences (even if not reaching the acoustic quality of the stimuli of Experiment 1A) reflect an improvement of the acoustic properties compared to previous stimuli using Neapolitan sixth chords. I: tonic chord, V/V: double dominant, $\flat\text{II}^6$: Neapolitan sixth chord, $\text{II}\downarrow$: major chord built on the lowered second degree.

values indicate a significant improvement of the sensory parameters compared to previous sequences using Neapolitan sixth chords [$\flat\text{II}^6$] (e.g., Jentschke, 2007, see Table 9.2 for pitch commonality values). A univariate ANOVA with the fixed factors Regularity (regular vs. irregular) and SequenceType (Jentschke (2007) vs. Present experiment) revealed a main effect of Regularity ($F(1, 44) = 8545.63, p < .0001$), indicating a higher pitch commonality in regular than in irregular sequences, a main effect of SequenceType ($F(1, 44) = 2347.46, p < .0001$), reflecting a higher pitch commonality in the present sequences compared to sequences using Neapolitan sixth chords (Jentschke, 2007), and an interaction of Regularity \times SequenceType ($F(1, 44) = 277.08, p < .0001$), indicating that the introduction of the out-of-key notes in the harmonic context had brought the pitch commonality values of the irregular sequences more in line with those of the regular stimuli, as intended.

In summary, the results of the current analyses illustrate that the new chord sequences take an intermediate position between the acoustically problematic Neapolitan chord sequences and the sequences of Experiment 1A in which the relation between acoustic similarity and music-syntactic regularity was even inverted (see Chapter 6.1). Note that balancing the acoustic similarity between final irregular chords and harmonic context more strongly would come to the expense of the detectability of the irregular chords (see Introduction of the present chapter), that should be kept high in the present stimuli to match as accurately as possible with the detectability of syntactic errors in language. Therefore, the present stimuli were taken as qualified candidates for a comparative study of music and language processing. In the following paragraphs, the behavioural and electrophysiological effects of

these stimuli in non-musicians will be presented. The EEG data will specifically focus on the impact of the remaining sensory irregularity of the II↓ chords.

9.2 Behavioural Experiment

9.2.1 Methods

Participants. To estimate the detectability of the irregular sequence endings, 14 right-handed non-musicians (8 women, mean age: 24.64 years, age range: 20-29 years, mean laterality quotient according to Oldfield (1971): 85.07%) participated in a behavioural experiment. None of the participants had ever learned to play a musical instrument, and musical training did not exceed typical school education. All participants reported to have normal hearing, and no neurological or psychiatric disease.

Stimuli. Participants were presented with the regular and irregular chord sequences described above and depicted in Figure 9.1. Both sequences were transposed to all twelve major keys, resulting in 24 different stimuli. Like in previous experiments (e.g., Koelsch et al., 2000, 2007; Koelsch & Sammler, 2008), the initial five chords were identical in both sequence types (regular and irregular): Dominant [V] - tonic [I] - subdominant [IV] - subdominant [IV] - dominant [V]. In regular sequences, the final chord was a tonic chord [I] (e.g., C-E-G in a C major sequence), irregular sequences ended on the major chord built on the lowered second degree of the scale [II↓] (e.g., D \flat -F-A \flat in C major).

Like in Experiment 1A, sound files of the sequences (see Figure 9.1) were generated using Cubase SX 2.0 (Steinberg Media Technologies, Hamburg, Germany) with a grand piano sound (Steinberg, The Grand). The presentation time of all chords was 500 ms, except the critical final chords which lasted 1000 ms and were followed by a 1500 ms pause. Across the experiment, each sequence was presented four times, resulting in 96 sequences in total. Regular and irregular sequences occurred equiprobably ($p = .5$) and were pseudorandomly intermixed. Consecutive sequences always had a different tonal key and not more than 3 sequences of the same type followed each other.

Procedure. During the experiment, participants were seated in a sound shielded room. Stimuli were presented via headphones (Sennheiser HD 202) using PRESENTATION 0.53 (Neurobehavioral Systems, Inc., Albany, Canada). Listeners were asked to indicate as quickly and accurately as possible via a left or right hand button press whether the final

chord was an appropriate or an inappropriate ending of the harmonic progression, i.e., whether the composer had intended to finish or to continue the chord sequence. Key assignment was counterbalanced across participants. Four sound examples and eight practise trials were provided for training before the beginning of the experiment. The duration of the experiment was approximately 10 minutes.

9.2.2 Results

Participants had on average 88.62% correct responses ($SD = 7.54\%$, range: 71.88 - 98.96%). The performance did not differ between regular ($M = 88.98\%$) and irregular sequence endings ($M = 88.24\%$; $p > .47$), whereas the mean reaction times were significantly shorter for final I ($M = 522.15$ ms) than for final II \downarrow chords ($M = 566.08$ ms; t -test for paired samples: $t(13) = -2.57$, $p < .024$). This result is in keeping with previous studies reporting faster reaction times for related than for less related sequence endings (e.g., Bigand & Pineau, 1997; Koelsch et al., 2007; Poulin-Charronnat et al., 2005; Tillmann, Bigand, Escoffier, & Lalitte, 2006).

The overall performance in the present experiment was significantly higher and reaction times were significantly shorter than in Experiment 1A⁴ employing more subtle harmonic violations (i.e., *double dominants*; t -test for independent samples for percent correct: $t(28) = 5.63$, $p < .001$; reaction times: $t(28) = 5.51$, $p < .001$). This indicates that, as intended, the present music syntactic violations were much better detectable than the ones used in Experiment 1A, leading to an increased performance approaching (even if still not reaching) the performance obtained in language experiments (e.g., Friederici et al., 1999; Hahne & Friederici, 1999).

9.2.3 Discussion

As intended, irregular II \downarrow chords of the present sequences were much better detected than irregular *double dominants* [V/V] in Experiment 1A (and also better than Neapolitan chords in previous studies; Koelsch et al., 2000, Experiment 3: 79% correct), thus, bringing the behavioural performance considerably more in line with the performance in language studies than previous musical stimuli.

Physically, the new chord sequences represent a compromise between a strong music-syntactic violation, and a mitigation of the confound of sensory and cognitive processes

⁴Datasets of all participants of the present experiment as well as the datasets of the non-musicians of Experiment 1A entered the analysis.

during listening (see Bharucha & Stoeckig, 1987; Bigand et al., 2003; Koelsch et al., 2007; Parncutt, 1989, and the Introduction of Chapter 6 for a comparison of sensory and cognitive accounts on the processing of harmonic structure). By incorporating all pitch classes of the final chords (including the out-of-key pitch classes of the irregular II \downarrow), the sensory similarity between the harmonic context and the final II \downarrow was considerably increased, representing an improvement of the acoustic properties of the new sequences compared to stimuli using Neapolitan chords (e.g., Jentschke, 2007; Koelsch et al., 2000; Koelsch, Fritz, et al., 2005; Loui et al., 2005). The objective to present easily detectable music-syntactic violations (to keep performance high) precluded, however, to increase the pitch commonality values to the same extent as in Experiment 1A, thus, not fully excluding the involvement of sensory processing during listening to the new sequences.

The extent of these sensory mechanisms may be estimated by comparing the electrophysiological effects of the present stimuli and the sequences of Experiment 1A. If the ERAN is partly determined by the acoustic differences between regular and irregular chords (but see Koelsch et al., 2007; Koelsch & Sammler, 2008, for arguments in favour of a mainly cognitive origin of the ERAN), its amplitude should be larger when elicited by the present sequences (still containing acoustic differences) than by the sequences employed in Experiment 1A (Set B, largely controlled for acoustic parameters). To test this assumption, an EEG experiment was conducted.

9.3 EEG Experiment

9.3.1 Methods

Participants. Twenty right-handed musically untrained students were invited (10 women, mean age: 24.65 years, age range: 17-30 years, mean laterality quotient according to Oldfield (1971): 87.5%). Participants had never learned to play a musical instrument and had no musical training besides typical school education. All participants reported normal hearing and no neurological or psychiatric disease. None of them had participated in the behavioural experiment.

Stimuli. The stimulus material of the behavioural experiment was employed with two modifications: The pause between consecutive chord sequences was reduced to 500 ms (as in a previous study; Koelsch & Sammler, 2008) because no response to the final chord was required. Furthermore, some of the sequences contained one chord being played by a deviant instrument (bells, VST-sound a1) other than the standard Grand Piano (Steinberg,

The Grand) to provide the participants with an easy detection task (see below). Such timbre deviants occurred with equal probability at any of the six chord positions. Across the experiment, 192 regular, 192 irregular sequences and 48 sequences containing a deviant instrument were presented, resulting in 432 sequences in total. Regular and irregular sequences were pseudorandomly intermixed as in the behavioural experiment.

Procedure. Participants listened to the chord sequences via loudspeakers in a sound proof cabin at a comfortable volume using PRESENTATION 0.53 (Neurobehavioral Systems, Inc., Albany, Canada). They were not informed about the regular and irregular sequence endings, but were asked to press a button whenever they detected a deviant instrument. Like in Experiment 1A, the session was divided into two blocks: During the first block, participants looked at a fixation cross while listening to the stimuli; during the second block, participants watched a silent movie without subtitles (e.g., an animal documentary, reduced to 1/4th of its original size to avoid eye movement artefacts). This “entertainment” was chosen to put less strain on the participants to allow the acquisition of more trials, hence, improving the signal-to-noise ratio (SNR). The duration of the experiment was approximately 30 minutes.

Data acquisition and analysis. The EEG was recorded with 22 Ag/AgCl electrodes placed according to the extended 10–20 system (cf. Sharbrough et al., 1991), referenced to the left mastoid (M1). Electrode positions were: AF7/8, AF3/4, AFZ, F7/8, F3/4, FZ, FT7/8, FC3/4, CZ, CP5/6, P7/8, P3/4, PZ. Additional electrodes were placed on the right mastoid (M2) and the nose tip (for later re-referencing), below and above the right eye (vertical EOG), as well as at the outer canthus of each eye (horizontal EOG; to monitor eye movements). The ground electrode was placed on the sternum. Impedances were kept below 5 k Ω . The recording was achieved with two synchronised PORTI-32/MREFA amplifiers (Twente Medical Systems International B.V., Enschede, NL), at a sampling rate of 250 Hz.

After the measurement, data were re-referenced to linked mastoids (i.e., the algebraic mean of the left and right mastoid electrodes) and filtered with a 0.5-20 Hz bandpass filter (fir, 1001 points, hamming window). To eliminate artefacts, a 200 ms and an 800 ms gliding window was centred around each sampling point. The relevant sampling point was rejected whenever the standard deviance of the signal within the window exceeded 25 μ V at any channel. Additionally, trials with typical eye blinks were marked and corrected by applying an electrooculogram correction tool (xeog, EEP software, ANT, Netherlands; see Friederici et al., 1999, for a detailed description of the tool). Finally, ERPs were calculated separately for regular and irregular trials using a 200 ms prestimulus baseline and a 1000 ms poststim-

ulus time window. Sequences containing deviant instruments were excluded from further analysis (because they were only employed to devise a task for the listeners, see above).

To statistically evaluate the ERP effects, mean amplitude values were calculated within a time window from 190 - 230 ms after stimulus onset (centred around the peak of the ERAN) for 4 Regions of Interest (ROIs): Left anterior (AF3, F3, F7), right anterior (AF4, F4, F8), left posterior (CP5, P3, P7), and right posterior (CP6, P4, P8). An ANOVA for repeated measures with the within-subjects factors Chord (regular vs. irregular), Hemisphere (left vs. right), and AntPost (anterior vs. posterior ROIs) was computed on these mean values. Like in Experiment 1A, the data of the two blocks were pooled because an ANOVA with the repeated measures factors Chord, Hemisphere, AntPost, and Block (fixation cross vs. movie) did not reveal any significant interaction involving Chord and Block (p 's > .581), indicating that the visual stimulation did not influence the ERAN amplitude. An analogous ANOVA was calculated for mean amplitude values between 450 and 700 ms after stimulus onset (as in Experiment 1A) to evaluate the N5 effect. Again, the data of the two blocks were pooled because no significant interaction of Chord \times Block was found (p 's > .166) in an ANOVA for repeated measures with the within-subjects factors Chord, Hemisphere, AntPost, and Block.

To compare the ERAN amplitudes elicited by the present stimuli and by the sequences of Experiment 1A, an ANOVA for repeated measures with the within-subjects factors Chord (regular vs. irregular), Hemisphere (left vs. right), AntPost (anterior vs. posterior), and the between-subjects factor SequenceType (Experiment 1A vs. Experiment 2A) was computed. Datasets of all participants of the present experiment as well as the datasets of the non-musicians of Experiment 1A entered the analysis. The ERAN time windows of both experiments (Experiment 1A: 160..200 ms; Experiment 2A: 190..230 ms) were retained.⁵ An analogous ANOVA was calculated for the time window of the N5 (450..700 ms).

9.3.2 Results

Participants detected on average 99.38% of the deviant instruments and had only 1.15% of false alarms, showing that they attended to the stimuli. Performance did not differ between the two blocks (fixation cross: $M = 99.58\%$; silent movie: $M = 99.17\%$; t -test for paired samples: $t(19) = 0.81$, $p > .427$) demonstrating that participants paid equally attention to the stimuli in both halves of the experiment.

⁵In both experiments, the statistical time window was centred around the peak of the ERAN. The different peak latencies may be due to the different types of sequences applied in Experiment 1A and 2A.

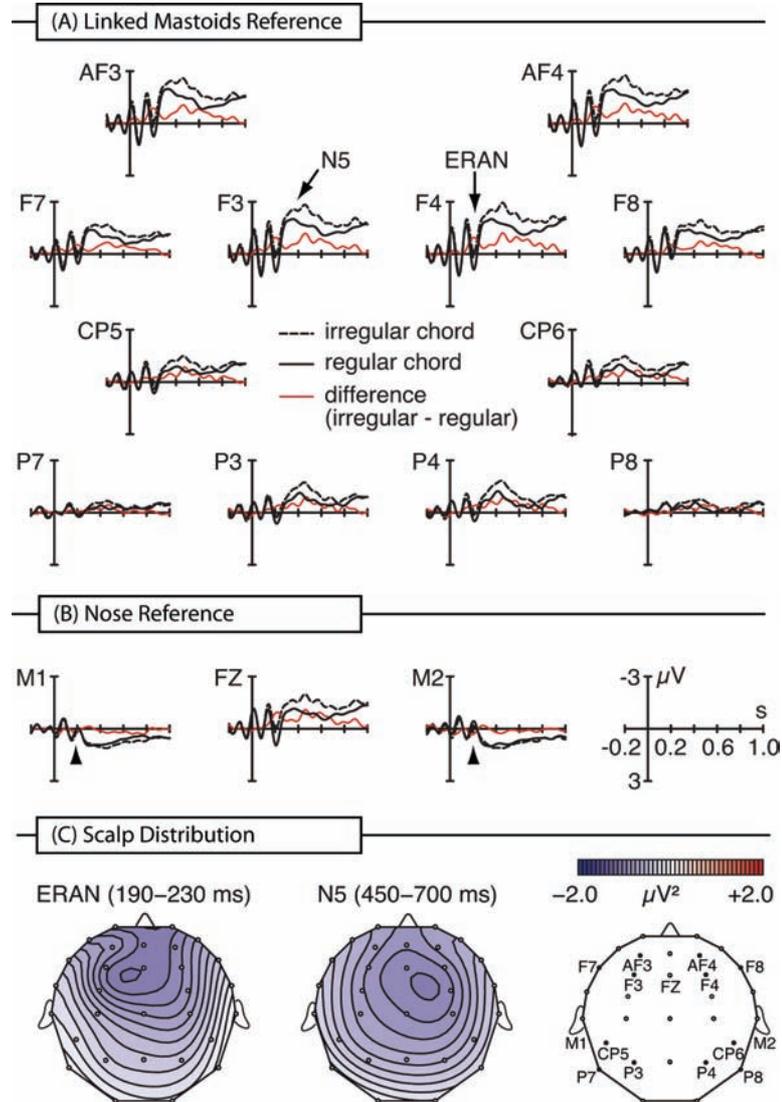


Figure 9.2: **A:** Potentials referenced to linked mastoids elicited by regular (solid line) and irregular chords (dashed line) as well as the difference wave (red line). An early negativity around 200 ms (the ERAN) as well as a later negativity peaking around 500 ms (the N5) were observed (see arrows). **B:** The ERAN inverted polarity at the mastoid electrodes (M1 and M2, see arrows). **C:** Both, ERAN and N5 had a frontal scalp distribution and were not lateralised.

As depicted in Figure 9.2 and Table 9.3, irregular chords elicited a frontally distributed negativity peaking around 210 ms after onset of the critical chord, i.e., an ERAN. Furthermore, an N5 was observed, i.e., a later negativity with frontal scalp topography starting around 400 ms after chord onset.

ROI	ERAN (190..230 ms)	N5 (450..700 ms)
left anterior	-0.76 (\pm 0.89)	-0.67 (\pm 0.54)
right anterior	-0.77 (\pm 0.84)	-0.73 (\pm 0.56)
left posterior	-0.21 (\pm 0.70)	-0.39 (\pm 0.48)
right posterior	-0.27 (\pm 0.84)	-0.47 (\pm 0.51)

Table 9.3: Mean ERAN and N5 amplitudes (μ V; \pm SD) elicited by II \downarrow in non-musicians in anterior and posterior ROIs.

ERAN time window (190..230 ms). Within the early time window, the ANOVA revealed a significant main effects of Chord ($p < .002$) indicating that irregular chords elicited an ERAN (see Table 9.4 for detailed statistical values). Furthermore, a significant interaction of Chord \times AntPost ($p < .007$) was found, demonstrating the frontal scalp distribution of the ERAN. The interaction of Chord \times Hemisphere did not reach significance ($p > .809$), illustrating a bilateral distribution of the effect which is in line with a number of recent studies (e.g., Leino et al., 2007; Loui et al., 2005; Miranda & Ullman, 2007; Steinbeis & Koelsch, 2008b).

N5 time window (450..700 ms). Within the later time window (450..700 ms), the ANOVA indicated a significant main effects of Chord ($p < .0001$) showing that irregular chords elicited an N5. No further interactions were found, demonstrating the broad scalp distribution of the negativity (see Table 9.4).

Experiment 1A vs. Experiment 2A. Contrary to our assumptions, the ERAN appeared to be larger, not smaller, when elicited by the acoustically “clean” stimuli employed in Experiment 1A (see Tables 6.2) compared to the acoustically less balanced chord sequences of the present experiment (see Table 9.3).

Within the ERAN time window, the ANOVA revealed a main effect of Chord ($p < .0001$), indicating that irregular chords elicited an ERAN. Furthermore, an interaction of Chord \times AntPost ($p < .001$; indicating the frontal scalp distribution of the ERAN), as well as a significant interaction of Chord \times SequenceType ($p < .05$) was observed, indicating that the *double dominants* [V/V] employed in Experiment 1A indeed elicited larger ERAN

Effect	ERAN (190..230 ms)		N5 (450..700 ms)	
	<i>F</i> (1, 19)	<i>p</i> -value	<i>F</i> (1, 19)	<i>p</i> -value
Chord	12.96	< .002	47.74	< .0001
Chord × Hemisphere	0.06	> .809	1.20	> .287
Chord × AntPost	9.17	< .007	3.24	> .087
Chord × Hemisphere × AntPost	0.11	> .748	0.18	> .674

Table 9.4: Summary of the ANOVAs of Chord × Hemisphere × AntPost for an early (ERAN) and a late (N5) time window. Only main effects and interactions involving the factor Chord are reported. Bold font indicates significant effects. The results show that irregular chords elicited a bilaterally distributed ERAN (main effect of Chord, interaction of Chord × AntPost, but no interaction of Chord × Hemisphere) as well as an N5 with broad scalp distribution (main effect of Chord, but no interactions of Chord × Hemisphere or AntPost).

amplitudes than the II_↓ chords used in the present experiment. The scalp distribution of the ERAN did not significantly differ between both sequence types (no significant 3- and 4-way interactions involving the factors Chord and SequenceType, see Table 9.5).

Effect	ERAN		N5	
	<i>F</i> (1, 30)	<i>p</i> -value	<i>F</i> (1, 30)	<i>p</i> -value
Chord	35.48	< .0001	41.32	< .0001
Chord × Hem	0.02	> .900	4.00	> .054
Chord × AntPost	22.06	< .0001	6.52	< .017
Chord × SequType	4.19	< .050	8.47	< .007
Chord × Hem × AntPost	0.38	> .540	0.01	> .910
Chord × Hem × SequType	0.23	> .633	0.47	> .496
Chord × AntPost × SequType	0.73	> .398	0.08	> .773
Chord × Hem × AntPost × SequType	1.09	> .304	0.14	> .710

Table 9.5: Comparison of the ERAN and N5 elicited in Experiment 1A and 2A. Only main effects and interactions involving the factor Chord of the ANOVAs of Chord × Hemisphere × AntPost × SequenceType are reported. Bold font indicates significant effects. The results show that the double dominants [V/V] employed in Experiment 1A elicited a larger ERAN but a smaller N5 than II_↓ presented in the Experiment 2A (see interaction of Chord × SequenceType).

Within the N5 time window, the ANOVA revealed likewise a main effect of Chord ($p < .0001$), indicating that irregular chords elicited an N5. Furthermore, a significant interaction of Chord × AntPost ($p < .017$; indicating the typical frontal scalp distribution of the N5), as well as an interaction of Chord × SequenceType was found ($p < .007$; see Table 9.5),

indicating that V/Vs elicited a smaller N5 than II \downarrow chords. No further interactions were observed, showing a similar scalp distribution of the N5 in both experiments.

9.3.3 Discussion

As expected, the newly created chord sequences elicited an ERAN as well as an N5 demonstrating that these stimuli trigger music-syntactic processing (Koelsch et al., 2000; Koelsch, 2005). Most intriguingly, the ERAN was larger when elicited by the acoustically well balanced V/Vs employed in Experiment 1A (see also Koelsch & Sammler, 2008) than by the present II \downarrow that reflect not only a harmonic but also a slight acoustic irregularity. This finding demonstrates that the ERAN is not driven by bottom-up sensory processes and relies to a considerable degree on top-down cognitive processes (see also Koelsch et al., 2007; Koelsch & Sammler, 2008). In other words, if the ERAN was related to the processing of acoustic features like sensory dissonance or pitch commonality (that were not entirely balanced in the present stimuli, but well controlled in Experiment 1A), the II \downarrow should have elicited a larger negativity than the V/Vs. The observation of the inverse result combined with the results of Experiment 1A, thus, clearly argue for a prevalence of cognitive over sensory mechanisms when listening to harmonic progressions. This idea is in keeping with studies disentangling the electrophysiological signatures of music-syntactic processing and sensory deviance detection, e.g., the ERAN and the MMN (e.g., Koelsch, Maess, et al., 2001; Koelsch, Gunter, et al., 2005; see Koelsch, in press for a review), or a P3 and a late slow wave (Regnault et al., 2001), associated with the processing of the deviant harmonic function of a chord or the irregular acoustic structure of a sound, respectively. Furthermore, this finding fits with the claim of several authors that the co-occurrence of acoustic and music-syntactic irregularity may perhaps have contributed to the internalisation of the harmonic structure of music (but see the data of Tillmann & McAdams, 2004, showing that learning of statistical regularities may take place independently from acoustical segmentation cues), but once established, this implicit knowledge gains a level of considerable autonomy and predominance over pure acoustic cues in adult listeners (e.g., Bharucha & Stoeckig, 1987; Bigand et al., 2003; Tekman & Bharucha, 1992, 1998).

The cognitive origin of the ERAN is further supported if one inspects the present results in light of studies on the relation between the ERAN amplitude and harmonic context build-up. It has been shown that the ERAN amplitude is modulated by the stability of key representation and the specificity of the listeners' expectations on upcoming events. For example, Koelsch et al. (2000) demonstrated that Neapolitan chords presented at the final position of an authentic cadence, violating the very specific expectation of a tonic chord, lead to a

significantly larger ERAN amplitude than the presentation of Neapolitan chords at the third position of the chord progression where they are less unexpected (see also Koelsch, Maess, et al., 2001; Maess et al., 2001). Applied to the present results, the incorporation of one out-of-key note into the harmonic context in Experiment 1A (e.g., F \sharp in C major; see Figure 6.1) compared to three out-of-key notes in the present stimuli (e.g., A \flat and D \flat in C major; see Figure 9.1), may have less perturbed the determination of the tonal centre and the formation of expectations on upcoming events, leading to a larger ERAN amplitude. Taken together, these results argue that the ERAN is essentially determined by top-down cognitive mechanisms.⁶

9.4 Conclusion

To summarise, the aim of the present study was to create and to acoustically, behaviourally, and electrophysiologically test new musical stimulus material containing easily detectable harmonic violations to approximate the degree of difficulty of the stimuli to language material (Friederici et al., 1993; Hahne & Friederici, 1999). At the same time, it was intended to keep the acoustic dissimilarity of the irregular chords with respect to the harmonic context as low as possible to avoid a confound of cognitive and sensory processing differences between expected and unexpected sequence endings. To this end, major chords built on the lowered second degree of the scale [II \downarrow] were employed, i.e., chords that were very similar to the Neapolitan chords used in previous studies (e.g., Jentschke, 2007; Koelsch et al., 2000; Maess et al., 2001; Steinbeis & Koelsch, 2008b), and represented a strong music-syntactic violation at the final position of a cadence. Like in Experiment 1A (Set B), all out-of-key pitch classes of these chords were incorporated into the initial five chords to increase the acoustic similarity between the irregular chords and the context. The acoustic properties of the present stimuli were, thus, considerably better controlled than in previous stimuli using Neapolitan chords.

As intended, the performance in detecting the irregular chords was significantly higher than in previous studies, yielding the best approximation to the performance in language experiments ever obtained with chord sequences that were in some respect balanced for acoustic deviance. Furthermore, the ERAN elicited by these stimuli was shown to be essentially dependent on top-down music-syntactic, not on bottom-up sensory processing. The present stimuli are, thus, particularly qualified for studies comparing music and language processing.

⁶Consequently, the results of Experiment 1A (see Chapter 6) which could have been explained by a sensory or a cognitive account, can be clarified in favour of cognitive mechanisms.

Chapter 10

Experiment 2B - Intracranial ERP Study

As lined out in Chapter 3, syntax processing in language and music is thought to rely on partially overlapping neural structures that are involved in a domain-general way in the analysis of rule-based sequential information (Koelsch & Siebel, 2005; Patel, 2003a). Likely candidates for such an overlap are the IFG and the STG, two brain areas that have been previously associated with syntax processing in language (Friederici, 2002; Friederici & Kotz, 2003) and music (Koelsch, 2005, 2006, see also Chapter 7). Yet, as explained in Chapter 8, the interpretation of these results in terms of a co-localisation of musical and linguistic syntax processing remains debatable for two reasons: First, the anatomical overlap has never been validated in a within-subjects design, but results from the comparison of peak coordinates between studies. Second, the argument of overlapping neural resources is exclusively based on group averages, risking to obtain an artificial overlap due to the smoothing of the natural anatomical and functional variability between subjects (see, e.g., Cohen et al., 2004; G. A. Ojemann & Mateer, 1979).

The present study was designed according to these considerations. A language and a music experiment was conducted with nine patients during the acquisition of Electro-Corticogram (ECoG) data from left and right perisylvian brain areas for presurgical evaluation of epilepsy. The electrocortical equivalents of the scalp-recorded ELAN and ERAN were identified in each patient and subjected to Brain Surface Current Density (BSCD) mapping in order to localise and compare their neural generators. It was hypothesised that:

1. Both phrase-structure violations in sentences and harmonic violations in chord progressions would elicit an early negativity with a peak latency around 200 ms.

2. The neural generators of both negativities would be located at identical or very similar coordinates within inferior frontal and anterior temporal brain areas.

10.1 Methods

10.1.1 Participants

Data were acquired from 11 adult patients undergoing presurgical evaluation of pharmacoresistant epilepsies by means of perisylvian subdural electrodes. One patient was excluded from the data analysis due to an extended haemorrhage underneath the electrode grid. A second patient had to be excluded due to almost permanent inter-ictal activity at the majority of the grid electrodes. The remaining 9 patients (3 women, 6 men) had a mean age of 31.56 years (range: 18-53 years). All patients were native German speakers, right-handed, and had a left hemisphere language dominance as assessed by standard fMRI protocols and/or electric stimulation. The average duration of school education was 10.33 years (range: 8-12 years). None of the patients was a professional musician. Six patients had learned to play an instrument during their childhood or youth, but were not actively playing any more (see Table 10.1 for details). Two patients (K.R. and S.R.²) had left ear hearing deficits. They were still included into the analysis because previous studies have shown that the ELAN and ERAN are reliably elicited if stimuli are presented with different intensities to both ears (Maidhof & Koelsch, in press), and that the ERAN is even elicited in cochlear implant users (Koelsch, Wittfoth, Wolf, Müller, & Hahne, 2004).

ID	Age	Gender	Handedness (LQ)	Language Dominance	School Education	Musical Training
K.H.	29	M	R (83)	left (fMRI)	12 years	2 years
G.M.	31	M	R (68)	left (fMRI)	9 years	0 years
S.R. ¹	18	M	R (75)	left (fMRI/e-stim.)	12 years	4 years
K.R.	43	F	R (100)	not tested	8 years	10 years
M.S.	19	M	R (90)	left (e-stim.)	9 years	0 years
B.N.	28	F	R (82)	left (fMRI)	12 years	4 years
W.O.	35	M	R (80)	left (e-stim.)	12 years	3 years
S.R. ²	53	M	R (100)	left (fMRI)	10 years	0 years
S.G.	28	F	R (80)	left (fMRI/e-stim.)	9 years	2 years

Table 10.1: Personal data of the patients. Gender: F = female, M = male. Handedness is indicated according to the Edinburgh Handedness Inventory (Oldfield, 1971): LQ = laterality quotient, R = right handed. Language dominance was assessed using standard fMRI protocols or electric stimulation (e-stim.). Musical training indicates the accumulated years of playing an instrument.

During presurgical evaluation, spontaneous brain activity was recorded invasively using various settings of strip and grid electrodes, as well as depth electrodes placed with the goal of localising suspected epileptogenic foci and identifying functional regions to be spared in surgery. In the present study, only subdural electrodes placed over lateral fronto-temporal brain areas were analysed. Six patients had electrode grids over left perisylvian brain areas, in three patients electrodes were placed over the right hemisphere. The mean duration of epilepsy was 19.56 years (range: 5-50 years) - aetiology differed between patients (see Table 10.2 for details). The research protocol was approved by the appropriate institutional review boards at the University Clinic in Freiburg and the University Clinic in Bonn. Prior to the study, written informed consent was obtained from each patient.

Table 10.2: Medical data of the patients. The diagnosis of epilepsy is indicated according to the nomenclature of the International League Against Epilepsy (ILAE): TLE = temporal lobe epilepsy, SPS = simple partial seizures, CPS = complex partial seizures, GTC = generalized tonic-clonic convulsions. AHS = amonshornsclerosis. Medication indicates the daily dose of the anticonvulsant (active pharmaceutical ingredient, API) at the day of testing. The column "Electrode Positions" specifies the configuration and localisation of the subdural grid and strip electrodes. The number of days between implantation and testing is indicated in the outer right column ("Days since Implantation").

ID	Duration of Epilepsy	Diagnosis (ILAE)	Pathology	Medication	Electrode Positions	Days s. Impl.
K.H.	22 years	TLE with SPS/CPS evolving to GTC	dysplasia, left hippocampus	1000 mg Levetiracetam 1500 mg Oxcarbazepin	4x8 left temp.	7
G.M.	18 years	TLE with SPS/CPS evolving to GTC	focal cortical dysplasia left temporo-mesial	300 mg Lamotrigin	4x8 left temp.	6
S.R. ¹	7 years	symptomatic focal epilepsy with SPS/CPS evolving to GTC	focal cortical dysplasia, left temporo-mesial	300 mg Oxcarbazepin	4x8 left temp.	5
K.R.	38 years	symptomatic focal epilepsy with CPS evolving to GTC	lesions, left temporo-occipito-mesial, insular, superior-temporal	no medication	1x6 right frontal to postcentral, 2x6 right temp. 1x6 right temp.	14
M.S.	16 years	symptomatic focal epilepsy with CPS	AHS left	3000 mg Levetiracetam	4x8 left temp.	12

ID	Duration of Epilepsy	Diagnosis (ILAE)	Pathology	Medication	Electrode Positions	Days s. Impl.
B.N.	9 years	TLE with SPS/CPS evolving to GTC	normal	no medication	4x8 right temp.	6
W.O.	11 years	symptomatic focal epilepsy with CPS evolving to GTC	heterotopia, periventricular left	350 mg Lamotrigin 2000 mg Levetiracetam	4x8 left temp.	16
S.R. ²	50 years	symptomatic focal epilepsy with CPS evolving to GTC	AHS, right	1200 mg Oxcarbazepin	4x8 right temp.	17
S.G.	5 years	cryptogenic focal epilepsy with CPS evolving to GTC	normal	400 mg Lamotrigin	4x8 left temp.	17

10.1.2 Stimulus Material

All patients participated in a music and a language experiment. The stimulus material was presented auditorily in both experiments and will be described in turn.

(A) Music

regular

irregular

V I IV IV V I

V I IV IV V II \downarrow

(B) Language

correct

Das Geheimnis wurde geflüstert.
[The secret was whispered.]
Np Aux Pp

incorrect

Der Plan wurde im geflüstert.
[The plan was in-the whispered.]
Np Aux P Pp

filler

Der Name wurde im Versteck geflüstert.
[The name was in-the cranny whispered.]
Np Aux P Np Pp

Figure 10.1: Stimulus material presented in Experiment 2B. Panel (A) depicts the regular and irregular chord sequences presented with equal probability ($p = .5$) randomly across all tonal keys (see Chapter 9 for more details). Regular sequences ended on a highly expected tonic chord [I], whereas irregular sequences ended on the major chord built on the lowered second degree [II \downarrow]. Panel (B) shows the sentence material presented in the language blocks. All sentences contained a noun phrase [Np], an auxiliary [Aux], and a past participle [Pp]. Incorrect sentences additionally contained an incomplete prepositional phrase, i.e., only a preposition [P] without a noun phrase [Np]. Filler sentences with a complete prepositional phrase, [P] and [NP], were included in the experiment to avoid that participants anticipated the word-category violation as soon as encountering the preposition.

Music Material. Participants were presented with the regular and irregular chord sequences that were described and evaluated in Experiment 2A (see Chapter 9) and are depicted in Figure 10.1 A. As in previous experiments (e.g., Koelsch et al., 2000, 2007; Koelsch & Sammler, 2008), the initial five chords were identical in both sequence types (regular and irregular): Dominant [V] - tonic [I] - subdominant [IV] - subdominant [IV] - dominant [V]. In regular sequences, the final chord was a Tonic [I] (e.g., C-E-G in a C major sequence), irregular sequences ended on the major chord built on the lowered second degree of the scale [II \downarrow] (e.g., D \flat -F-A \flat in C major).

Like in Experiment 2A, chord sequences were presented with a grand piano sound. Infrequently one sequence contained a chord played by a deviant instrument. The presentation time of all chords was 500 ms, except the critical final chords which lasted 1000 ms and were followed by a 500 ms pause. Across the experiment, participants listened to 144 reg-

ular and 144 irregular sequences as well as 36 sequences containing a deviant instrument resulting in 324 sequences in total.¹ Regular and irregular sequences were pseudorandomly intermixed. Consecutive sequences always had a different tonal key and not more than 3 sequences of the same type (regular/irregular) followed each other. Patients were not informed about the different sequence endings but were asked to press a button whenever they detected a chord played by a deviant instrument.

Language Material. In the language blocks of the experiment, patients were presented with short sentences (mean duration: 1738 ms, range: 1268-2670 ms; taken with permission from Hahne & Friederici, 1999, see Appendix A) that were either syntactically correct or incorrect (see Figure 10.1 B). Correct sentences consisted of a noun phrase [Np], an auxiliary [Aux], and a past participle [Pp] (e.g., *Das Geheimnis wurde geflüstert.* - *The secret was whispered.*). Each correct sentence had a syntactically incorrect counterpart consisting of a similar noun phrase, the same auxiliary, and past participle. To violate phrase-structure, a preposition [P] was inserted before the past participle (e.g., *Der Plan wurde im geflüstert.* - *The plan was in-the whispered.*). Since German grammar demands a preposition to be followed by a noun phrase, the immediate succession of a past participle represents a word-category violation. To ensure that participants were not able to anticipate the upcoming syntactic violation as soon as a preposition was encountered, a third category of correct filler sentences was presented, containing a noun phrase, an auxiliary, a preposition followed by a noun phrase, and a past participle (e.g., *Der Name wurde im Versteck geflüstert.* - *The name was in-the cranny whispered.*). Sentences were spoken by a professional female speaker (see Hahne & Friederici, 1999, for a detailed description of the stimulus generation).

Across the experiment, participants listened to 132 correct, 132 incorrect, 66 filler sentences and 48 sentences containing a word spoken by a male (and not the standard female) voice.² Patients were not informed about the syntax violations but were asked to press a button whenever they detected the male voice. Sentences were presented with a pause of 2 seconds between consecutive trials.

10.1.3 Procedure

The experiment was conducted at bedside. Stimuli were presented via headphones (Koss Porta Pro, Milwaukee, WI, USA) with a Laptop (HP compaq nx7010) using PRESENTA-

¹Patients K.H., G.M., and M.S. completed only 2/3 of the music experiment, resulting in 96 regular, 96 irregular sequences, and 24 sequences containing a deviant instrument, i.e., 216 in total.

²Patients K.H., G.M., and M.S. completed only 2/3 of the language experiment, resulting in 88 correct, 88 incorrect, 44 filler sentences, and 32 sentences containing a voice deviant.

TION 0.70 (Neurobehavioral Systems, Inc., Albany, CA, USA). After having given written consent, the patients were carefully instructed to pay attention to the sentences and chord sequences and to press a button whenever they detected a deviant instrument or male voice. Six to eight practise trials were conducted to make clear that the patients had understood the instruction. Music and language stimuli were presented separately in 12 short blocks with a duration of about 3 minutes each. Music and language blocks alternated, counterbalanced across patients.

To test the patients' ability to explicitly discriminate syntactically correct and incorrect stimuli, one music and one language block were added at the end of the session. Now, patients were informed about the regular and irregular chord sequence endings as well as the syntactic violations within the sentences and asked to indicate via button press, whether the final chord/the sentence was regular/correct or irregular/incorrect. Prior to the music task, participants received a short training, ranging from 8 to 40 trials (depending on the need of practise). Afterwards, their performance was tested during the random presentation of 24 regular and 24 irregular sequences. Similarly, patients received 6 to 12 training trials in the language task before they were presented with 24 correct, 24 incorrect and 12 filler sentences. Patients were instructed to respond quickly within a 2 seconds time window after the onset of the critical chord or word. In total, the session lasted approximately 90 minutes (pauses included).

10.1.4 Data Acquisition and Analysis

Data were collected in the Section Epileptology of the Neurocenter at the University Hospital in Freiburg (Germany), as well as in the Clinic for Epileptology at the University Hospital in Bonn (Germany). The EEG signal was recorded from subdural grid and strip electrodes as well as from depth electrodes placed according to medical needs. In Freiburg, EEG data acquisition was performed with a Neurofile NT digital video EEG system (IT-med, Usingen, Germany). In Bonn, data were recorded with the digital EPAS system (Schwarzer, Munich, Germany) and its implemented Harmonie EEG software (Stellate, Quebec, Canada). Depending on the amplifier, the data were sampled at 256, 1000, or 1024 Hz. To synchronise the electrophysiological recordings with behavioural events, the experimental computer sent pulses through the parallel port via an optical isolator into an unused recording channel or digital input on the amplifier. For all patients, the exact locations of the electrodes were determined by means of coregistered and normalised pre- and postoperative magnetic resonance images (Kovalev et al., 2005). Only data from electrodes placed on lateral fronto-temporo-parietal brain areas were analysed.

Data processing was done with EEP 3.2 (ANT Software, Enschede, Netherlands). In a first step, channels with aberrant inter-ictal activity or technical artefacts (mean = 1.33 channels; range: 0-5 channels) were identified by an experienced epileptologist and excluded from the analysis. Data were re-referenced to the average reference of the remaining electrodes of the grid, and the sampling rate in all data sets was adjusted to 500 Hz after antialias filtering with a 250-Hz lowpass filter (fir, 241 or 247 points depending on whether the previous sampling rate was 1000 or 1024 Hz, blackman window). Subsequently, data were filtered using a 0.4-Hz highpass filter (fir, 6931 points, blackman window; to eliminate slow drifts and to adjust the baseline), and a 25-Hz lowpass filter (fir, 213 points, blackman window; to eliminate fast oscillations). Afterwards, the data were visually inspected, and epochs containing inter-ictal activity or technical artefacts were manually rejected under supervision of an epileptologist. In a final step, data were averaged for each condition (regular chord, irregular chord, correct past participle, incorrect past participle) in a 1000 ms poststimulus window.

The ERAN and ELAN were calculated as difference potentials between ERPs following the irregular chord / incorrect past participle and ERPs following the regular chord / correct past participle. Time windows for the early negativities in language and music were identified in each patient by visual inspection of the data. Each time window was centred around the peak of the greatest negativity occurring between 100 and 300 ms after onset of the critical chord or word. This late offset of the latency window was chosen because most patients were heavily medicated at the time of measurement (see Table 10.2), possibly delaying ERP components. Subsequently, the mean amplitudes of the regular/correct and the irregular/incorrect condition within the chosen time window was compared at each electrode by means of *t*-tests for independent samples (Bonferroni-corrected).

In a second processing step, Brain Surface Current Density mapping (BSCD; Knösche, Praamstra, Stegeman, & Peters, 1996; Knösche et al., 1999) was applied to localise the distributed neural sources of the observed effects. Contrary to common dipolar models, this method does not require any a priori knowledge on the nature and number of the generators, but allows to reconstruct distributed sources of arbitrary shape and extent (see Michel et al., 2004, for a comprehensive review on dipolar vs. distributed source models). Based on the Minimum Norm algorithm (Hämäläinen & Ilmoniemi, 1994) this approach restricts the localisation of neural generators to the cortical surface. This constraint is mainly motivated by the substantial concerns that have been raised about the validity of the depth-solution of source models (see, e.g., Knösche et al., 1999). Activity is, thus, reconstructed on a 2-dimensional plane at a constant depth from the inner surface of the skull.

To date, BSCD mapping has never been applied to intracranial data, and more generally, the question arises whether source modelling algorithms may yield reliable results regarding

the restricted coverage of the brain by, e.g., 4×8 or 8×8 electrode grids. Indeed, several studies have already successfully applied various source modelling methods like multiple source modelling (i.e., a dipolar model; Baumgartner et al., 1991) or distributed source modelling (i.e., LORETA; Korzyukov et al., 2007) yielding plausible results. In fact, the spatial resolution (a prerequisite for reliable source estimations) of the intracranial potentials largely excels the one achieved with scalp EEG, thus, providing optimal signal quality for source estimations, although it cannot be excluded that solutions become a little shaky at bordering electrodes of the grid. In general, one has to be aware that the electrode grid captures only a cutout of the brain activity during the task consequently leading to generator solutions including only parts of a possibly more widespread neural network. Therefore, the coverage of the perisylvian brain regions within the present experiment allowed to find sources within the respective inferior fronto-parietal and temporal brain areas but not in more dorsal frontal structures or even contralateral brain areas.

BSCD mapping was applied on the peak of the difference waves occurring between 100 and 300 ms after onset of the critical element using ASA 2.32 (ANT Software, Enschede, Netherlands). The volume conductor model was made up by one compartment for the cortical surface of the individual MNI scaled brains. This head model was tessellated with 5168 triangles (7 mm edge length), reconstruction surface was defined in a depth of 7 mm, and 2586 triplets of orthogonal dipoles were equidistantly placed on this surface (distance 7 mm). Their magnitudes were computed using the minimum-norm least-squares (MNLS) method assuming a noise level of 20% of the signal maximum (Knösche et al., 1999).

10.2 Results

10.2.1 Language

Patients detected on average 99.31% of the voice deviants and had on average 0.32% of false alarms showing that they attended to the stimulus material. All patients performed well above chance level when asked to detect the syntactic errors within the sentences, as assessed in the final block of the session (mean: 94.45%, *SD*: 6.91%, range: 79.17-100%) showing their sensitivity to the syntactic errors (see Table 10.3).

Figure 10.2 and Figure 10.3 illustrate the brain responses elicited by correct and incorrect sentences in patients with electrodes in the left (Figure 10.2) or right (Figure 10.3) hemisphere (see Figures B.1 to B.9 in Appendix B for the complete data sets of all patients). In all participants, word-category violations elicited an early negativity with a mean peak latency of 193 ms after onset of the final word (range: 140-160 ms; see left columns and

Patient	Language		Music	
	%correct	<i>p</i> -value	%correct	<i>p</i> -value
<i>Left hemisphere</i>				
K.H.	100.00%	< .001	77.08%	< .001
G.M.	79.17%	< .001	56.25%	> .160
S.R. ¹	89.58%	< .001	97.92%	< .001
M.S.	91.67%	< .001	70.83%	< .001
W.O.	100.00%	< .001	50.00%	> .440
S.G.	100.00%	< .001	70.83%	< .001
<i>Right hemisphere</i>				
K.R.	93.75%	< .001	64.58%	< .020
B.N.	97.92%	< .001	89.58%	< .001
S.R. ²	97.92%	< .001	50.00%	> .440

Table 10.3: Behavioural performance of each patient when asked to discriminate correct and incorrect sentences in the language experiment, and regular and irregular chord sequences in the music experiment. *P*-values indicate whether patients performed above ($p \leq .05$) or below ($p > .05$) chance level (50%) as tested with binomial tests.

blue regions in the topography maps). Additionally, most of the patients showed a simultaneous early positivity (see right columns and red regions in the topography maps; see Table B.1 in Appendix B for statistics at single electrodes). This polarity inversion might indicate the contribution of a source with tangential orientation relative to the brain surface, possibly located within the superior temporal plane as reported by previous MEG studies (e.g., Gross et al., 1998; Friederici, Wang, et al., 2000).

The position of the effect maxima (see Table B.1 in Appendix B) as well as the global topography of the potentials considerably differed between individuals, most presumably due to the natural variability of brain activity across participants as well as the different cortical folding in the single subjects (see, e.g., Cohen et al., 2004; G. A. Ojemann & Mateer, 1979). It should be mentioned that topographic differences do not necessarily indicate distinct spatial configurations of the neural generators (e.g., McCarthy & Wood, 1985; Urbach & Kutas, 2002).³ The intricate potential topographies with several positive and negative

³As pointed out by Urbach and Kutas (2002), identical generators differing in relative strength may produce largely different topographic patterns (see McCarthy & Wood, 1985; Picton et al., 2000, for attempts to eliminate the impact of generator magnitudes). Furthermore, adding one generator to an otherwise identical configuration equally results in highly different patterns neglecting the similarity of the other sources. Finally, a different orientation of one of the generators (which may be situated only some millimetres apart but is tilted due to the cortical folding) may result in a completely different distribution. Taken together, the distribution of brain potentials is largely determined by the relative strength, orientation and number of underlying sources, thus, precluding to infer different spatial configurations of generators from merely different topographic pat-

peaks suggest the activity of multiple sources possibly with partly radial and partly tangential orientations. The identification of the underlying generators may be achieved by applying source localisation methods as the Brain Surface Current Density (BSCD) mapping described in section 10.2.3.

Notably, effects were observed irrespective of whether electrodes were implanted in the left or the right hemisphere which is consistent with previous studies reporting a bilateral network involved in the generation of the scalp recorded ELAN (e.g., Friederici, Wang, et al., 2000; Gross et al., 1998; Knösche et al., 1999). Apart from that, the highly similar peak latencies of the present potentials and the scalp recorded ELAN (e.g., Hahne & Friederici, 1999), as well as the polarity inversion (see Maidhof & Koelsch, in press) suggest that the observed effects reflect an electrocortical equivalent of the ELAN.

10.2.2 Music

Patients detected on average 94.91% of the deviant instruments and had on average only 0.37% false alarms showing that they attended to the stimuli. When asked to discriminate regular and irregular sequences (as assessed in the final block of the experiment), patients performed on average around 69.67% (*SD*: 16.7%, range: 50-97.92%). Six patients performed above chance, three patients were at chance level as revealed by binomial tests (see Table 10.3).

In five of the nine patients, an early negativity with a mean peak latency of 189 ms after onset of the irregular chords was observed (range: 166-204 ms; see left column and blue regions in the topography maps in Figure 10.4). As in the language experiment, almost all of these patients also showed a simultaneous early positivity at neighbouring electrodes (see right column and red regions in the topography maps in Figure 10.4; see Table B.2 in Appendix B for statistical values at single electrodes), suggesting the contribution of a tangentially oriented source, and possibly mimicking the polarity inversion observed at mastoidal leads when scalp recorded potentials are referenced to a nose electrode (e.g., Koelsch et al., 2000; Koelsch, in press). Furthermore, the effects were observed irrespective of which hemisphere was investigated, supporting the notion of a bilateral neural network involved in the processing of musical syntax, which is in line with previous studies (e.g., Maess et al., 2001; Koelsch, Fritz, et al., 2005).

As in the language experiment, the position of the effect maxima (see Tables B.1 and B.2 in Appendix B) as well as the global topography of the potentials considerably differed be-

terns. One way to address this pertinent question is to model the underlying generators by means of source localisation procedures (see Michel et al., 2004, for a review on the different approaches).

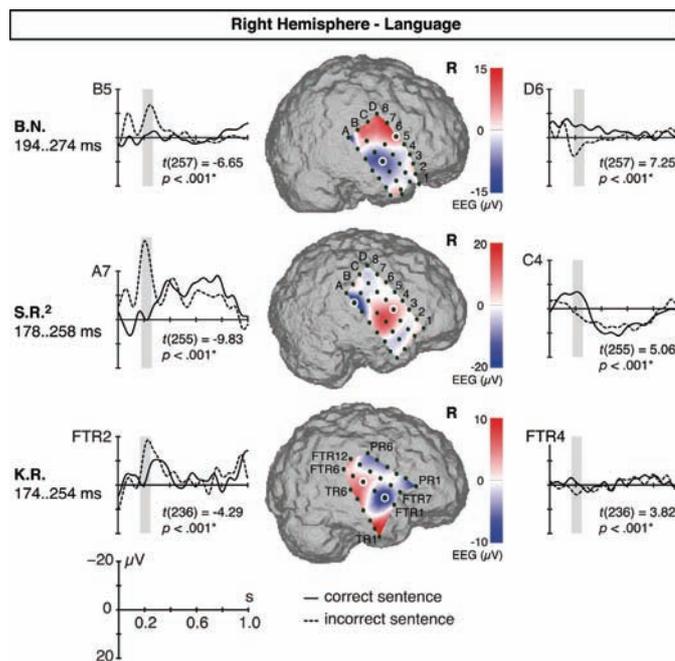


Figure 10.3: ERPs of three patients with electrodes covering the perisylvian area within the right hemisphere during the language experiment. Left: ERPs elicited by correct (solid line) and incorrect (dotted line) final words. All patients showed a significant early negativity peaking between 100 and 300 ms after onset of the critical words. The time window for statistical testing (indicated left to the diagram) is shaded in grey, statistical values are depicted below each diagram, * indicate significance after Bonferroni-correction. Right: Within the same time window, a simultaneous early positivity was observed in all patients suggesting the contribution of a tangentially oriented source. Middle: Individual, MNI-scaled brains of all patients with a reconstruction of the individual electrode positions (Kovalev et al., 2005). Topography maps depict the difference of the mean potentials within the statistical time window (i.e., incorrect - correct sentences). Blue indicates a negativity, red indicates a positivity. Electrodes depicted in the left and right columns are marked by a white circle.

tween individuals. The natural variability of brain activity across participants as well as the different cortical folding in the single subjects may account for this finding (see, e.g., Cohen et al., 2004; G. A. Ojemann & Mateer, 1979). Note further that topographic differences do not necessarily indicate distinct spatial configurations of the underlying neural generators (e.g., McCarthy & Wood, 1985; Urbach & Kutas, 2002, see also 10.2.1).

The absence of effects in four patients may be due to different reasons: a) The relevant brain areas were perhaps not covered by the electrodes that were mainly placed over temporal, less so over relevant frontal brain regions, b) the signal-to-noise ratio may have been too low to capture the effect in these patients, or c) music-syntactic processing may be deficient in these patients. There is some support for the latter option, given that the behavioural performance of these four patients ($M = 60.42\%$, $SEM = 4.58\%$) did not pass chance level as revealed by a one-sample t -test with the test-value 50 ($t(3) = 2.27$, $p > .107$). On the other hand, patients in whom the early negativity was observed, performed significantly above chance ($M = 77.08\%$, $SEM = 8.26\%$; $t(3) = 3.28$, $p < .030$), and scored tendentially higher than the patients without early negativity as revealed by a Mann-Whitney U -test ($U = 4$, $p < .069$, one-tailed).

Taken together, although effects were less pronounced in the music than the language experiment, the similarity between the intracranially recorded ERPs and the scalp recorded ERAN, specifically their similar peak latency as well as the polarity inversion, suggests that the present effect represent an electrocortical equivalent of the ERAN recorded with surface electrodes. The intricate potential topographies with several positive and negative peaks suggest the activity of multiple sources possibly with partly radial and partly tangential orientations. The identification of the underlying generators may be achieved by applying source localisation methods as the Brain Surface Current Density (BSCD) mapping described below (see section 10.2.3).

10.2.3 Language vs. Music

Patients' performance to detect male voices and deviant instruments did not differ (t -test for paired samples: $t(8) = 1.71$; $p > .125$) indicating that the task was similarly easy in both experiments. On the other hand, the performance of patients to detect syntactic errors in sentences was significantly higher than to discriminate regular and irregular chords (t -test for paired samples: $t(8) = 4.12$; $p < .004$).

For the comparison of the neural generators of the effects in the language and the music experiment, BSCD mapping was applied (Knösche et al., 1996, 1999).⁴ The results are illustrated in Figure 10.5 and Table 10.4 for all patients exhibiting early negativities in both the language and the music experiment (see Figure B.19 and Table B.3 in Appendix B for the results of G.M., M.S., W.O., and K.R. in the language experiment). Major sources included the anterior, mid, and posterior superior and middle temporal gyrus bilaterally, extending into adjacent inferior frontal and inferior parietal brain areas. Note that the exact generator configurations (like the topographies described above) markedly varied between participants, reflecting the natural heterogeneity of brain functions across individuals.

Remarkably, despite the interindividual variability, within each patient the sources of both the language and the music effect were located in intriguingly similar brain areas (Figure 10.5 and coordinates in Table 10.4). Depending on the extent of the individual network, the points of major overlap were situated within the anterior (K.H., S.G.), mid (S.R.¹, S.R.², B.N.), and posterior superior temporal gyrus (B.N., S.R.²) with some overlap in inferior frontal and inferior parietal brain regions (K.H., S.G.; see also Figure 10.7). That means, despite the fact that in each patient a slightly differently configured neural network was involved, parts of this individual network were recruited for the processing of both musical and linguistic syntax.

Interestingly, the relative strength of the fronto-temporal generators appeared to differ depending on whether music or language was presented. Visual inspection of the data suggested a stronger predominance of temporal over frontal sources in the language than in the music experiment, and a stronger involvement of the frontal lobe in the processing of musical compared to linguistic syntax (see Figures 10.6 and 10.7). To statistically test this observation, the magnitudes of the effect maxima in the frontal (i.e., the magnitude of the local maximum anterior of the Central fissure and superior of the Sylvian fissure) and the temporal lobe (i.e., inferior of the Sylvian fissure) were identified in each patient for both experiments. These values were z-transformed separately for the language and the music data with respect to the magnitudes of all dipoles in the respective hemisphere. In case no maximum could be found in one of the lobes or conditions, the value was set to zero. Non-parametric Wilcoxon-tests were computed for the group of five patients. Statistics revealed indeed a significantly stronger involvement of the temporal than the frontal lobe in the language ($Z = -2.02$, $p < .044$; which is in line with the findings of Friederici, Wang, et al.,

⁴Note that the intricate potential topographies with several positive and negative peaks observed in the present study do not yield reliable information about the nature and number of the underlying generators. Therefore, a comparison of the signal distributions is not suited to draw conclusions on the spatial similarity or difference of the underlying generator configurations (see McCarthy & Wood, 1985; Urbach & Kutas, 2002, and Section 10.2.1).

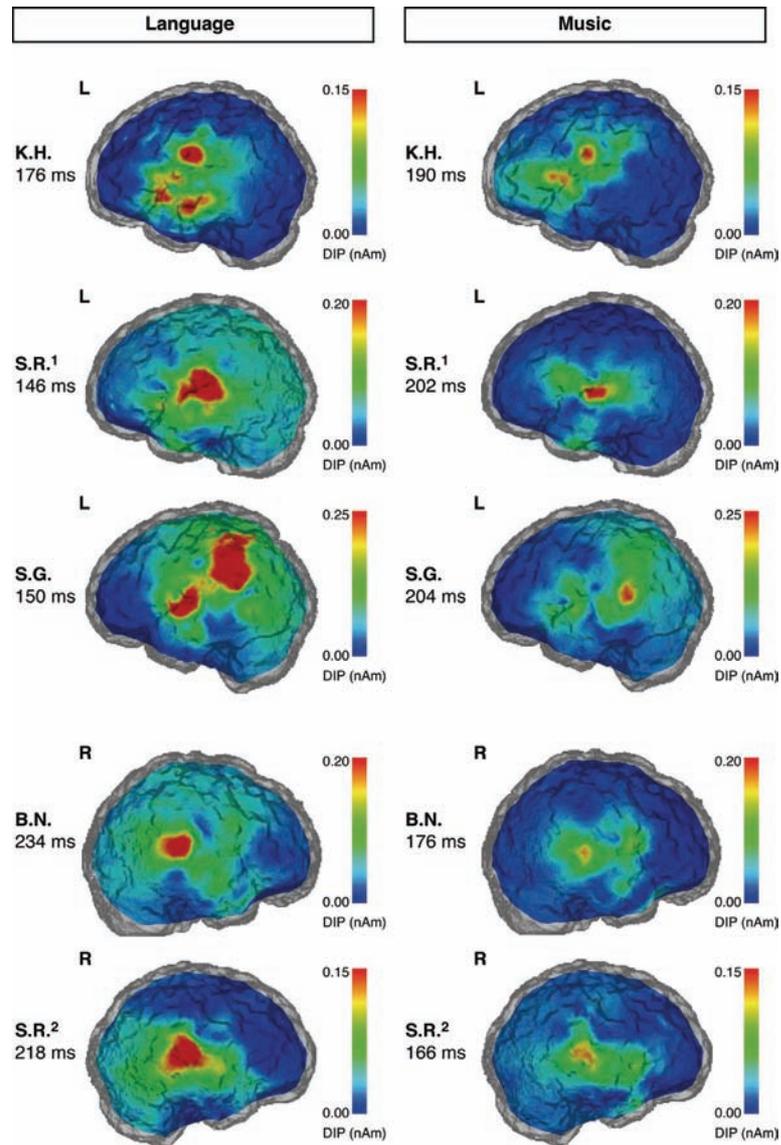


Figure 10.5: Results of the Brain Surface Current Density (BSCD) mapping for the five patients showing effects in the language (left) and the music experiment (right).

2000), but not in the music experiment ($Z = -0.94, p > .345$). Furthermore, the frontal lobe was tentatively more strongly involved in the music than in the language task ($Z = -1.75, p < .081$; see also Figure 10.6), whereas the temporal lobe involvement did not significantly differ between experiments ($Z = -.14, p > .893$). Taken together, the anatomically overlapping neural networks involved in syntax processing in music and language differed with respect to the relative weighting of their constituents.

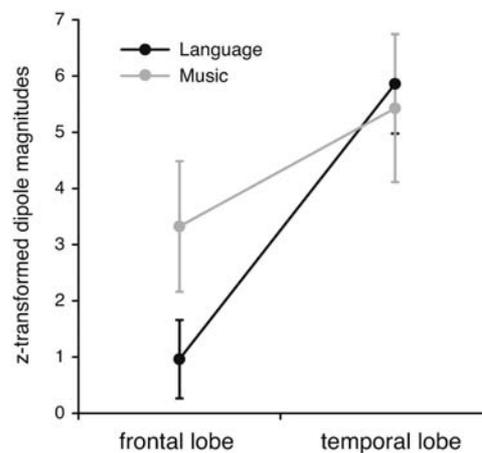


Figure 10.6: Illustration of the different weighting of frontal and temporal lobe generators in the processing of phrase-structure violations in language (orange) and harmonic expectancy violations in music (blue). Error bars indicate one standard error of mean (SEM).

Another important finding concerns the orientation of the sources. Figure 10.7 depicts the rotation of the generators that were located at the same or very similar coordinates in the music and the language experiment. As can be clearly seen, the orientation of the dipoles, despite their identical coordinates, differed considerably between domains. These results suggest that the externally very similar neural networks recruited for the analysis of syntactic relations in music and language may inhere a more sophisticated internal structure that differentiates between the analysis of musical and linguistic irregularities.

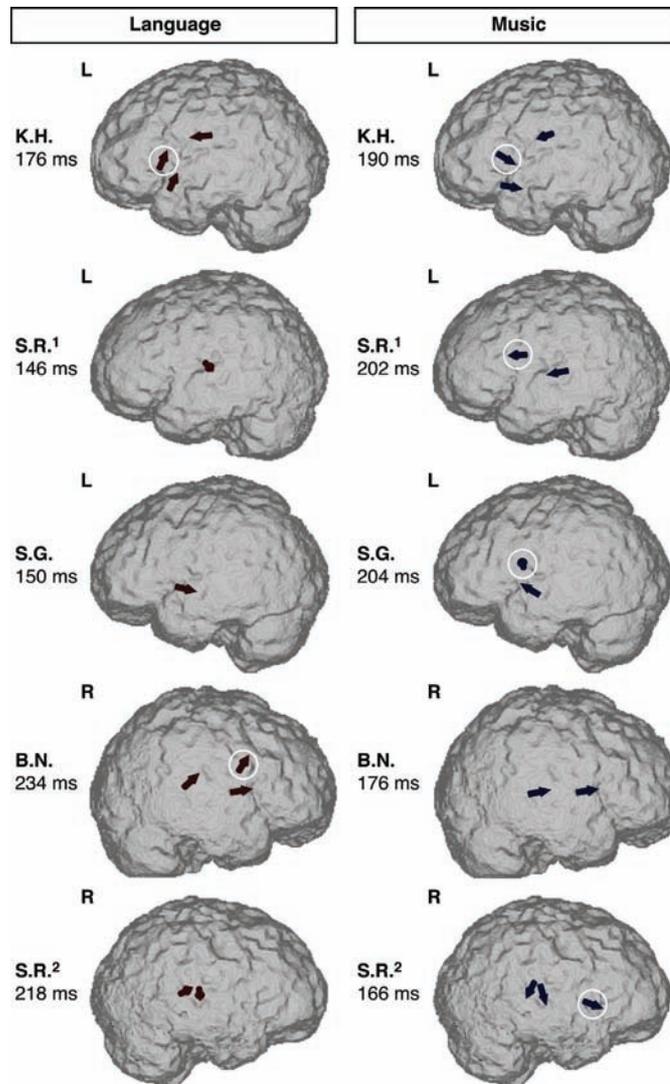


Figure 10.7: Rotation of the perisylvian sources with identical or nearby coordinates in the language and the music experiment depicted separately for each patient. For illustration, magnitude differences between generators were eliminated. Frontal sources (i.e., within the IFG or vIPMC) are marked by white circles. These graphs illustrate a) the remarkable overlap of the macroscopic brain regions involved in the processing of musical and linguistic syntax, b) the apparently different weighting of frontal and temporal sources in the language and the music experiment, and c) the different rotation of the dipoles, indicating the complex internal structure of the underlying brain regions.

Table 10.4: Results of the BSCD mapping. Coordinates indicate the localisation of the local maxima of sources underneath and in the close vicinity of the electrode grid. Their magnitudes are indicated in nAm or z-transformed with respect to the magnitude of all generators within the respective hemisphere. Only maxima with z-values > 1.00 are reported. Coordinates refer to the stereotactic space of the Montreal Neurological Institute (MNI; Evans et al., 1994; Mazziotta et al., 1995). Bold font indicates sources that entered the analysis on the different relative magnitudes of the generators (see Figure 10.6). BA: Brodman's area, a: anterior, m: mid, p: posterior, STG: superior temporal gyrus, MTG: middle temporal gyrus, ITG: inferior temporal gyrus, TP: temporal pole, SF: Sylvian fissure, STS: superior temporal sulcus, IFG: inferior frontal gyrus, p. op.: pars opercularis, p. or.: pars orbitalis, prec. g.: precentral gyrus, postc. g.: postcentral gyrus, SMG: supramarginal gyrus, IPL: inferior parietal lobe.

Language										Music				
x	y	z	nAm	z-value	region	BA	x	y	z	nAm	z-value	region	BA	
<i>Left hemisphere</i>														
K.H.														
-59	-12	21	0.22	6.47	postc. g.	1/2/3	-59	-12	21	0.15	6.59	postc. g.	1/2/3	
-53	7	-12	0.16	4.57	aSTG	22	-52	15	4	0.14	5.94	IFG, p. op.	44	
-59	-9	-18	0.15	4.34	mMTG	21	-54	5	1	0.13	5.62	aSF	-	
-51	14	-6	0.14	4.08	aSF	-	-61	-35	28	0.08	2.79	SMG	40	
-62	-19	-12	0.13	3.70	mMTG	21	-58	-39	34	0.06	1.87	IPL	7	
-56	0	4	0.13	3.69	aSF	-	-44	25	-15	0.05	1.64	IFG, p. or.	47	
-52	15	4	0.12	3.27	IFG, p. op.	44	-49	11	-17	0.05	1.49	aSTG	22	
-55	-17	39	0.06	1.36	postc. g.	1/2/3								
-61	-36	17	0.06	1.31	SMG	40								
-60	-34	31	0.06	1.26	IPL	7								
S.R. ¹														
-62	-18	6	0.25	5.98	mSTG	22	-63	-22	2	0.22	7.80	mSTG	22	

Language										Music											
x	y	z	nAm	z-value	region	BA	x	y	z	nAm	z-value	region	BA	x	y	z	nAm	z-value	region	BA	
-63	-26	4	0.24	5.64	mSTG	22	-61	-13	-1	0.21	7.69	mSTG	22								
-61	-15	18	0.24	5.53	postc. g.	1/2/3	-55	9	15	0.12	4.09	IFG, p. op.	44 /								
-59	-5	3	0.22	4.97	mSTG	22	-55	7	8	0.12	4.04	prec. g.	6								
												IFG, p. op.	44 /								
												prec. g.	6								
-51	13	-10	0.14	2.72	TP	38	-45	1	-39	0.09	2.79	aITG	20								
-59	-9	-17	0.14	2.49	mMTG	21	-36	-5	-43	0.07	1.86	aITG	20								
-41	1	-41	0.12	1.86	aITG	20	-60	-11	-21	0.06	1.30	mMTG	21								
							-58	-15	-27	0.05	1.14	mMTG	21								
S.G.																					
-59	-41	27	0.52	6.46	SMG	40	-62	-42	4	0.24	6.42	pMTG	21								
-59	-11	3	0.37	4.35	mSTG	22	-57	-2	-7	0.17	3.94	aSTG	22								
-57	-2	-7	0.34	3.93	aSTG	22	-57	-48	32	0.14	2.98	SMG	40								
-45	-47	48	0.31	3.48	IPL	7	-62	-23	0	0.12	2.60	mSTG	22								
-46	-39	50	0.29	3.20	IPL	7	-63	-31	-9	0.11	2.20	mMTG	21								
-51	-35	48	0.25	2.63	IPL	7	-51	14	-9	0.11	2.09	aSF	-								
-61	-21	16	0.21	1.94	postc. g.	1/2/3	-45	-47	48	0.10	1.82	IPL	7								
-62	-29	12	0.20	1.89	pSTG	22	-56	3	13	0.10	1.81	prec. gyr.	6								
-57	-57	-7	0.17	1.37	pMTG	21	-63	-25	-16	0.10	1.69	mMTG	21								
							-46	-39	50	0.09	1.53	IPL	7								

		Language					Music							
	x	y	z	nAm	z-value	region	BA	x	y	z	nAm	z-value	region	BA
<i>Right hemisphere</i>														
B.N.														
	65	-33	12	0.26	8.39	pSTG	22	66	-31	3	0.17	7.16	pSTG	22
	66	-22	-7	0.12	2.92	mSTS	-	60	4	4	0.08	1.59	mSF	-
	61	-7	-23	0.09	1.73	mMTG	21	66	-19	-2	0.12	4.57	mSTG	22
	60	4	4	0.08	1.59	mSF	-	59	-2	-22	0.08	2.12	aMGT	21
	60	5	24	0.08	1.54	prec. g.	6	63	-14	22	0.06	1.85	postc. g.	1/2/3
	61	-6	-14	0.08	1.52	mSTS	-	34	22	-31	0.05	1.48	TP	38
	45	16	-33	0.07	1.13	TP	38	34	14	-41	0.05	1.22	TP	38
								38	23	-29	0.04	1.04	TP	38
S.R.²														
	67	-36	6	0.19	6.44	mSTS	-	67	-26	3	0.13	6.74	mSTG	22
	67	-26	3	0.19	6.34	mSTG	22	67	-36	6	0.13	6.32	mSTS	-
	68	-26	13	0.18	5.88	pSTG	22	55	13	-5	0.10	4.78	IFG, p. op.	44
	62	-6	-6	0.11	3.20	mSTG	22	46	13	-34	0.06	2.21	TP	38
	50	21	-16	0.06	1.09	TP	38	66	-34	25	0.05	1.91	SMG	40

10.3 Discussion

The aim of the present experiment was to clarify whether musical and linguistic syntax are processed in distinct or overlapping cerebral structures. To this end, the intracranial equivalents of the scalp-recorded ELAN and ERAN (indices of linguistic and musical syntax processing) were identified, and Brain Surface Current Density (BSCD) mapping was used to localise and compare their neural generators.

Word-category violations in sentences and harmonic irregularities in chord progressions both elicited early negativities with a peak latency of about 200 ms. Furthermore, simultaneous positivities were observed in both modalities suggesting the contribution of sources with tangential orientation relative to the brain surface, possibly situated within the supratemporal plane. Taken together, these activation patterns are consistent with the latency and the typical polarity inversion of the scalp-recorded ERAN and ELAN at mastoid leads when referenced to nose electrode (e.g., Hahne & Friederici, 1999; Koelsch et al., 2000; Koelsch, in press; Maidhof & Koelsch, in press), suggesting that the observed effects represent the electrocortical equivalents of the scalp-recorded ERAN and ELAN.

Notably, in both modalities, effects were observed in the left and the right hemisphere, arguing in favour of bilateral networks involved in musical and linguistic syntax processing. In the music domain, this finding is largely consistent with, firstly, bilateral generator solutions observed by previous MEG source localisation studies (Koelsch, Maess, et al., 2001; Maess et al., 2001), secondly, the bilateral distribution of the scalp-recorded ERAN elicited by the chord sequences used in the present study (see Chapter 9) or reported by a number of other studies (e.g., Leino et al., 2007; Loui et al., 2005; Steinbeis & Koelsch, 2008b), as well as, thirdly, the mainly bilateral (even though right dominant) brain activation patterns found in fMRI studies when presenting harmonic violations in chord sequences (Koelsch, Schröger, & Gunter, 2002; Koelsch & Siebel, 2005; Tillmann, Janata, & Bharucha, 2003; Tillmann, Koelsch, et al., 2006).

The bilateral effects elicited by the word-category violations deserve more extensive comments, since they add one more piece of evidence to the language capacities of the right hemisphere. Bilateral brain activations have been observed during a number of fMRI experiments on language processing (e.g., S. Brown et al., 2006; Friederici & Alter, 2004; M. Meyer et al., 2000; Price et al., 2005), and likewise bilateral generators have been identified for the scalp-recorded ELAN by means of source modelling (Gross et al., 1998; Knösche et al., 1999; Friederici, Wang, et al., 2000). Opinions converge on the involvement of the right hemisphere in the maintenance of coarser word meanings (Jung-Beeman, 2005), or the analysis of suprasegmental aspects of language, like sentence prosody (e.g., M. Meyer

et al., 2002, 2004; Friederici & Alter, 2004; Eckstein & Friederici, 2006; Friederici et al., 2007).

Consistent with the latter hypothesis, a recent ERP study (Eckstein & Friederici, 2006) investigating the interaction of initial phrase-structure building (as typically indexed by the ELAN) and prosody processing, observed a bilaterally distributed (instead of left lateralised) early negativity when the critical word contained both syntactic and prosodic violations. This topography shift was taken to reflect the recruitment of additional right hemispheric neural resources for the processing of the prosodic violations (see also Friederici et al., 2007, for interactions of syntactic and prosodic processing). Note that the sentence material used in the present study likewise contained a double violation, as the final word of the incorrect sentences was not only syntactically inadequate (past participle instead of the expected noun phrase) but was also prosodically unexpected when untimely turning to sentence-final prosody. Therefore, the bilateral activation pattern may be explained by an interaction of syntactic and prosodic processes (see also Brauer & Friederici, 2007).

The sources identified by the BSCD mapping within inferior frontal, superior temporal and inferior parietal brain areas are in large parts consistent with previous studies, demonstrating the validity of this method when applied to intracranial data. Generators localised within the inferior frontal lobe (IFL) are well in line with a number of previous MEG, EEG and fMRI studies that have reported an involvement of the IFG and the deep frontal operculum in the processing of word-category violations (e.g., Friederici et al., 1999; Friederici, Wang, et al., 2000; Friederici, Rüschemeyer, et al., 2003; Friederici, Bahlmann, et al., 2006; Knösche et al., 1999). Likewise, the involvement of the IFG, the ventral premotor cortex, and the anterior insula has been frequently shown during the processing of harmonic irregularities (Koelsch, Maess, et al., 2001; Maess et al., 2001; Koelsch, Schröger, & Gunter, 2002; Koelsch, Fritz, et al., 2005; Tillmann, Janata, & Bharucha, 2003; Tillmann, Koelsch, et al., 2006), and the processing of musical relations in melodies (Schmithorst, 2005; Krumhansl, 2004; Platel et al., 1997; Zatorre et al., 1994). Second, temporal lobe recruitments have been frequently reported by studies presenting phrase-structure violations in sentences (Friederici, Rüschemeyer, et al., 2003; Rüschemeyer et al., 2005; Brauer & Friederici, 2007), or harmonic (Koelsch, Schröger, & Gunter, 2002; Koelsch, Fritz, et al., 2005; Tillmann, Koelsch, et al., 2006) and melodic violations in music (Schmithorst, 2005; Platel et al., 1997). Finally, also the supramarginal gyrus is a well-known constituent of the neural network processing musical (e.g., Koelsch, Fritz, et al., 2005; Platel et al., 1997; Schmithorst, 2005; Tillmann, Janata, & Bharucha, 2003) and linguistic material (e.g., Bahlmann, Rodriguez-Fornells, Rotte, & Münte, 2007; Corina et al., 1999; Démonet, Price, Wise, & Frackowiak, 1994; Ravizza, Delgado, Chein, Becker, & Fiez,

2004), most often associated with short-term memory for pitch (e.g., Gaab et al., 2003; Vines, Schneider, & Schlaug, 2006) and phonological information (e.g., Henson, Burgess, & Frith, 2000; Paulesu et al., 1993; Thierry, Boulanouar, Kherif, Ranjeva, & Démonet, 1999). Taken together, this correspondence of previous fMRI studies and the present findings cross-validated the generator solutions gained by the BSCD mapping.

The localisation of the effect maxima within each domain largely differed between individuals, most presumably due to the natural variability of brain activity and anatomy (see, e.g., Cohen et al., 2004; G. A. Ojemann & Mateer, 1979). It cannot be excluded that also the individual history of epilepsy and eventual cerebral malformations have contributed to the interindividual heterogeneity of the results. It is noteworthy, that the observed variability, hence, justifies the approach of the present study to examine the brain potentials at single subject level to avoid the blurring of the effect maxima by averaging.

Although the generators were spatially differently configured between patients, the within-subject comparisons of the BSCD mapping of both experiments revealed a remarkable overlap of parts of these individual networks in the processing of musical and linguistic syntax. That means, even if in each patient a slightly different neural network was activated, parts of this subject specific network were involved in the perception of both music and language. Hence, the combined findings lend strong support for the hypothesis of brain regions that process musical and linguistic regularities in a domain-general way (e.g., Koelsch & Siebel, 2005; Patel, 2003b).

The present data seem to emphasise the temporal lobe as main convergence zone of musical and linguistic syntax processing, given that in all patients points of overlap were situated in the anterior, mid, or posterior STG. This finding is in line with fMRI studies showing temporal lobe involvement in both language (e.g., Friederici, Meyer, & von Cramon, 2000a; Friederici, Rüschemeyer, et al., 2003; M. Meyer et al., 2000; Rüschemeyer et al., 2005) and music (e.g., Koelsch, Gunter, et al., 2002; Koelsch, Fritz, et al., 2005; Platel et al., 1997; Tillmann, Koelsch, et al., 2006). Nevertheless, in light of the idea that mainly frontal brain areas host domain-general processing mechanisms (e.g., Janata & Grafton, 2003; Koelsch & Siebel, 2005; Patel, 2003a, see also Experiment 1B), it appears surprising that only one patient exhibited an equivalent overlap in the IFL (see K.H. in Figure 10.7). One explanation may be that the relevant frontal brain areas simply have not been sampled in the present study. Since the electrode grids were implanted for the diagnosis of temporal lobe epilepsy they mainly covered the temporal lobe most often only touching on the most inferior portion of the IFG.⁵ Due to the excellent spatial resolution of intracranial measures, it is conceiv-

⁵While 61.17% of the contacts were placed on the temporal, and 21.61% on the parietal lobe, only 17.22% of the electrodes were located on frontal brain regions (including the IFG and the precentral gyrus).

able that the present recordings were essentially blind to a great part of the relevant brain activity. However, an explanation along these lines cannot explain why substantial frontal lobe involvement was found in the present music (but less so in the language) experiment.

Indeed, the temporal and frontal network constituents were found to be differently weighted depending on whether music or language was presented. Activity during phrase-structure violations showed a clear temporal predominance which is consistent with the results of a previous MEG source localisation study (see Friederici, Wang, et al., 2000). Likewise, harmonic irregularities activated temporal brain regions promoting the overlap in these brain areas. On the other hand, the processing of word-category violations relied in only two participants (K.H. and B.N.) on the frontal lobe, considerably reducing the probability to find an overlap in these areas.

It remains to be discussed whether the different involvement of frontal and temporal resources is a characteristic difference between syntax processing in language and music or whether it emerges from differential processing demands of the musical and linguistic material. It is well-known that the activation of the IFG is particularly modulated by an increase of processing costs, depending either on the complexity of the stimulus material or on the experience of the listeners. For example, a number of imaging studies on language observed increased activations within the IFG with increasing syntactic complexity due to, e.g., non-canonical word order or long-distance dependencies requiring augmented syntactic processing (e.g., Ben-Shachar et al., 2003; Bornkessel et al., 2005; Caplan et al., 1999; Fiebach et al., 2005; Friederici, Bahlmann, et al., 2006; Friederici, Fiebach, et al., 2006). Similar results have been found in music studies, showing stronger activations of the right IFG with increasing difficulty of a pitch memory task (e.g., Zatorre et al., 1994; Zatorre, 2001; see also Gaab et al., 2003 for the modulation of left IFG activity). The impact of the listener's expertise has been demonstrated in second language learners (Rüschmeyer et al., 2005) as well as six year old children (Brauer & Friederici, 2007) who exhibited enhanced activations in left BA 44/45 during the processing of word-category errors compared to adult native speakers, taken to reflect the enhanced syntactic processing in these individuals due to their lower linguistic sophistication.⁶

Along these lines, the stronger frontal involvement during the present music than the language experiment may be due to the lower expertise of the patients with the music compared to the language material, and therefore enhanced syntactic processing during the perception of the chord sequences. This argument is endorsed by the fact that all patients were non-musicians and performed considerably lower in the music than the language task.

⁶fMRI studies on music-syntactic processing in comparably young children (but see Koelsch, Fritz, et al., 2005, for a study with 10-year olds) or individuals from different musical cultures are still missing.

Alternatively, the musical and linguistic stimuli themselves may have differed in syntactic processing demands. For example, while the detection of the phrase-structure violations may have mainly relied on the identification of a *local* mismatch, e.g., the identification of the erroneous past participle in the context of the preposition, the detection of the irregular chords may have involved the integration of successive chords at a more *global* level.

The idea of a local mismatch detection in the language experiment finds support in a number of studies investigating *syntactic priming*,⁷ showing that grammatical (e.g., *ein Falter*) and ungrammatical two-word utterances (e.g., **ein faltet*; Hasting, Kotz, & Friederici, 2007; see also Pulvermüller, Shtyrov, & Ilmoniemi, 2003; Pulvermüller & Shtyrov, 2003; Shtyrov et al., 2003 for similar experiments with morphosyntactic violations) elicit a similar ERP like the phrase-structure violations in the present experiment, a so-called *syntactic MMN* (e.g., Pulvermüller et al., 2003; Pulvermüller & Shtyrov, 2003; Shtyrov et al., 2003).⁸ This ERP component is reminiscent of the ELAN with regard to latency, topography, and most of the functional characteristics. Furthermore, both components can be elicited even if subjects do not attend to the stimulus material (ELAN: e.g., Jentschke et al., 2005, 2008; Maidhof & Koelsch, in press; syntactic MMN: e.g., Hasting et al., 2007; Pulvermüller et al., 2003; Shtyrov et al., 2003). Finally, the neural generators of both components have been localised in similar cerebral regions, i.e., in the (left) superior temporal cortex with less pronounced frontal lobe contribution (ELAN: e.g., Friederici, Wang, et al., 2000; syntactic MMN: e.g., Pulvermüller et al., 2003; Pulvermüller & Shtyrov, 2003; Pulvermüller, Shtyrov, Ilmoniemi, & Marslen-Wilson, 2006; Shtyrov et al., 2003). These combined findings converge on the interpretation that ELAN and syntactic MMN may reveal similar syntactic brain mechanisms, namely local structure building. Consequently, it is highly likely that the effects observed in the present experiment mainly express local processes at the level of word pairs. In other words, the observed effects may reflect the detection of the word-category mismatch in ungrammatical phrases like **im geflüstert* compared to grammatical word pairs like *wurde geflüstert*, hence, somehow economising the computation of global inter-item relationships as supported by the frontal lobe. This assumption could be tested in future studies.

In contrast, the perception of harmonic irregularities in music largely depends on the computation of inter-item relations at a more global level, thus, most presumably strongly re-

⁷*Syntactic priming* denotes the facilitation of word processing in a grammatically correct sequence (e.g., Pulvermüller, 2002).

⁸In the relevant literature, the syntactic MMN is thought to be based on the matching of item-related properties (e.g., word-category or morphemes indicating case marking) against a template of legal serial order. At a neuronal level, these templates may correspond to the so-called *sequence detectors* proposed by Pulvermüller (2002), i.e., neuronal units that link syntactic elements (e.g., lexical categories) that are likely to occur in succession.

lying on frontal lobe resources. As demonstrated by behavioural studies with eight-chord sequences, “harmonic expectancies not only occur sequentially from chord to chord” (Bigand & Parncutt, 1999, p. 188), but are largely dependent on the integration of harmonic functions across an extended musical context. This idea is supported by ERP studies showing that the ERAN amplitude is significantly smaller if an irregular Neapolitan chord is presented after a short (two chords) compared to a long context (four chords). This finding shows that the extraction of the tonal centre of a musical sequence, which is the prerequisite to detect a harmonic violation, requires the integration of a (sufficient) number of musical events (e.g., Koelsch et al., 2000; Maess et al., 2001, see also the results of Experiment 2A).

In sum, the different weighting of frontal and temporal network constituents in the processing of the syntactic irregularities in language and music may be related to the differential dependence on the surrounding context in both experiments. Whereas a very local context may have been sufficient to detect the phrase-structure violations in the sentences, the identification of the harmonic irregularities may have depended on the integration of a more global context, requiring augmented syntactic processing possibly along with greater working memory resources, thus, leading to more pronounced frontal activations.⁹ It would be desirable to avoid these confounds in future comparative studies on music and language, by presenting, e.g., sentences that require a similar degree of computations on the contextual items like chord sequences.

Most interestingly, the dipoles that were located at identical coordinates in the music and the language experiment exhibited different rotations, indicating that they are subserved by microscopically different neuronal configurations. Methods with higher spatial resolution and depth information¹⁰ are required to clarify the nature and relationship of these configurations. Taken together, this finding demonstrates that the internal structure of externally similar brain activation patterns may be more sophisticated than initially thought, justifying the use of methods like intracranial recordings that combine excellent temporal and spatial resolution.

10.4 Conclusion

In sum, the within-subject comparison of perisylvian electrocortical potentials showed that initial structure building processes in music and language are subserved by apparently

⁹To give a more precise idea, the global context of the musical sequences lasted 2000 ms, whereas the local context of the sentences had a duration of on average 241 ms, clearly reflecting different working memory requirements.

¹⁰Note that the BSCD mapping projects all brain activity to the cortical surface and is thus blind to the depth of sources (see Section 10.1).

highly similar anatomical regions. Areas of main overlap were found in the superior temporal lobe of both hemispheres, although the exact localisation considerably differed between participants. Further overlap was observed in the left inferior frontal lobe, however, less pronounced which may be attributed either to the position of the electrode grids covering only the most inferior portion of the frontal lobe, or to the differential processing demands of the musical and linguistic material with respect to working memory load, individual expertise of the listener, or dependence on local and global contextual information. Finally, the different rotation of the dipoles at identical coordinates suggests a sophisticated internal structure of the underlying brain tissue.

Chapter 11

Summary and General Discussion

The purpose of the present dissertation was to investigate the *neuroanatomical* overlap of musical and linguistic syntax processing, aiming to complement the growing literature on a *functional* overlap of syntactic analysis between both domains (Fedorenko et al., 2007; Koelsch, Gunter, et al., 2005; Patel et al., 2008; Slevc et al., 2007; Steinbeis & Koelsch, 2008b).

The work focused on the inferior frontal gyrus (IFG) and the (anterior) superior temporal gyrus (aSTG) as likely candidates for domain-general processing of syntax as proposed by a number of independent language (Friederici, 2002) and music studies (Koelsch & Siebel, 2005). Two different approaches were chosen to address the question of neuroanatomical overlap in these areas:

Experiment 1B investigated the ERAN, an ERP elicited by music-syntactic irregularities (Koelsch et al., 2000), in two patient groups with core lesions in classical “language areas”, i.e., within the left IFG or the left aSTG. It was hypothesised that lesions in these areas known to be crucially involved in syntax processing in language would lead to parallel deficits in the music domain.

Experiment 2B studied musical and linguistic syntax processing within subjects by means of intracranial ERP recordings in left and right perisylvian brain areas. The intracranial equivalents of the scalp-recorded ERAN and ELAN (Friederici et al., 1993), two ERP components that indicate syntactic processing in music and language respectively, were identified, and their generators were modelled using Brain Surface Current Density mapping (BSCD; Knösche et al., 1999). It was hypothesised that the sources of these effects would be localised in overlapping brain regions within the temporal and inferior frontal lobe.

The results of both studies are summarised in Table 11.1 and will be discussed below, separately for the IFG and the STG.

	Inferior Frontal Gyrus		Superior Temporal Gyrus	
	Left	Right	Left	Right
Experiment 1B	YES	–	?	–
			(recovery)	
Experiment 2B	YES	?	YES	YES
		(grid position)		

Table 11.1: Summary of the results of Experiments 1B and 2B regarding the neuroanatomical overlap of musical and linguistic syntax processing in the inferior frontal and the superior temporal lobe of both hemispheres. “YES” indicates that evidence for an overlap was found. “?” means that no direct evidence was found, however, most presumably due to methodological reasons as specified in brackets (see text for details), demanding future research. “–” indicates that no right hemisphere structures were investigated in Experiment 1B.

Before turning to the results, it should be mentioned that for both patient studies, new stimulus material was created and evaluated in psychoacoustic, behavioural and electrophysiological terms (Experiment 1A and 2A). Both pilot studies were particularly designed to tease apart the impact of sensory and cognitive deviance of harmonically irregular chords on the generation of the ERAN (see also Bigand et al., 2003; Koelsch et al., 2007). In Experiment 1A, a robust ERAN was observed despite the fact that music-syntactically irregular chords were in sensory terms *less* deviant from the previous context than regular chords, demonstrating that the ERAN is not merely elicited by acoustic irregularities (see also Koelsch et al., 2007). This finding was supported by Experiment 2A showing that the ERAN may be even *larger* when elicited by music-syntactically irregular chords in which sensory deviance was minimised compared to stimuli that were irregular in terms of both musical syntax *and* acoustics. Taken together, both studies added strong evidence that the ERAN does not crucially depend on sensory deviance but mainly reflects cognitive aspects of music-syntactic processing (see also Koelsch & Sammler, 2008).

11.1 Inferior Frontal Gyrus

Both Experiment 1B and 2B found evidence for a domain-general role of the left inferior frontal lobe in syntax processing in music and language.

Experiment 1B. In Experiment 1B, patients with core lesions in the left IFG exhibited an ERAN that was more frontally distributed and (nominally) more right lateralised than in healthy controls, indicating that the observed negativity was generated by a configuration of neural sources that differed from the one in intact brains. The scalp topography conforms to a breakdown of the left frontal generator, and a predominant involvement of the sources in the contralesional right hemisphere (Koelsch, Fritz, et al., 2005; Maess et al., 2001).

Furthermore, the ERAN amplitude in left IFG patients was significantly correlated with the time since brain injury. That means, the ERAN amplitude was considerably reduced in patients with recent brain injury (6 months), but showed a normal amplitude in patients with chronic lesions (7 years). This finding indicates that the left IFG is an originally essential generator of the ERAN, but that its drop-out may be gradually compensated over the years by anatomical and/or functional reorganisation processes in perilesional and/or contralesional brain areas (Schuppert et al., 2003).

Finally, patients performed at chance level when asked to discriminate regular and irregular chords, indicating a persistent deficit in the recognition, integration and prediction of sequential musical information.

These combined findings support the notion that the left IFG is *essentially* involved in the generation of the ERAN, and is, thus, a crucial constituent of the distributed neural network of musical syntax processing (Koelsch, Gunter, et al., 2002; Koelsch, Fritz, et al., 2005; Krumhansl, 2004; Tillmann, Janata, & Bharucha, 2003; Tillmann, Koelsch, et al., 2006). Relating this result to previous studies in the language domain that show the necessity of the left inferior frontal lobe for linguistic syntax processing (e.g., Caplan & Futter, 1986; Caplan et al., 1996; Caramazza & Zurif, 1976; Davis et al., 2008; Friederici et al., 1998, 1999; Friederici & Kotz, 2003; Schwartz et al., 1980) it can be concluded that this brain region is indeed a convergence zone of syntactic analysis in the music and the language domain.

Experiment 2B. A convergence of musical and linguistic syntax processing within the left IFG was also strongly supported by the results of patient K.H. in Experiment 2B. In this patient, the frontal source maxima of the early effects elicited by phrase structure violations in language and by harmonic irregularities in music emerged at *identical* coordinates (see Table 10.4) within the opercular part of the left IFG.

In patients S.R.¹ and S.G. with similar left hemisphere grid positions no such overlap was found because, surprisingly, no frontal source maxima were detected in the language task (but in the music experiment; see Figure 10.5). It is conceivable that in these cases the

frontal brain activity escaped the recordings during the language experiment due to the limited number of frontal electrodes covering only the very inferior portion of the IFG and precentral gyrus. On the other hand, the processing of phrase-structure violations does not only depend on frontal, but in large parts also on superior temporal brain areas (Friederici, Wang, et al., 2000; Friederici, Rüschemeyer, et al., 2003). Hence, patients S.R.¹ and S.G. perhaps omitted the syntactic-relational processes of the IFG, and relied instead predominantly on temporal regions that are thought to serve the matching of incoming items against the template of the local phrase structure (see Figure 10.5 and section 11.2; Pulvermüller & Shtyrov, 2006; Shtyrov et al., 2003; see also Hasting et al., 2007 for similar considerations).

A similar reasoning might apply to the missing frontal overlap in the two patients with right hemisphere grids, thus, leaving unresolved whether musical and linguistic syntax processing converge in the right inferior frontal lobe. All in all, further research is clearly necessary to confirm the domain-general role of the left IFG and to clarify a possible overlap within the right IFG.

Summary and Discussion. In sum, Experiments 1B and 2B converge on the notion that the left IFG serves syntactic processing in both music and language. This result adds anatomical evidence to the Shared Syntactic Integration Resource Hypothesis (SSIRH; Patel, 2003a) that assumes domain-general syntactic processes within frontal brain areas. Hence, the left IFG may represent the anatomical convergence zone that accounts at least partly for previously reported functional interactions of syntax processing in music and language, such as the competition effects observed as soon as syntactic errors are presented simultaneously in both modalities (Fedorenko et al., 2007; Koelsch, Gunter, et al., 2005; Slevc et al., 2007; Steinbeis & Koelsch, 2008b), the influence of musical training on verbal abilities (Belin et al., 1996; Chan et al., 1998; Ho et al., 2003; Jentschke et al., 2005; Schlaug et al., 2008), or conversely, the impaired musical processing in individuals with language deficits (e.g., Jentschke et al., 2008; Patel et al., 2008; Schuppert et al., 2000). More broadly, these combined data provide a framework for therapies that employ music in the treatment of developmental or acquired language disorders. One promising approach is the Melodic Intonation Therapy (MIT), that aids the recovery of expressive language functions in non-fluent aphasics by means of singing and rhythmic hand tapping (see Albert, Sparks, & Helm, 1973; Sparks & Holland, 1976, for an explanation of the method; see Belin et al., 1996; Schlaug et al., 2008; Sparks, Helm, & Albert, 1974; Wilson, Parsons, & Reutens, 2006, for the beneficial effects of MIT).

Although the present study may indicate *where* musical and linguistic syntax processing converge, it remains to be specified *which* domain-general cognitive operations may be sup-

ported by this area. The relevant literature on (left) IFG functions (see also Chapters 1 and 2) reveals two likely candidates of domain-general aspects of syntax processing: First, a number of music (Koelsch, 2005, 2006) and language studies (Bornkessel et al., 2005; Friederici, 2002; Friederici, Bahlmann, et al., 2006; Friederici, 2006a) converge on the importance of the IFG in the recognition and on-line integration of hierarchical dependencies of incoming items, thus, suggesting operations of *syntactic integration* to be shared between domains. Other research in music (Gaab et al., 2003; Koelsch et al., in press; Zatorre et al., 1994; Zatorre, 2001) and language (Baddeley, 2003; Caplan & Waters, 1999; Fiebach et al., 2005; Koelsch et al., in press; Stowe et al., 2005; Vigneau et al., 2006) highlights the involvement of the IFG and adjacent superior frontal areas in working memory tasks, proposing that musical and linguistic syntax processing may recruit domain-general syntactic *working memory* functions. Future research will be needed to tease apart these accounts, even though both views may be mutually not exclusive, because relational computations among sequentially incoming items evidently require a short-term retention and manipulation of these elements in memory. On a more general level, both accounts converge on a superordinate procedural (rather than conceptual) role of the IFG in the extraction of an internal hierarchical structure from a sequential input, providing one key to meaning (Steinbeis & Koelsch, 2008b; Ullman, 2001).

It is important to note that sequence processing is not only crucial for language and music perception, but is central to many aspects of animal and human behaviour, from locomotion, through reaching and grasping to the control of logical reasoning (Houghton & Hartley, 1996). With regard to the domain-general role of the IFG in processing sequential information, it may not come as a surprise that activations in the left IFG (BA 44) and the adjacent vIPMC (BA 6) have also been reported during a variety of non-linguistic and non-musical experiments involving sequential ordering, like the perception, mental imagery and execution of oro-facial, oro-laryngeal, and hand actions (for reviews see Binkofski & Buccino, 2004; Buccino, Binkofski, & Riggio, 2004; Craighero, Metta, Sandini, & Fadiga, 2007; Rizzolatti & Craighero, 2004). Like music or language, actions are no random organisations of motor elements. On the contrary, movements must be organised according to certain principles to be efficient with respect to a goal (e.g., to open a bottle), and to be meaningful to the observer. These principles, or motor representations, may be considered as kind of an “action syntax” that (de)codes abstract motor behaviour (Fadiga, 2008; Greenfield, 1991; Rizzolatti & Arbib, 1998). Furthermore, actions as well as language and music have been considered as vehicle for human (gestural or vocal) communication (Rizzolatti & Arbib, 1998; Rizzolatti & Craighero, 2004). Within this framework, the left IFG may be the crucial instance that decodes structure to access meaning, thus, standing in the service of communication in a domain-general way.

11.2 Superior Temporal Gyrus

Experiment 1B. Patients with lesions including the left aSTG exhibited an intact ERAN and normal sensitivity to harmonic closure. Although these results seem to suggest a rather minor role of the aSTG in music-syntactic processing, and would thus, argue against a domain-general involvement of this area in syntactic structure building, the highly likely impact of reorganisation processes (since data were acquired about seven years after brain injury) demands further investigations before drawing a final conclusion in this respect (Schuppert et al., 2003).

Experiment 2B. Nevertheless, the distributed source modelling of the intracranial potentials provided strong evidence for a domain-general role of the left and right STG in the processing of structural regularities. In all participants, a part of the source maxima of the ERPs elicited by phrase-structure violations in language and by harmonic irregularities in music were localised at *identical* coordinates within the STG.

Most interestingly, these sources (despite their identical coordinates) exhibited different orientations in the music and the language experiment, suggesting that they rely on microscopically different neuronal configurations. The exact nature and relationship of these configurations remains to be specified with methods yielding a higher spatial resolution as well as depth information. Taken together, the present finding indicates that the internal structure of the brain areas underlying musical and linguistic syntax processing may be more sophisticated than initially believed.

Summary and Discussion. Although future research is clearly necessary, the data of Experiment 2B strongly propose that the STG plays a domain-general role in the processing of structure in music and language, substantiating the presumption of a temporal overlap raised by previous independent language (e.g., Friederici, Wang, et al., 2000; Friederici, Rüschemeyer, et al., 2003; Rüschemeyer et al., 2005) and music studies (e.g., Koelsch, Gunter, et al., 2002; Koelsch, Fritz, et al., 2005; Maess et al., 2001; Tillmann, Koelsch, et al., 2006).

The anatomical convergence of musical and linguistic syntax processing within the STG fits well with a number of music (e.g., Griffiths et al., 1998; Griffiths, 2001) and language studies (e.g., Pulvermüller, 2002; Pulvermüller & Shtyrov, 2003) that converge on the importance of the STG in the *detection of a sequence* based on the computation of (low-level

syntactic) relations between consecutive items.¹ The role of the ATL in *working memory* functions reported by several studies (Zatorre & Samson, 1991; Zatorre et al., 1994; Zatorre, Bouffard, & Belin, 2004) is certainly related to these operations. Furthermore, the posterior STG including the planum temporale (PT) has been associated with the processing of “prosodic” features, i.e., aspects like accentuation and boundary marking in both language (Friederici & Alter, 2004; M. Meyer et al., 2002, 2004) and music (Nan, Knösche, Zysset, & Friederici, 2008). Notably, in both domains, aspects of accentuation and intonational phrasing are tightly bonded to syntactic structure. In language, prosodic features guide syntactic parsing and resolve syntactic ambiguity (e.g., Eckstein & Friederici, 2006; Friederici & Alter, 2004; Friederici et al., 2007; M. Meyer et al., 2004; Steinhauer et al., 1999). Likewise in music, harmonically stable elements are typically accentuated and mark phrase endings, facilitating the sequencing of the auditory input (see Chapter 3.2.2). The aforementioned fMRI studies in both domains are consistent with a special role of the (right) posterior STG in the *integration of local (syntactic) and global (“prosodic”) information* to build a coherent percept (see also Griffiths & Warren, 2002, for the role of the PT in spectrotemporal integration). It may be speculated that the stimulus material employed in Experiment 2B particularly triggered these (shared) processes, since incorrect sentences demanded the integration of incongruent syntactic and prosodic information (see Discussion of Experiment 2B), and irregular chord sequences required the integration of harmonically unstable chords that were accentuated at the end of phrases. Taken together, the domain-general role of the STG may be summarised as the analysis and integration of the spectrotemporal features of incoming sounds (presumably by grouping mechanisms akin to the Gestalt principles) to form a sound-based representation of speech or music that can be subjected to higher order processes like the ones subserved by the closely interconnected inferior frontal lobes.

11.3 Concluding Remarks

The present dissertation aimed at elucidating whether syntax processing in language and music relies partly on similar neuroanatomical structures. Points of convergence were found in the left inferior frontal gyrus as well as the superior temporal lobes bilaterally. This overlap proposes that, with respect to syntax processing, language and music can serve as foils for each other, helping to conceptually integrate neuroimaging data from both domains

¹Within this context, Griffiths (2001) proposed so-called *pitch sequence detection areas* in the anterior and posterior STG that become activated during the processing of diatonic melodies contrasted against a regular pitch “staircase”. In the language domain, Pulvermüller (2002) assumed syntactic *sequence detectors* within the superior temporal cortex that are thought to account for syntactic priming.

and, hence, to increase our understanding of the functional architecture of the human brain (Janata & Grafton, 2003; Price et al., 2005; Shalom & Poeppel, 2008).

11.4 Future Perspectives

During the analysis and interpretation of the present data, a series of new questions arose while others remained unresolved, opening a field for future work.

Transcranial Magnetic Stimulation. The most pertinent question that emerged from Experiment 1B was whether patients with more recent lesions in the left aSTG show deficits in music-syntactic processing. Likewise, the residual deficits observed in the left IFG patients should be replicated in patients with “younger” lesions, in order to test whether the assumption of reorganisation processes holds. One way to minimise reorganisation processes would be to conduct a study with functional instead of anatomical lesions, for example, induced by means of Transcranial Magnetic Stimulation (TMS; Walsh & Pascual-Leone, 2003). Slow inhibitory TMS pulses (1 Hz) could be administered off-line to those areas within the left IFG or left aSTG that have been identified by a previous fMRI localiser scan as being involved in syntax processing in individual volunteers. An amplitude reduction of the ERAN recorded immediately after the TMS (i.e., during the temporary functional deficit; Nyffeler et al., 2006) compared to the ERAN recorded in the same individual after sham TMS (i.e., without magnetic interference), would strongly argue for the functional role of the stimulated region in musical syntax processing.

Electrocortical Mapping. Alternatively, the processing of musical syntax could be mapped using cortical stimulation. This is one standard method to identify, e.g., language relevant cortical areas in patients before neurosurgery. During various tasks like naming, counting, reading etc., weak electrical currents are administered to the cortical surface via intracranially placed electrodes (Boatman, 2004; G. A. Ojemann, Ojemann, Lettich, & Berger, 1989; J. G. Ojemann, Ojemann, & Lettich, 2002). A disruption of behaviour during stimulation indicates that the brain tissue underneath the electrode is functionally relevant for the actual task. A similar mapping could be obtained for musical syntax processing, by using, e.g., a behavioural harmonic priming paradigm (e.g., Patel et al., 2008; Tillmann et al., 2007).

Recovery of musical syntax processing. Although receptive amusia is quite common after brain injury (e.g., Kohlmetz, Altenmüller, Schuppert, Wieringa, & Münte, 2001; Schuppert et al., 2000), to date, only very little is known about the neurorehabilitation of musical deficits. While a number of studies focused on the recovery of low-level acoustic analysis

(e.g., Ilvonen et al., 2003; Kohlmetz et al., 2001), systematic experiments on higher order music processing remain sparse (Schuppert et al., 2003). Repeated EEG and fMRI examinations with parallel testing of musical abilities from the acute to the chronic stage could yield important insights into the dynamics of reorganisation in the music system (e.g., the interplay of peri- and contralesional areas) and possible parallels to language recovery (e.g., Saur et al., 2006). In this context, the ERAN could serve as important indicator for the implicit processing of musical structure. The chord sequence paradigm applied in the present study appears to be particularly suited to investigate music perception also in severely impaired patients, because it does not require focused attention (e.g., Koelsch et al., 2000; Maidhof & Koelsch, in press) or motor responses like other tasks described in the literature (e.g., Griffiths, Dean, Woods, Rees, & Green, 2001; Peretz et al., 2003; Schuppert et al., 2003; Tillmann et al., 2007).

Neuroanatomical overlap in the right hemisphere. The present dissertation tested the hypothesis of domain-generality predominantly within the left hemisphere as the major seat of the language faculty. However, evidence for the linguistic capacities of the right hemisphere is rapidly growing (e.g., Friederici & Alter, 2004; Jung-Beeman, 2005; M. Meyer et al., 2002, 2004; Price et al., 2005). Since music processing likewise recruits bilateral networks (e.g., Ayotte et al., 2000; Koelsch, Fritz, et al., 2005; Liégeois-Chauvel et al., 1998; Parsons, 2001; Platel et al., 1997), it becomes conceivable that music and language perception may share resources within the right hemisphere. Preliminary evidence for the partial convergence of musical and linguistic syntax processing in the right superior temporal lobe has been provided by Experiment 2B. These findings are promising and should be confirmed and extended in future work.

Frontal grid positions. The most pertinent question raised by Experiment 2B was whether grids centred on the inferior frontal instead of temporal lobe would have gathered clearer evidence for shared resources within the IFG, a question that could be addressed in future investigations.

Depth information. The present study showed that BSCD mapping is a powerful tool in the localisation of generators of intracranially recorded potentials. However, this method eliminates any depth information by projecting all activity to the cortical surface (Knösche et al., 1999). This may be critical, especially within the perisylvian brain region, because generators may be located within varying depths of the Sylvian fissure (one possible reason for the different orientation of the otherwise identical generators observed in the present study) or in the deep frontal operculum instead of the IFG (see Friederici, Bahlmann, et al., 2006; Friederici, Fiebach, et al., 2006, for different functions of these areas in syntax processing). Based on the present results, further analyses could be conducted applying

alternative source localisation methods that are able to estimate the depth of current generators, yielding valuable information about the proximity or distance of the sources involved in musical and linguistic syntax processing. Alternatively, this question could be studied by means of depth electrodes reaching into the Sylvian fissure or insula (see Liégeois-Chauvel et al., 1991).

Connectivity. Although music and language may be processed in partly similar brain areas, the functional connectivity patterns between these regions may considerably differ between domains. These differences and similarities could be investigated by techniques such as dynamic causal modelling in fMRI (Friston, Harrison, & Penny, 2003) or coherence analysis in EEG and MEG (Patel & Balaban, 2000).

Other syntactic violations. The present study compared the neural correlates of harmonic structure building in music and initial phrase structure building in language. These are, however, only facets of syntax processing in both domains, and there is no reason to believe that those are the best for probing anatomical relations between musical and linguistic syntax processing. Future research could be extended on the comparison of other structural aspects, like rhythm and metre in music (e.g., Abecasis, Brochard, Granot, & Drake, 2005) or morphosyntax in language (e.g., Gunter et al., 2000).

Music, Language, and Motion. Most intriguingly, the left IFG has not only been associated with the processing of musical and linguistic sequences, but also with the perception, recognition, and execution of oro-facial, oro-laryngeal, and hand actions (see section 11.1). It appears tempting to run studies that aim to integrate these findings, e.g., by extending their focus on the interplay between language, music and *gestures*, all of them requiring the coding and decoding of ordered sequences in the service of communication.

Part III

Appendix

Appendix A

Sentence Material Used in Experiment 2B

Table A.1: Sentence material used in Experiment 2B

001	correct	Die Forelle wurde geangelt.
001	incorrect	Der Karpfen wurde im geangelt.
002	correct	Die Tante wurde geärgert.
002	incorrect	Die Mutter wurde im geärgert.
002	filler	Der Onkel wurde im Bett geärgert.
003	correct	Die Torte wurde gebacken.
003	incorrect	Der Kuchen wurde im gebacken.
004	correct	Das Baby wurde gebadet.
004	incorrect	Die Schwester wurde im gebadet.
004	filler	Das Kind wurde im Teich gebadet.
005	correct	Der Strohstern wurde gebastelt.
005	incorrect	Die Maske wurde im gebastelt.
006	correct	Der Schneemann wurde gebaut.
006	incorrect	Die Burg wurde im gebaut.
006	filler	Die Hütte wurde im Ferienlager gebaut.
007	correct	Der Postbote wurde gebissen.
007	incorrect	Der Polizist wurde ins gebissen.
008	correct	Die Trompete wurde geblasen.
008	incorrect	Die Posaune wurde zur geblasen.

008	filler	Das Waldhorn wurde zur Jagd geblasen.
009	correct	Das Spiegelei wurde gebraten.
009	incorrect	Das Fleisch wurde zum gebraten.
010	correct	Die Reise wurde gebucht.
010	incorrect	Die Fahrt wurde im gebucht.
010	filler	Der Urlaub wurde im Reisebüro gebucht.
011	correct	Die Höhle wurde gebuddelt.
011	incorrect	Die Grube wurde unterm gebuddelt.
012	correct	Das Hemd wurde gebügelt.
012	incorrect	Die Hose wurde am gebügelt.
012	filler	Die Bluse wurde am Freitag gebügelt.
013	correct	Das Karussell wurde gedreht.
013	incorrect	Die Schraube wurde im gedreht.
014	correct	Das Kind wurde geduscht.
014	incorrect	Das Nilpferd wurde am geduscht.
014	filler	Das Nashorn wurde am Morgen geduscht.
015	correct	Das Korn wurde geerntet.
015	incorrect	Das Getreide wurde im geerntet.
016	correct	Die Maus wurde gefangen.
016	incorrect	Der Fußball wurde vorm gefangen.
016	filler	Der Ball wurde vorm Tor gefangen.
017	correct	Der Hof wurde gefegt.
017	incorrect	Die Treppe wurde am gefegt.
018	correct	Der Geburtstag wurde gefeiert.
018	incorrect	Die Party wurde im gefeiert.
018	filler	Das Fest wurde im Garten gefeiert.
019	correct	Der Räuber wurde gefesselt.
019	incorrect	Der Cowboy wurde am gefesselt.
020	correct	Die Landschaft wurde gefilmt.
020	incorrect	Der Löwe wurde im gefilmt.
020	filler	Der Elefant wurde im Zoo gefilmt.
021	correct	Das Loch wurde geflickt.
021	incorrect	Die Hose wurde am geflickt.
022	correct	Das Geheimnis wurde geflüstert.
022	incorrect	Der Plan wurde im geflüstert.
022	filler	Der Name wurde im Versteck geflüstert.

023	correct	Der Lehrer wurde gefragt.
023	incorrect	Der Zauberer wurde im gefragt.
024	correct	Die Banane wurde gefressen.
024	incorrect	Das Stroh wurde im gefressen.
024	filler	Das Futter wurde im Stall gefressen.
025	correct	Das Fass wurde gefüllt.
025	incorrect	Die Tonne wurde beim gefüllt.
026	correct	Das Baby wurde gefüttert.
026	incorrect	Die Gans wurde im gefüttert.
026	filler	Die Kuh wurde im Stall gefüttert.
027	correct	Das Brot wurde gegessen.
027	incorrect	Das Eis wurde im gegessen.
028	correct	Der Tunnel wurde gegraben.
028	incorrect	Der Kanal wurde am gegraben.
028	filler	Das Loch wurde am Morgen gegraben.
029	correct	Die Wurst wurde gegrillt.
029	incorrect	Das Schnitzel wurde beim gegrillt.
030	correct	Der Bruder wurde gehauen.
030	incorrect	Der Freund wurde beim gehauen.
030	filler	Die Schwester wurde beim Streit gehauen.
031	correct	Das Zimmer wurde geheizt.
031	incorrect	Die Küche wurde am geheizt.
032	correct	Die Musik wurde gehört.
032	incorrect	Das Konzert wurde im gehört.
032	filler	Das Gebrüll wurde im Zelt gehört.
033	correct	Der Hund wurde geimpft.
033	incorrect	Die Kusine wurde vorm geimpft.
034	correct	Der Tiger wurde gejagt.
034	incorrect	Der Wolf wurde im gejagt.
034	filler	Der Wal wurde im Meer gejagt.
035	correct	Der Schatz wurde geklaut.
035	incorrect	Der Lutscher wurde im geklaut.
036	correct	Die Nuss wurde geknackt.
036	incorrect	Das Haselnuss wurde vorm geknackt.
036	filler	Die Walnuss wurde vorm Backen geknackt.
037	correct	Das Essen wurde gekocht.

037	incorrect	Das Ei wurde am gekocht.
038	correct	Die Oma wurde geküsst.
038	incorrect	Der Clown wurde am geküsst.
038	filler	Der Opa wurde am Abend geküsst.
039	correct	Die Glocke wurde geläutet.
039	incorrect	Das Glöckchen wurde vorm geläutet.
040	correct	Das Gedicht wurde gelernt.
040	incorrect	Das Alphabet wurde im gelernt.
040	filler	Das Gedicht wurde im Unterricht gelernt.
041	correct	Das Buch wurde gelesen.
041	incorrect	Das Märchen wurde im gelesen.
042	correct	Der Koch wurde gelobt.
042	incorrect	Die Freundin wurde im gelobt.
042	filler	Die Schülerin wurde im Unterricht gelobt.
043	correct	Der Brand wurde gelöscht.
043	incorrect	Das Feuer wurde beim gelöscht.
044	correct	Der Rasen wurde gemäht.
044	incorrect	Das Gras wurde am gemäht.
044	filler	Die Wiese wurde am Donnerstag gemäht.
045	correct	Das Bild wurde gemalt.
045	incorrect	Die Schnecke wurde im gemalt.
046	correct	Der Keller wurde gemauert.
046	incorrect	Die Garage wurde im gemauert.
046	filler	Die Wand wurde im Keller gemauert.
047	correct	Die Wohnung wurde gemietet.
047	incorrect	Das Haus wurde im gemietet.
048	correct	Die Farbe wurde gemischt.
048	incorrect	Das Müsli wurde fürs gemischt.
048	filler	Der Beton wurde fürs Fundament gemischt.
049	correct	Die Kuh wurde gemolken.
049	incorrect	Die Kuh wurde im gemolken.
050	correct	Die Wunde wurde genäht.
050	incorrect	Der Rock wurde am genäht.
050	filler	Das Kleid wurde am Samstag genäht.
051	correct	Die Schokolade wurde genascht.
051	incorrect	Der Pudding wurde vorm genascht.

052	correct	Die Tür wurde geöffnet.
052	incorrect	Der Behälter wurde im geöffnet.
052	filler	Die Dose wurde im Zelt geöffnet.
053	correct	Der Motor wurde geölt.
053	incorrect	Das Türschloss wurde im geölt.
054	correct	Die Tasche wurde gepackt.
054	incorrect	Der Rucksack wurde im gepackt.
054	filler	Der Koffer wurde im Hotel gepackt.
055	correct	Das Auto wurde geparkt.
055	incorrect	Der Bus wurde am geparkt.
056	correct	Die Kartoffel wurde gepellt.
056	incorrect	Die Mandarine wurde zum gepellt.
056	filler	Die Wurst wurde zum Abendbrot gepellt.
057	correct	Die Melodie wurde gepfiffen.
057	incorrect	Das Kinderlied wurde beim gepfiffen.
058	correct	Die Blume wurde gepflanzt.
058	incorrect	Der Strauch wurde im gepflanzt.
058	filler	Der Baum wurde im Wald gepflanzt.
059	correct	Das Obst wurde gepflückt.
059	incorrect	Die Birne wurde im gepflückt.
060	correct	Der Angriff wurde geplant.
060	incorrect	Die Reise wurde beim geplant.
060	filler	Der Ausflug wurde beim Mittagessen geplant.
061	correct	Die Zitrone wurde gepresst.
061	incorrect	Die Apfelsine wurde vorm gepresst.
062	correct	Die Nase wurde geputzt.
062	incorrect	Das Fenster wurde im geputzt.
062	filler	Der Stiefel wurde im Flur geputzt.
063	correct	Der Schmuck wurde geraubt.
063	incorrect	Der Videorekorder wurde beim geraubt.
064	correct	Die Pfeife wurde geraucht.
064	incorrect	Die Zigarre wurde beim geraucht.
064	filler	Die Zigarette wurde beim Fest geraucht.
065	correct	Die Kleidung wurde gereinigt.
065	incorrect	Der Teppich wurde vorm gereinigt.
066	correct	Der Verletzte wurde gerettet.

066	incorrect	Der Verunglückte wurde im gerettet.
066	filler	Der Matrose wurde im Sturm gerettet.
067	correct	Die Kugel wurde gerollt.
067	incorrect	Der Reifen wurde ins gerollt.
068	correct	Die Ärztin wurde gerufen.
068	incorrect	Die Tochter wurde zum gerufen.
068	filler	Der Arzt wurde zum Kranken gerufen.
069	correct	Das Holz wurde gesägt.
069	incorrect	Das Brett wurde im gesägt.
070	correct	Der Sand wurde geschaufelt.
070	incorrect	Der Lehm wurde vorm geschaufelt.
070	filler	Der Schnee wurde vorm Haus geschaufelt.
071	correct	Der Sack wurde geschleppt.
071	incorrect	Der Schrank wurde beim geschleppt.
072	correct	Die Tür wurde geschlossen.
072	incorrect	Das Geschäft wurde am geschlossen.
072	filler	Der Laden wurde am Samstag geschlossen.
073	correct	Die Tablette wurde geschluckt.
073	incorrect	Die Medizin wurde im geschluckt.
074	correct	Der Tee wurde geschlürft.
074	incorrect	Die Milch wurde vom geschlürft.
074	filler	Die Suppe wurde vom Löffel geschlürft.
075	correct	Der Weihnachtsbaum wurde geschmückt.
075	incorrect	Das Klassenzimmer wurde fürs geschmückt.
076	correct	Die Petersilie wurde geschnitten.
076	incorrect	Die Hecke wurde beim geschnitten.
076	filler	Das Haar wurde beim Frisör geschnitten.
077	correct	Der Brief wurde geschrieben.
077	incorrect	Die Postkarte wurde zum geschrieben.
078	correct	Die Straee wurde gesperrt.
078	incorrect	Die Autobahn wurde am gesperrt.
078	filler	Der Weg wurde am Mittwoch gesperrt.
079	correct	Die Brücke wurde gesprengt.
079	incorrect	Der Turm wurde am gesprengt.
080	correct	Die Fremdsprache wurde gesprochen.
080	incorrect	Die Nachricht wurde aufs gesprochen.

080	filler	Der Text wurde aufs Band gesprochen.
081	correct	Das Geschirr wurde gespült.
081	incorrect	Die Tasse wurde am gespült.
082	correct	Das Fahrrad wurde gestohlen.
082	incorrect	Der Fernseher wurde beim gestohlen.
082	filler	Das Radio wurde beim Einbruch gestohlen.
083	correct	Die Wand wurde gestrichen.
083	incorrect	Das Tor wurde am gestrichen.
084	correct	Der Pullover wurde gestrickt.
084	incorrect	Die Mütze wurde vorm gestrickt.
084	filler	Der Schal wurde vorm Winter gestrickt.
085	correct	Das Lied wurde gesungen.
085	incorrect	Das Wanderlied wurde im gesungen.
086	correct	Das Paket wurde getragen.
086	incorrect	Die Mappe wurde unterm getragen.
086	filler	Die Zeitung wurde unterm Arm getragen.
087	correct	Der Verlierer wurde getröstet.
087	incorrect	Der Pechvogel wurde am getröstet.
088	correct	Der Kaffee wurde getrunken.
088	incorrect	Der Saft wurde beim getrunken.
088	filler	Der Kakao wurde beim Essen getrunken.
089	correct	Der Sprung wurde geübt.
089	incorrect	Der Tanz wurde vorm geübt.
090	correct	Der Klassensprecher wurde gewählt.
090	incorrect	Der Kanzler wurde am gewählt.
090	filler	Der Präsident wurde am Sonntag gewählt.
091	correct	Der Betrüger wurde gewarnt.
091	incorrect	Der Verbrecher wurde beim gewarnt.
092	correct	Das Auto wurde gewaschen.
092	incorrect	Der Pullover wurde am gewaschen.
092	filler	Das T-Shirt wurde am Dienstag gewaschen.
093	correct	Die Medaille wurde gewonnen.
093	incorrect	Der Preis wurde im gewonnen.
094	correct	Der Ball wurde geworfen.
094	incorrect	Der Stock wurde ins geworfen.
094	filler	Der Stein wurde ins Wasser geworfen.

095	correct	Das Fleisch wurde gewürzt.
095	incorrect	Der Salat wurde beim gewürzt.
096	correct	Der Zahn wurde gezogen.
096	incorrect	Der Wagen wurde übers gezogen.
096	filler	Der Schlitten wurde übers Eis gezogen.

Appendix B

Results of Individual Patients in Experiment 2B

B.1 ERPs

Figures B.1 to B.9 show the ERPs elicited by syntactically correct (solid line) and incorrect (dotted line) words for each patient. Figures B.10 to B.18 show the ERPs elicited by harmonically regular (solid line) and irregular (dotted line) chords for each individual. The time window for statistical testing is shaded in grey. In patients without significant effects (only in the music experiment), the timespan from 100 to 300 ms which was scanned for discernable peaks is highlighted. Significant differences revealed by t -tests for independent samples remaining after Bonferroni-correction are marked by an asterisk (*). Additionally, the individual MNI-scaled brains are shown with the individual localisation of the electrodes (Kovalev et al., 2005). Open circles indicate electrodes that were excluded from the analysis due to technical or epileptic artefacts.

Tables B.1 and B.2 show the statistical values of the t -tests calculated for each electrode in each patient separately for the language and the music experiment. Bold font indicates effects remaining after Bonferroni correction.

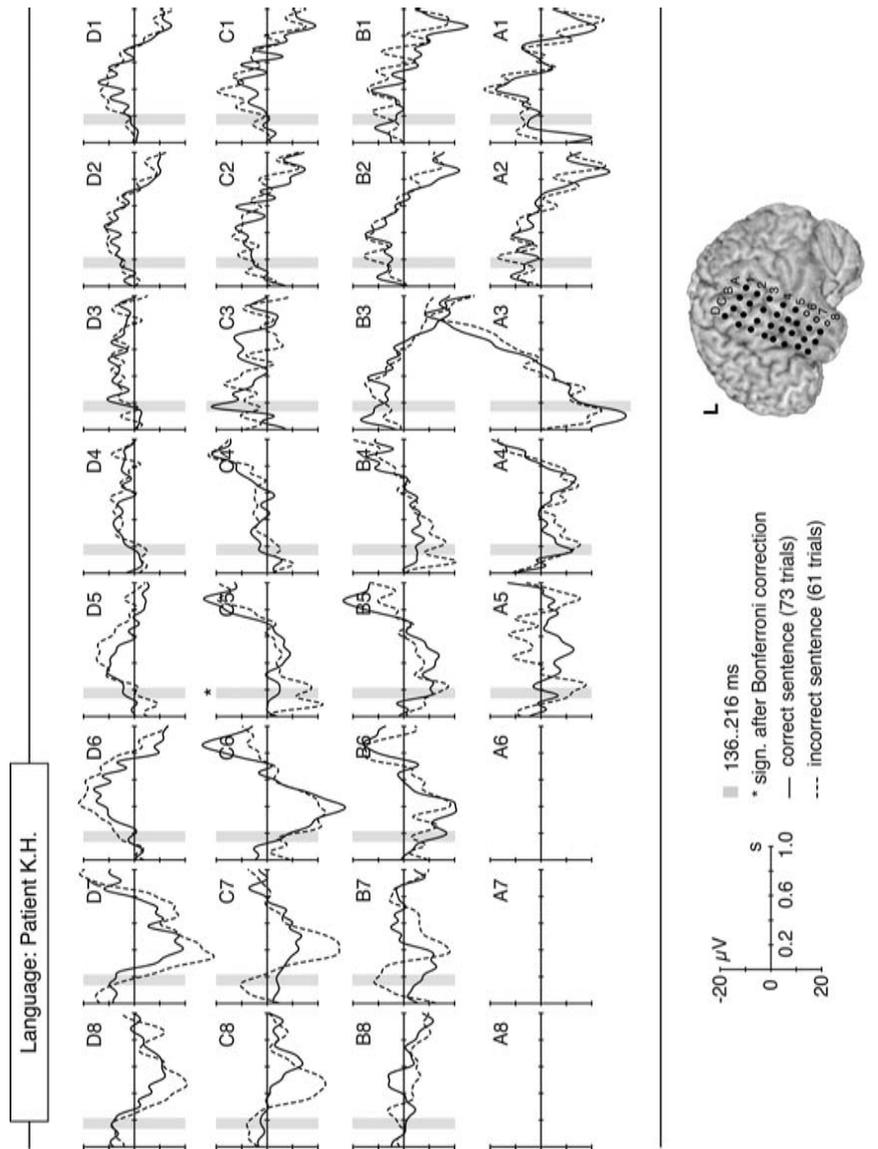


Figure B.1.: ERPs of patient K.H. in the language experiment

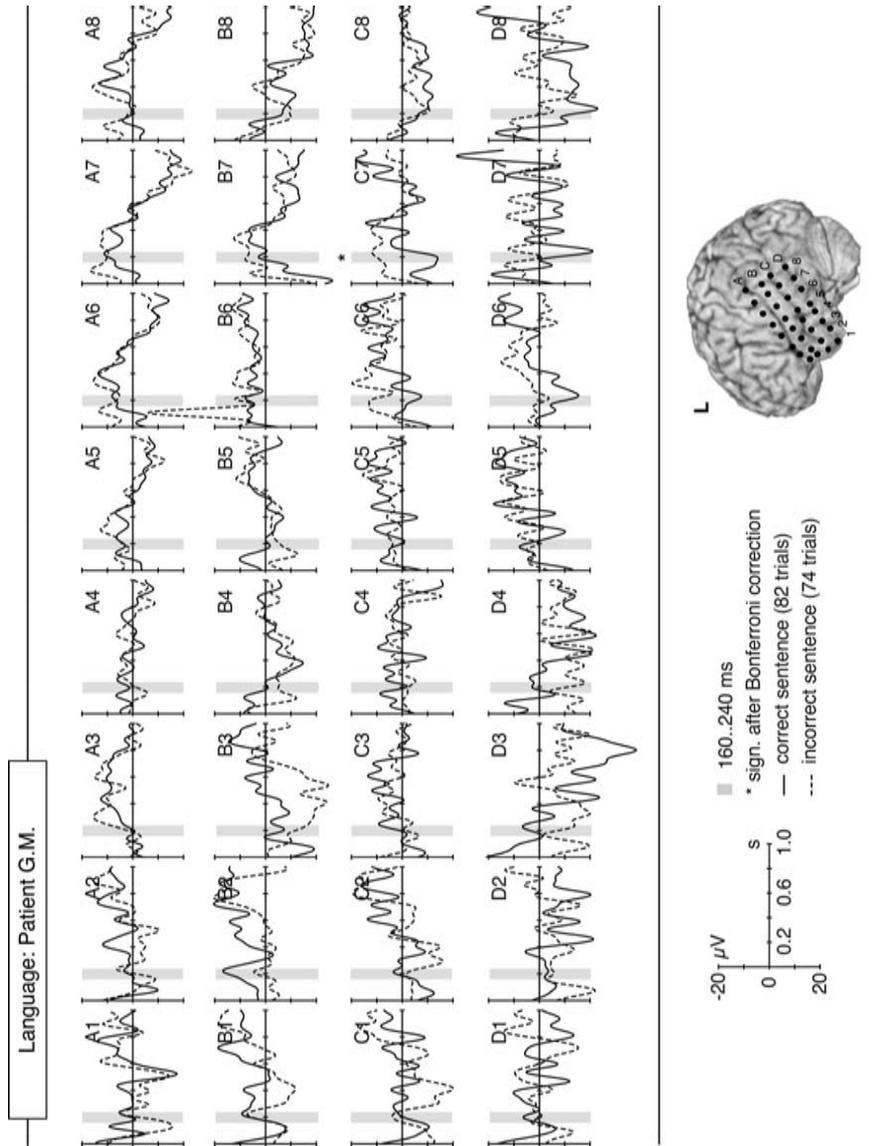


Figure B.2: ERPs of patient G.M. in the language experiment

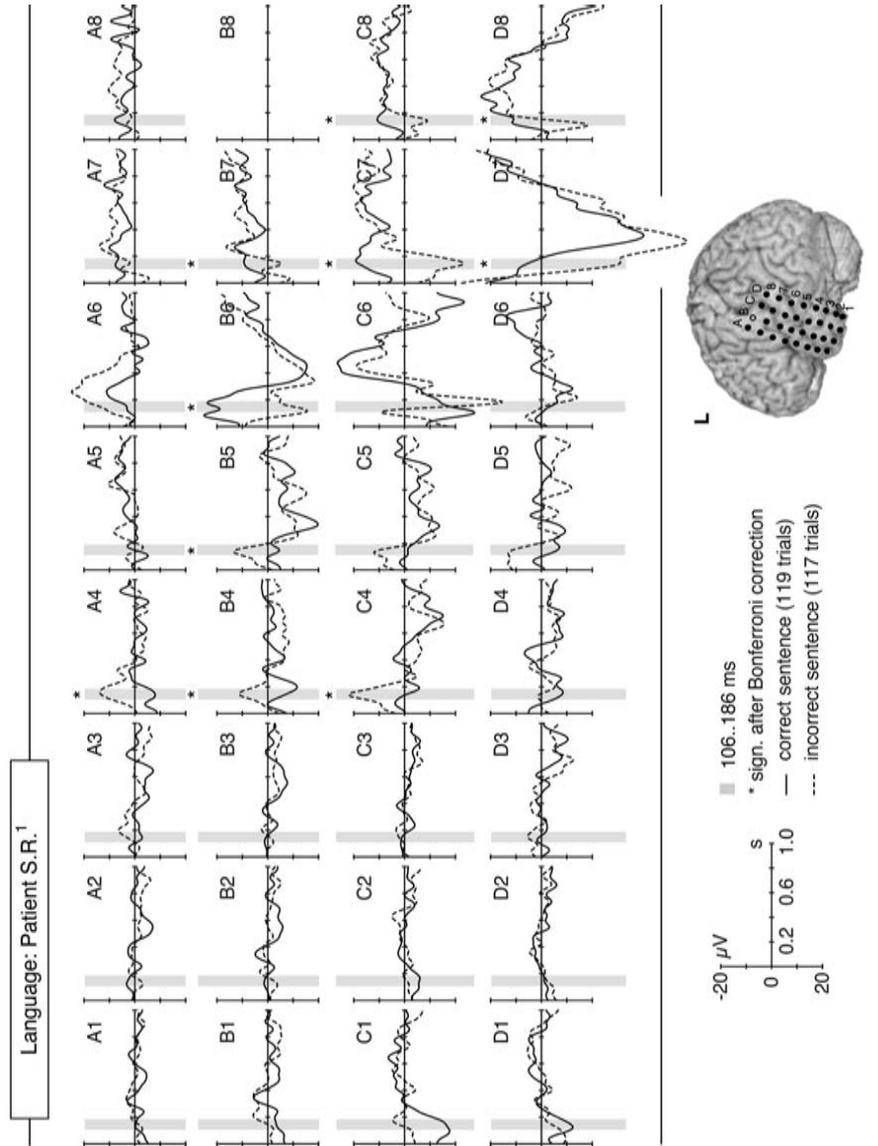


Figure B.3: ERPs of patient S.R.¹ in the language experiment

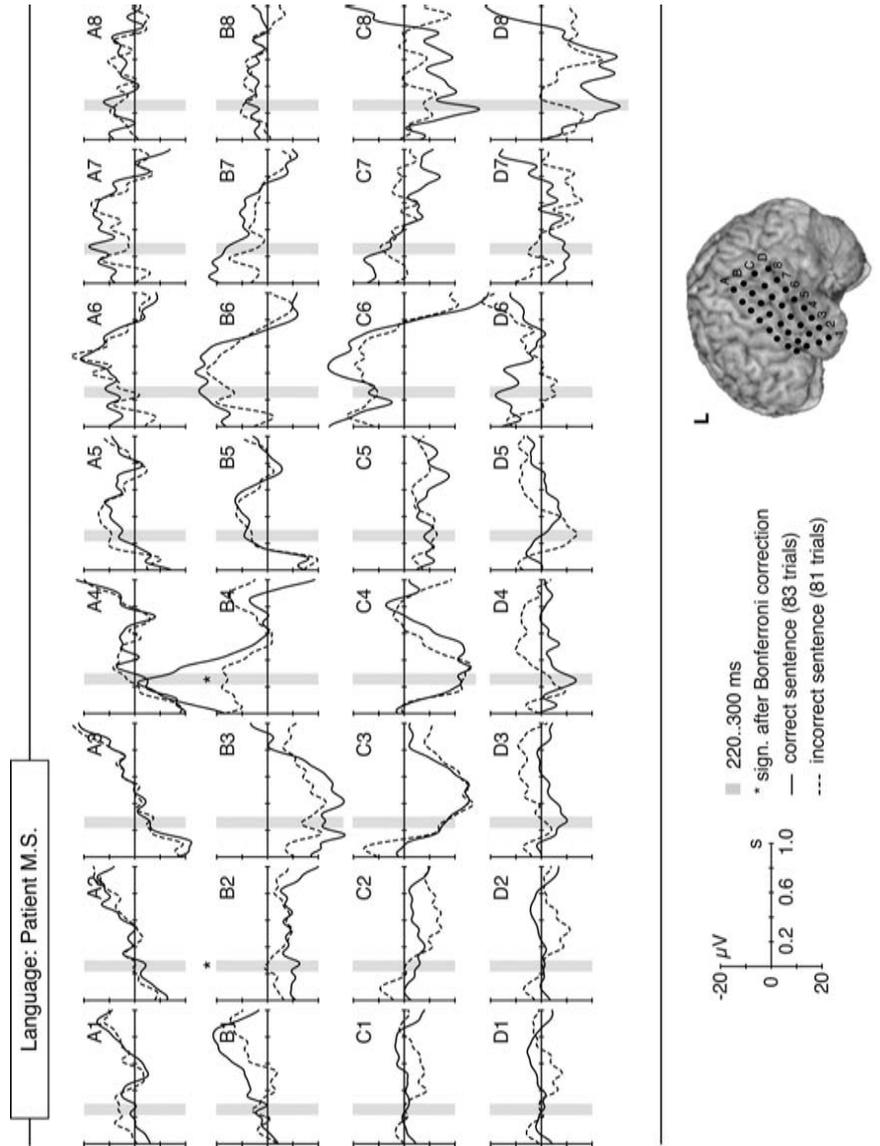


Figure B.4: ERPs of patient M.S. in the language experiment

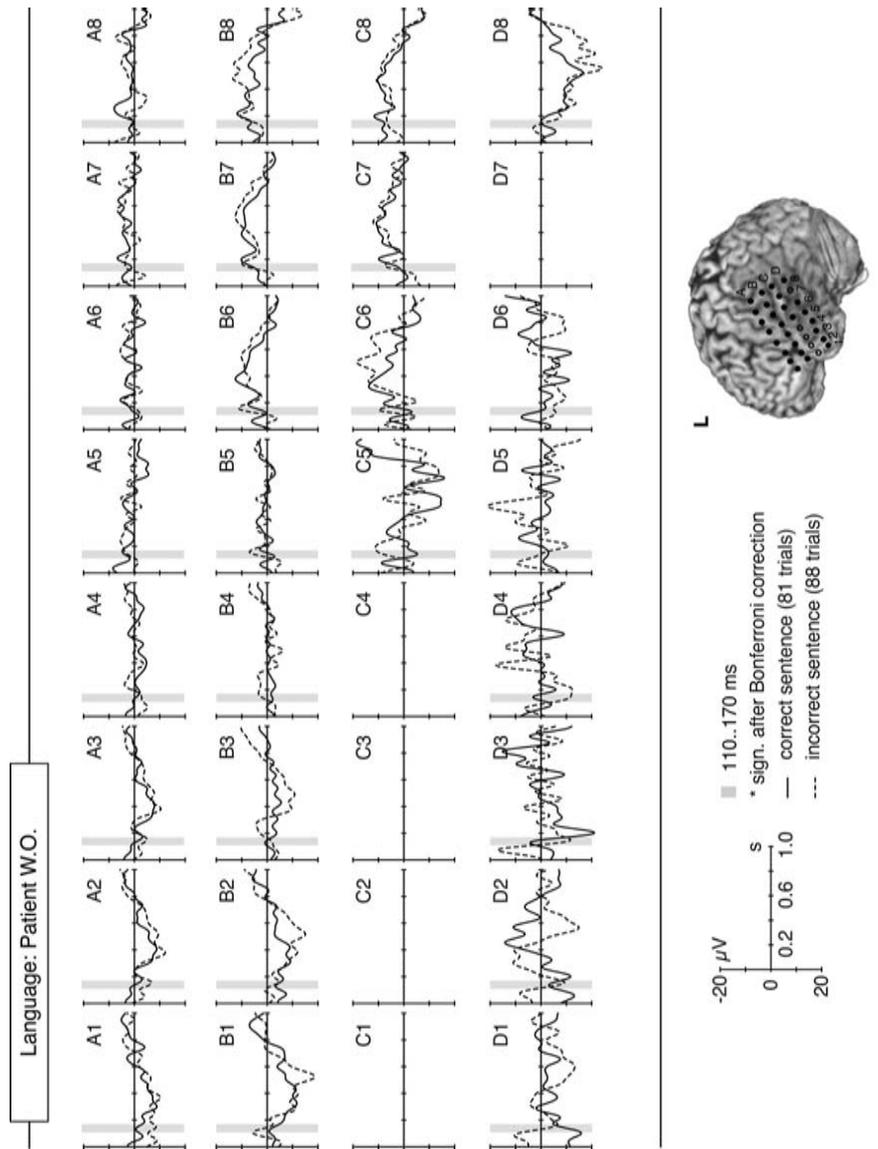


Figure B.5: ERPs of patient W.O. in the language experiment

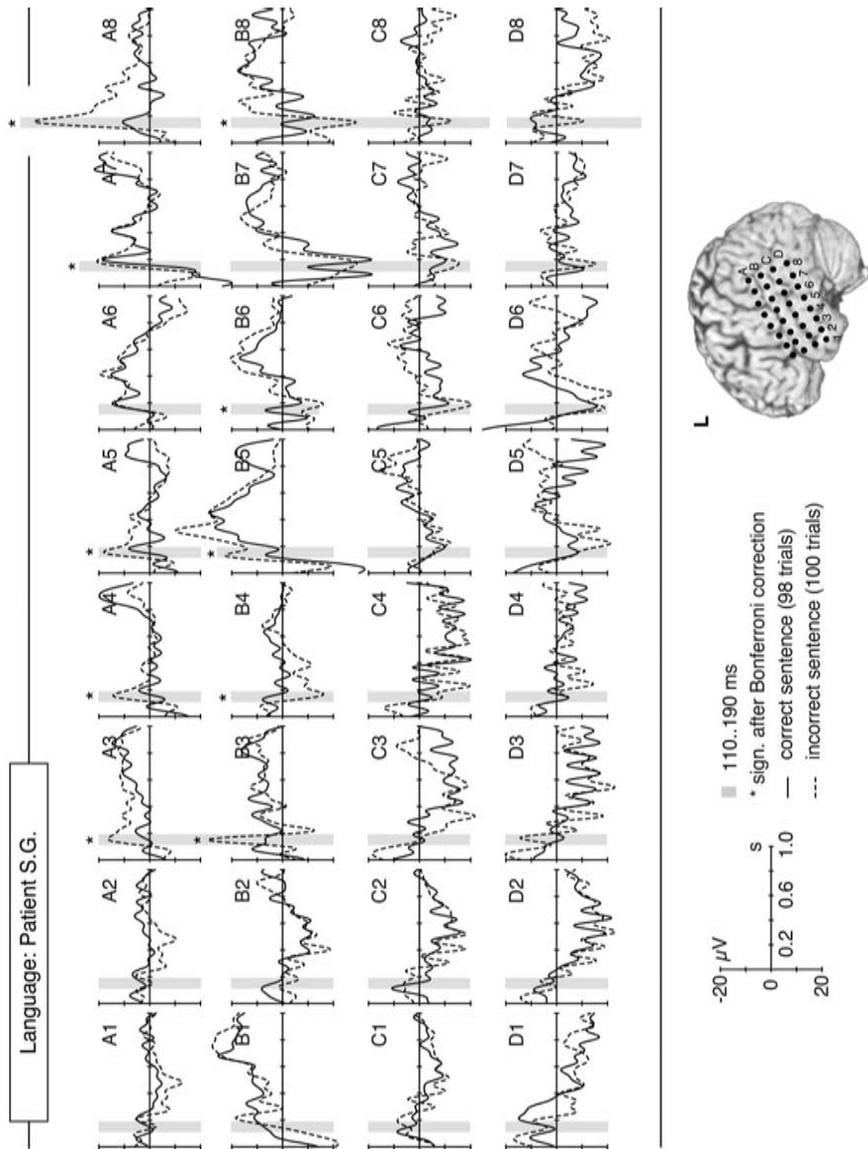


Figure B.6: ERPs of patient S.G. in the language experiment

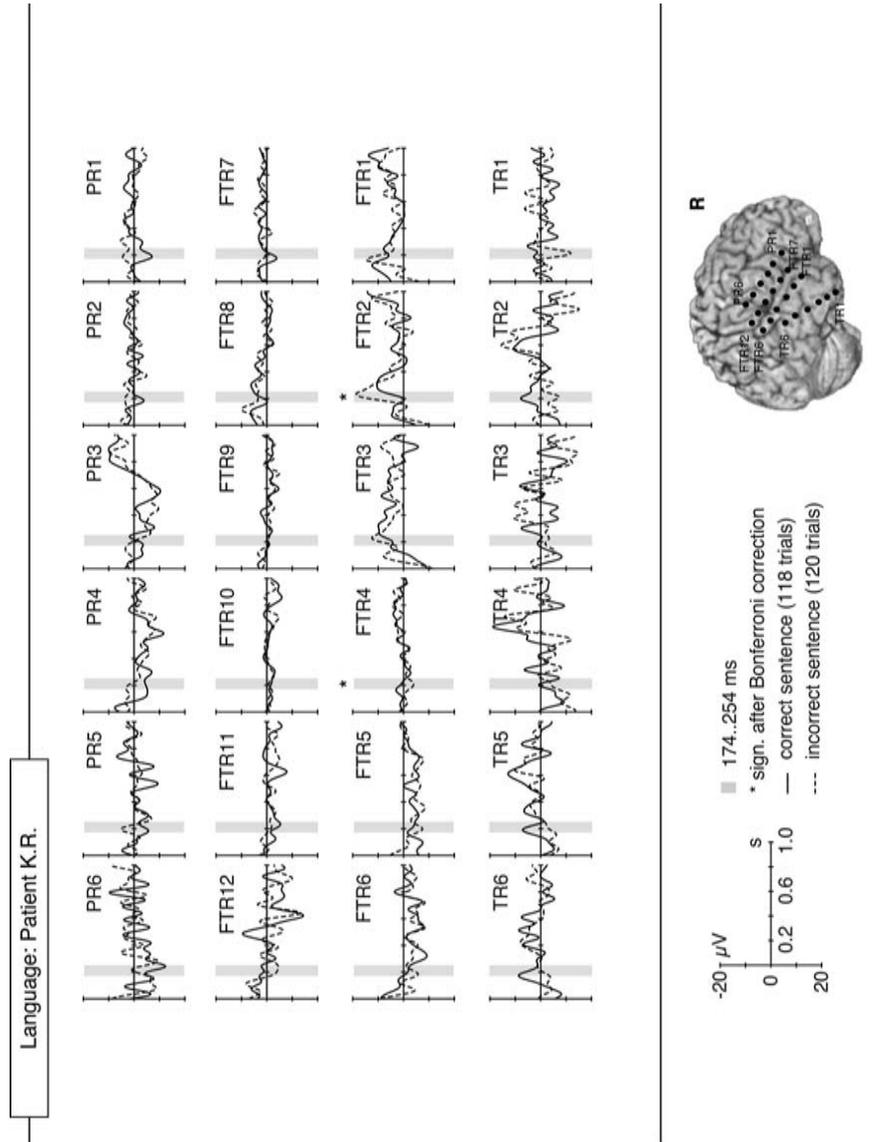


Figure B.7: ERPs of patient K.R. in the language experiment

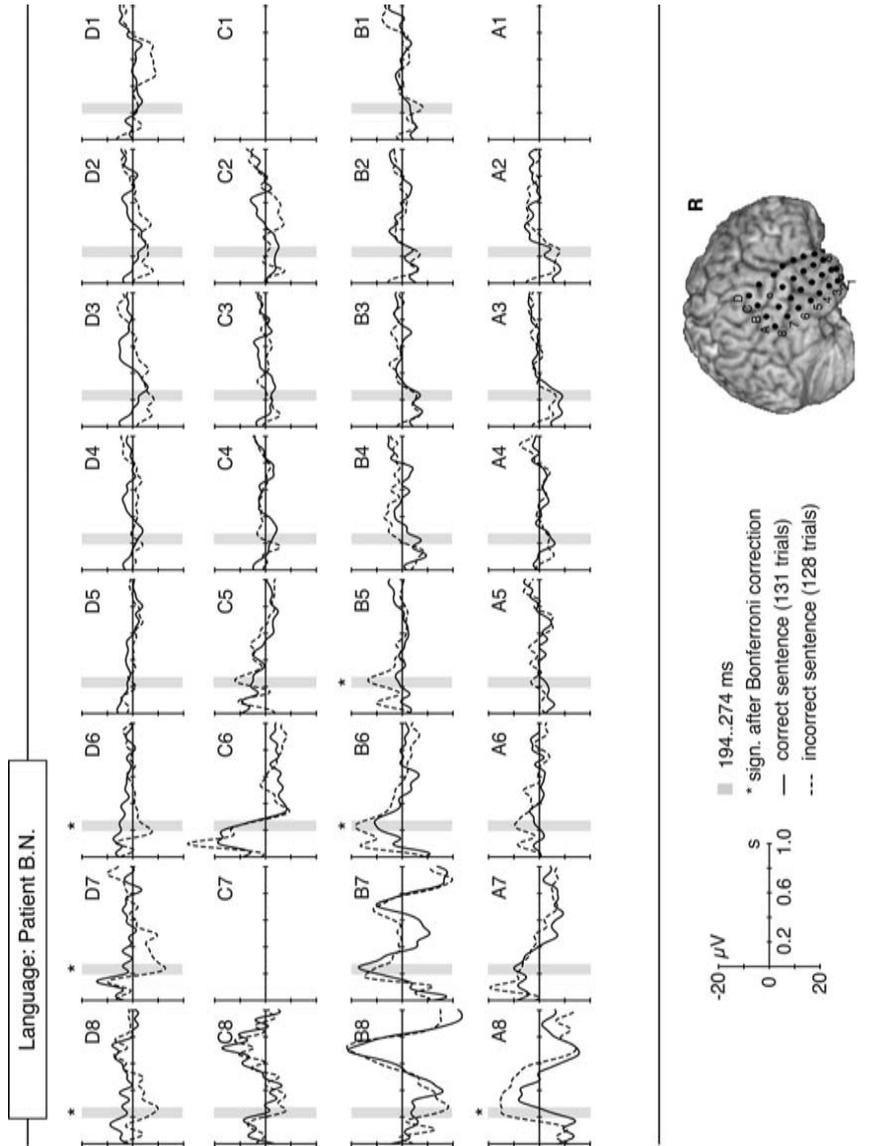


Figure B.8: ERPs of patient B.N. in the language experiment

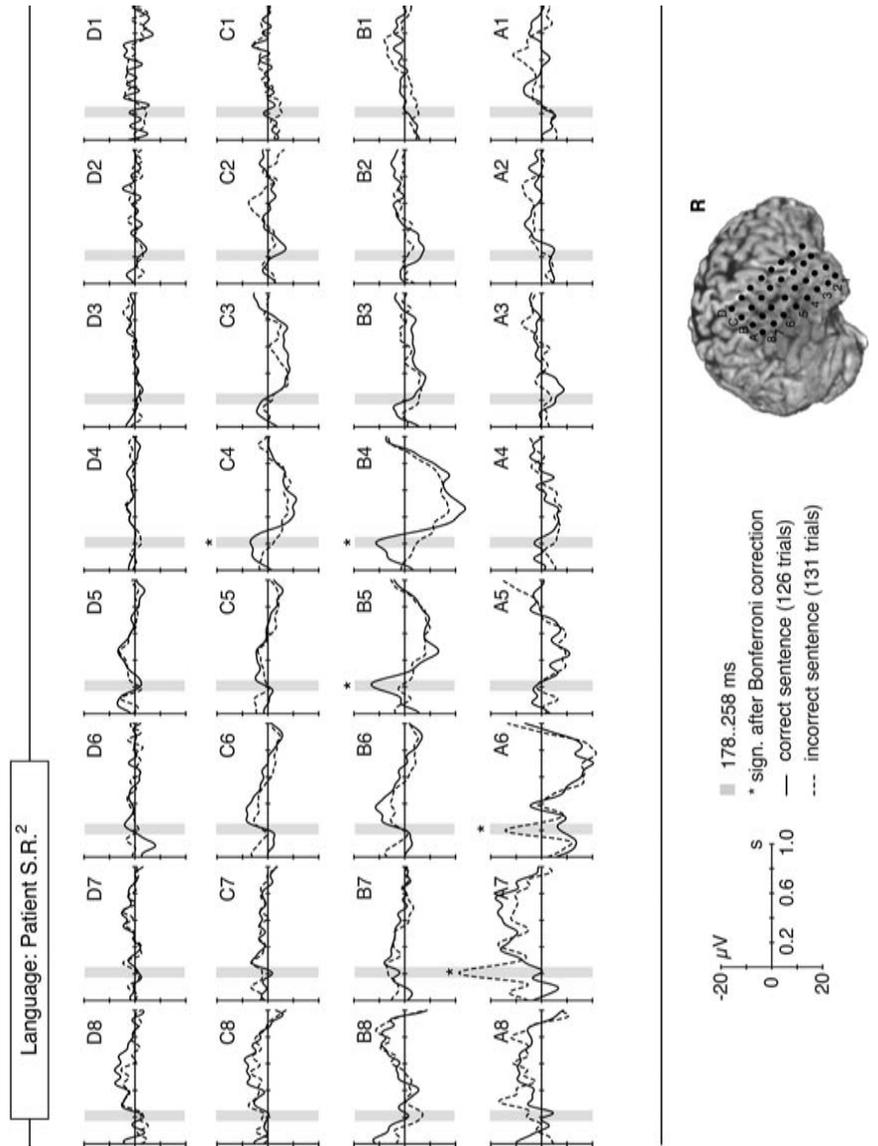


Figure B.9: ERPs of patient S.R.² in the language experiment

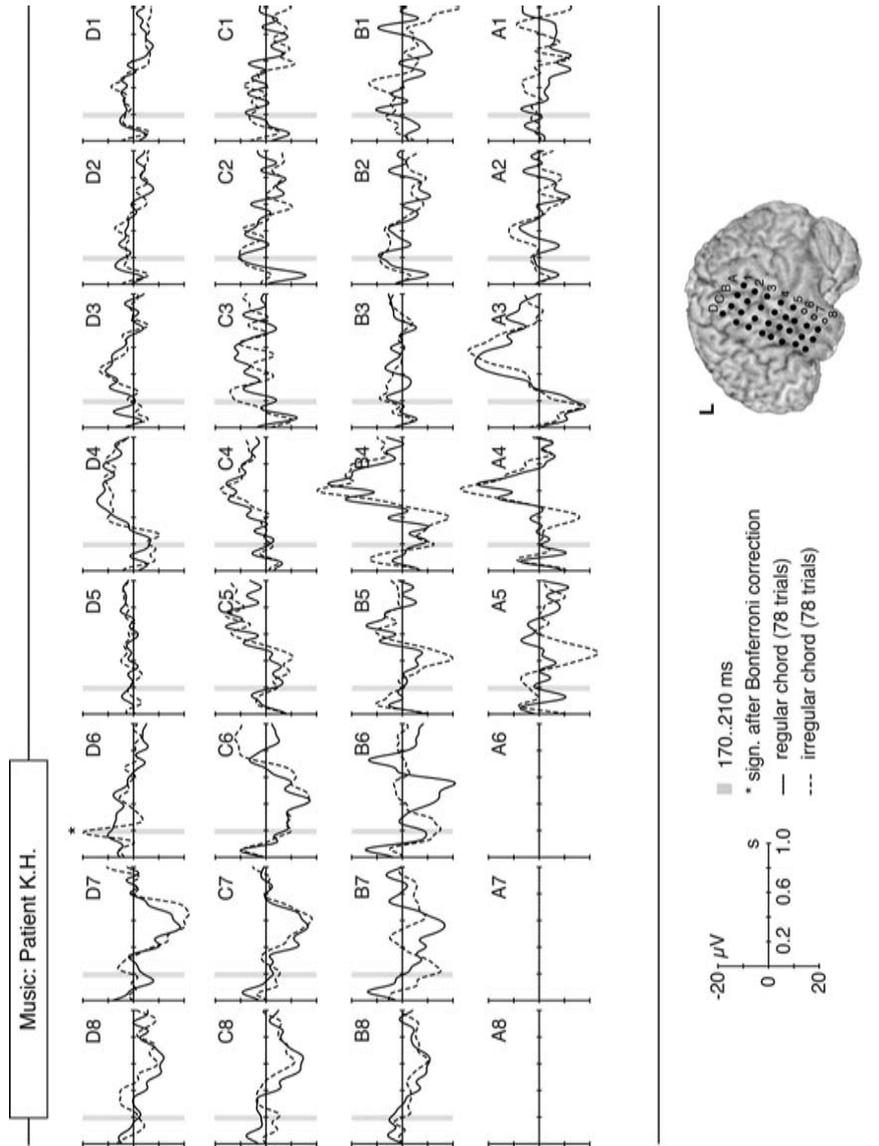


Figure B.10: ERPs of patient K.H. in the music experiment

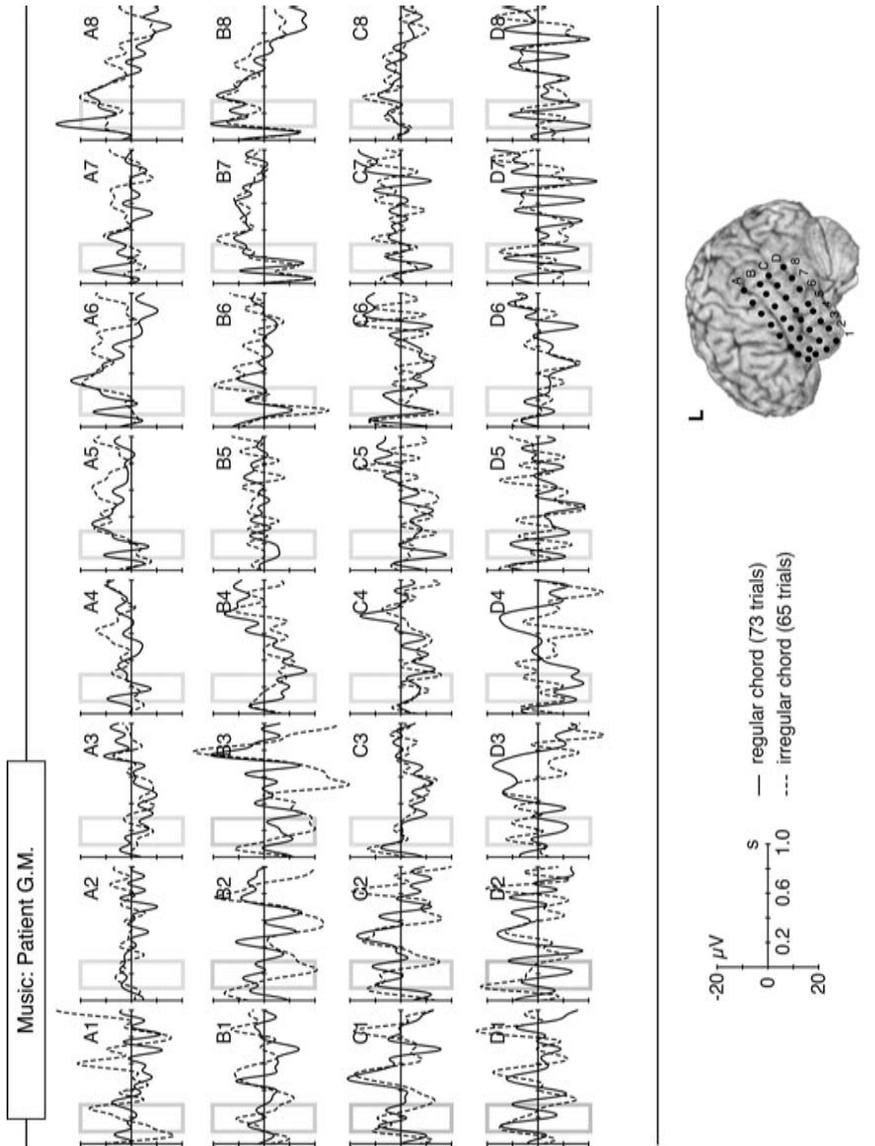


Figure B.11: ERPs of patient G.M. in the music experiment

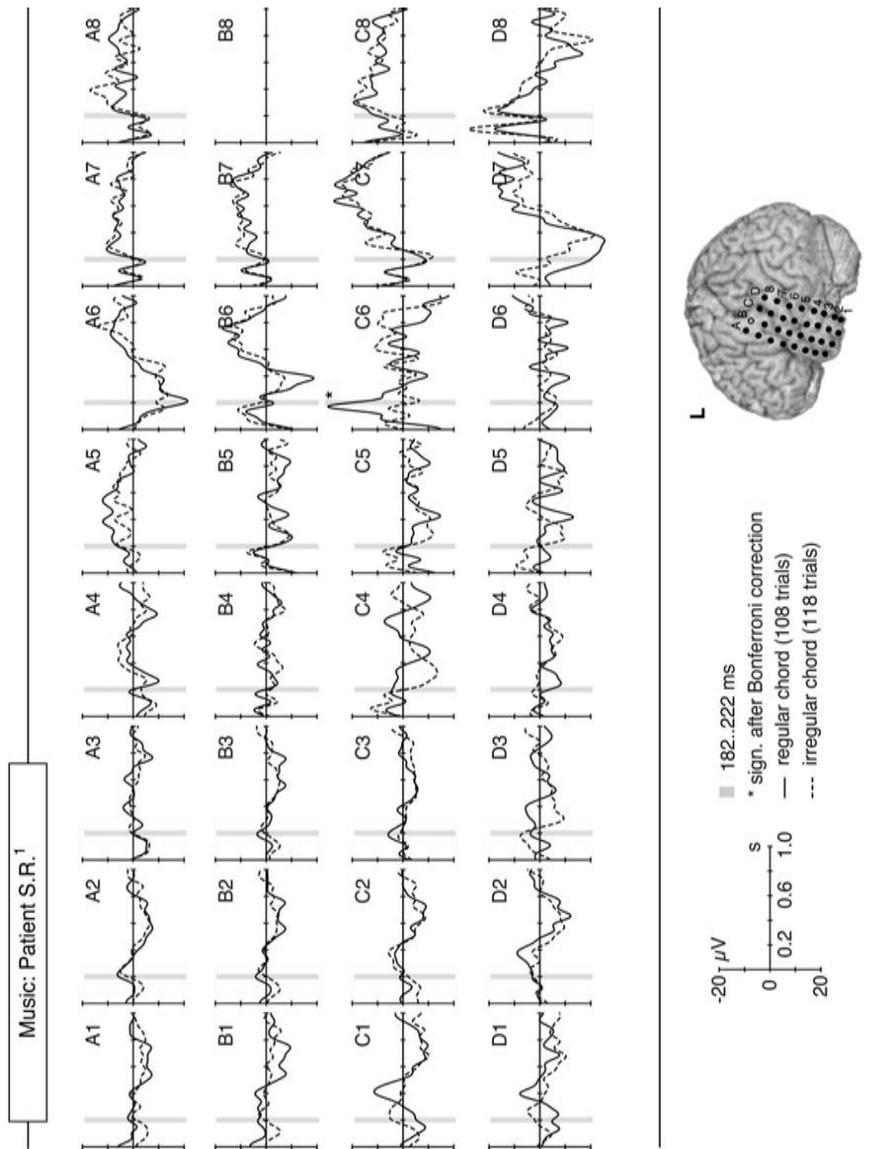


Figure B.12: ERPs of patient S.R.¹ in the music experiment

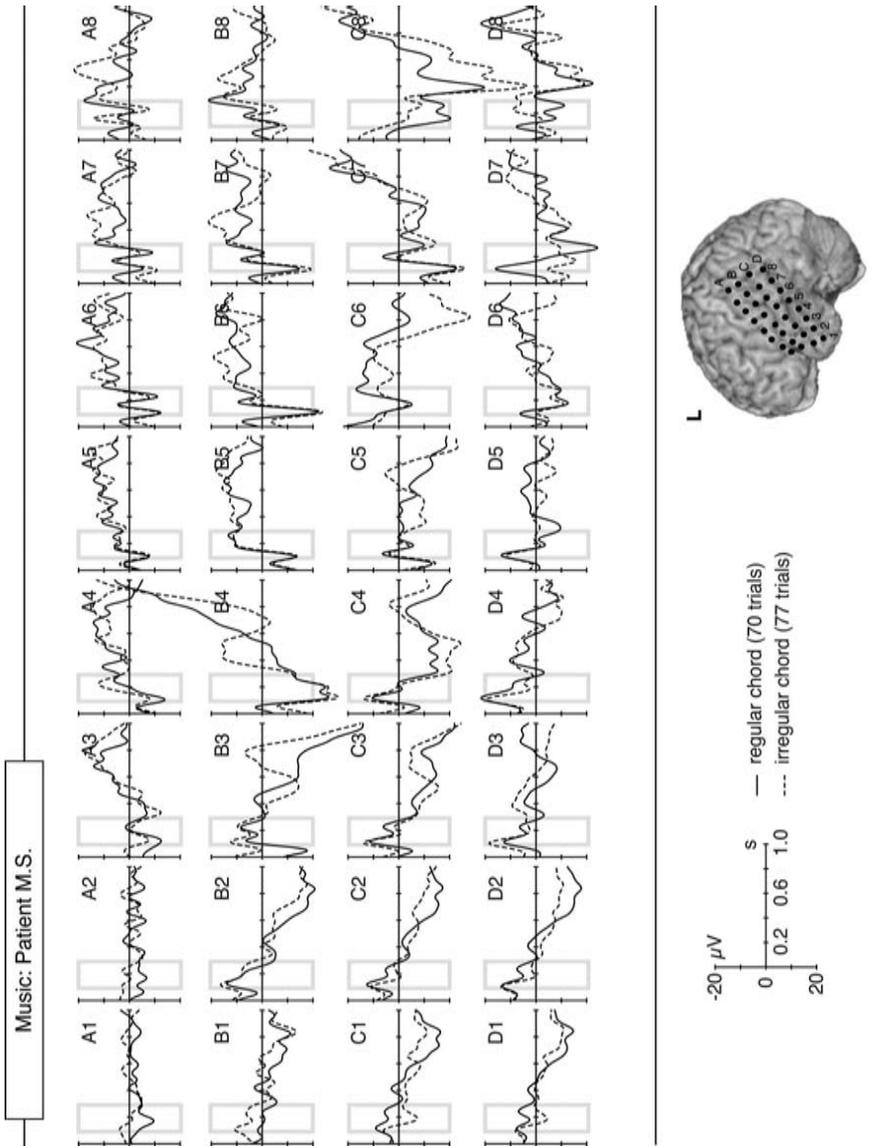


Figure B.13: ERPs of patient M.S. in the music experiment

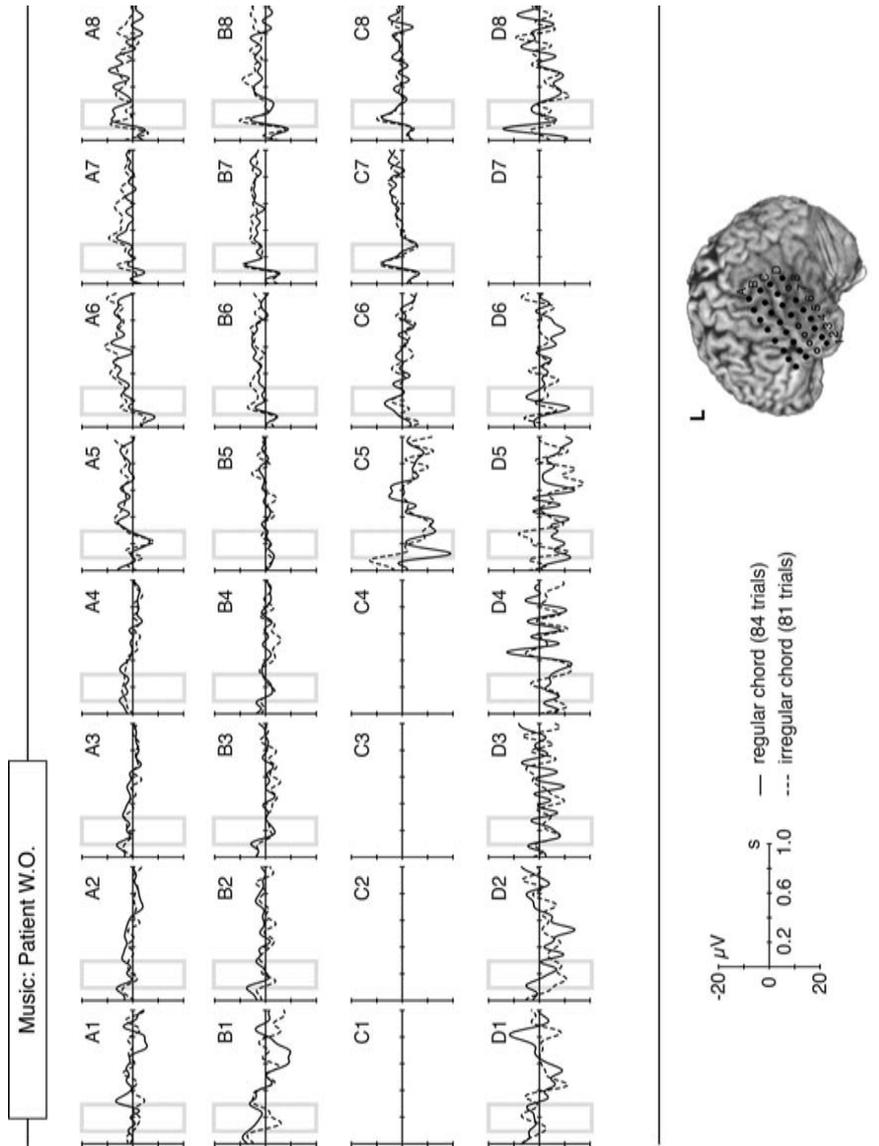


Figure B.14: ERPs of patient W.O. in the music experiment

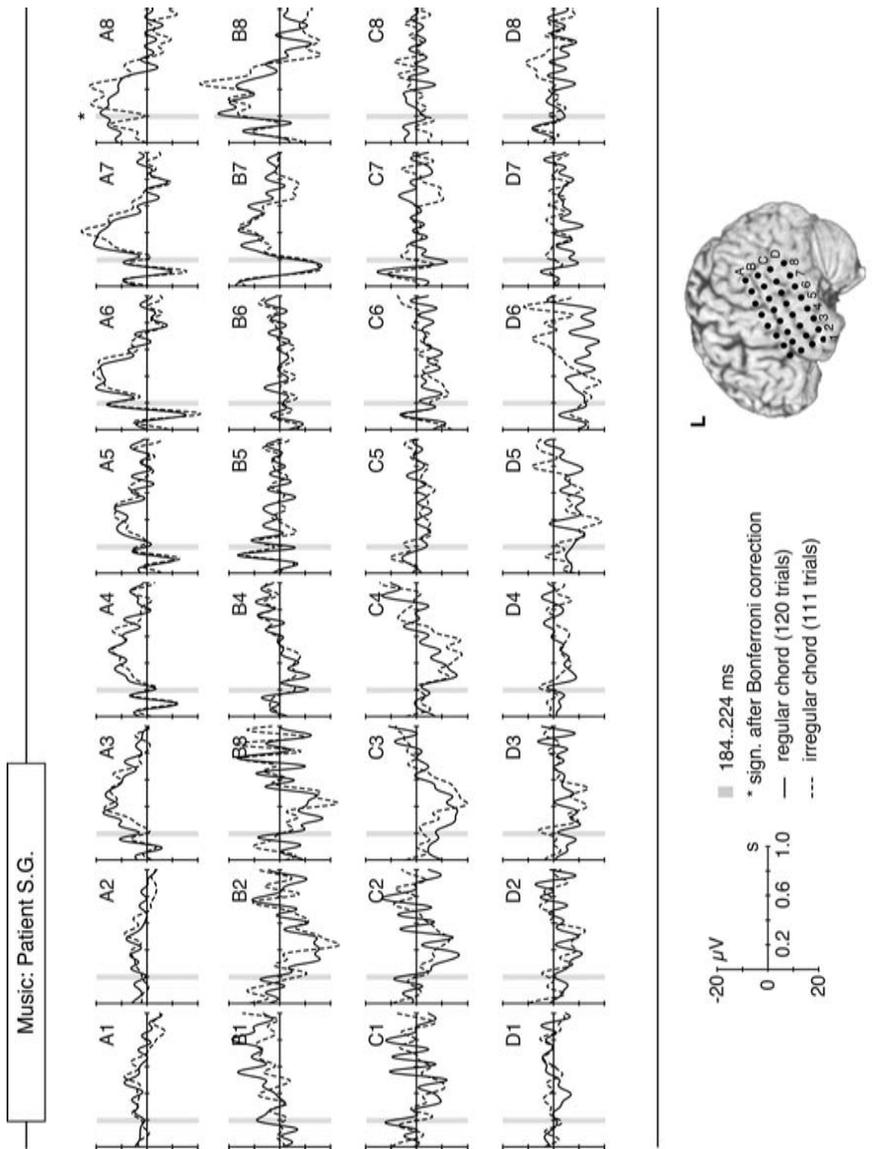


Figure B.15: ERPs of patient S.G. in the music experiment

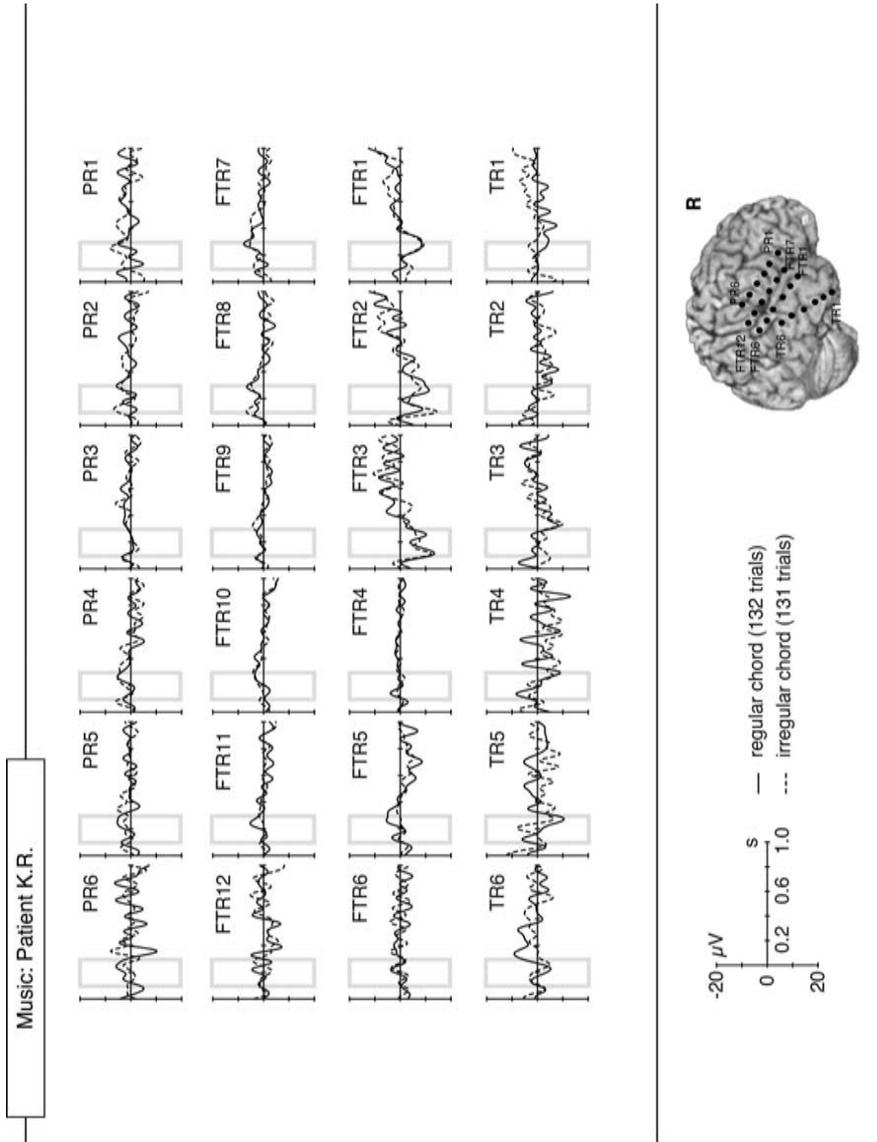


Figure B.16: ERPs of patient K.R. in the music experiment

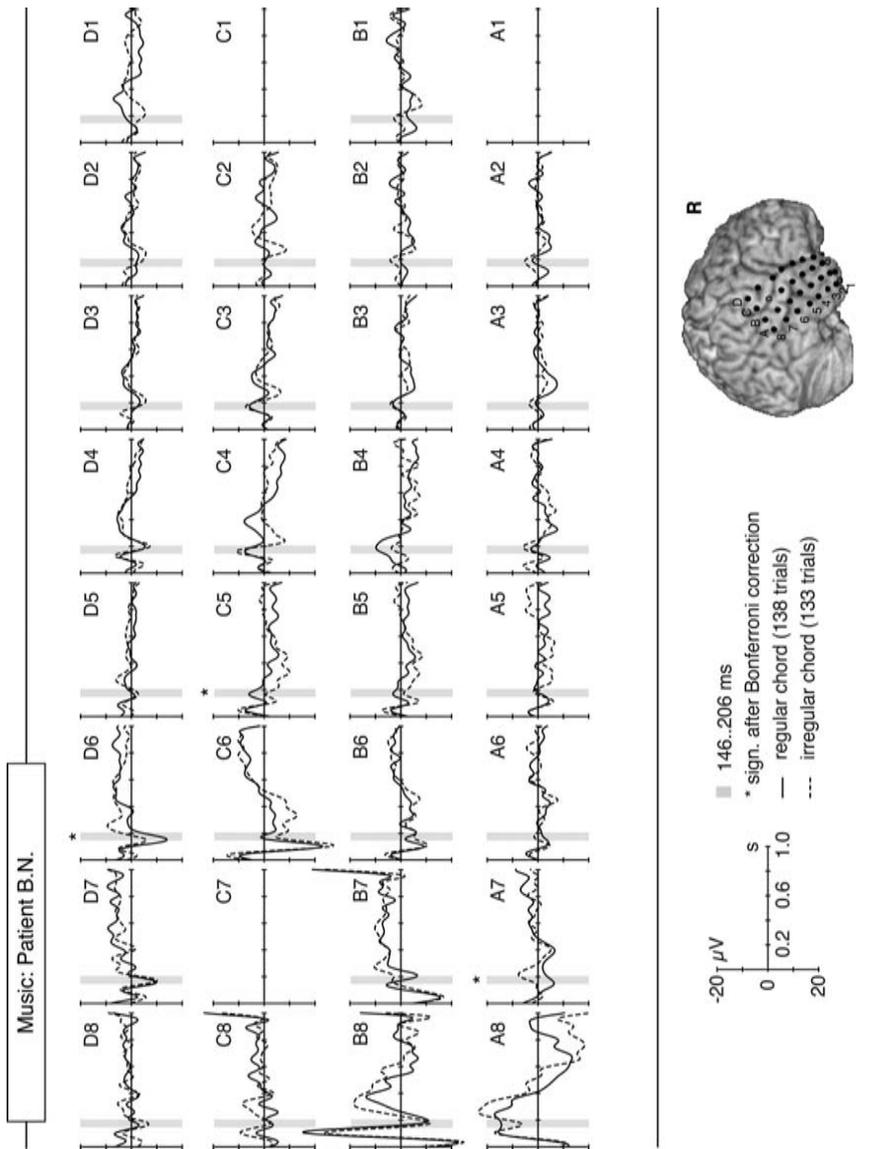


Figure B.17: ERPs of patient B.N. in the music experiment

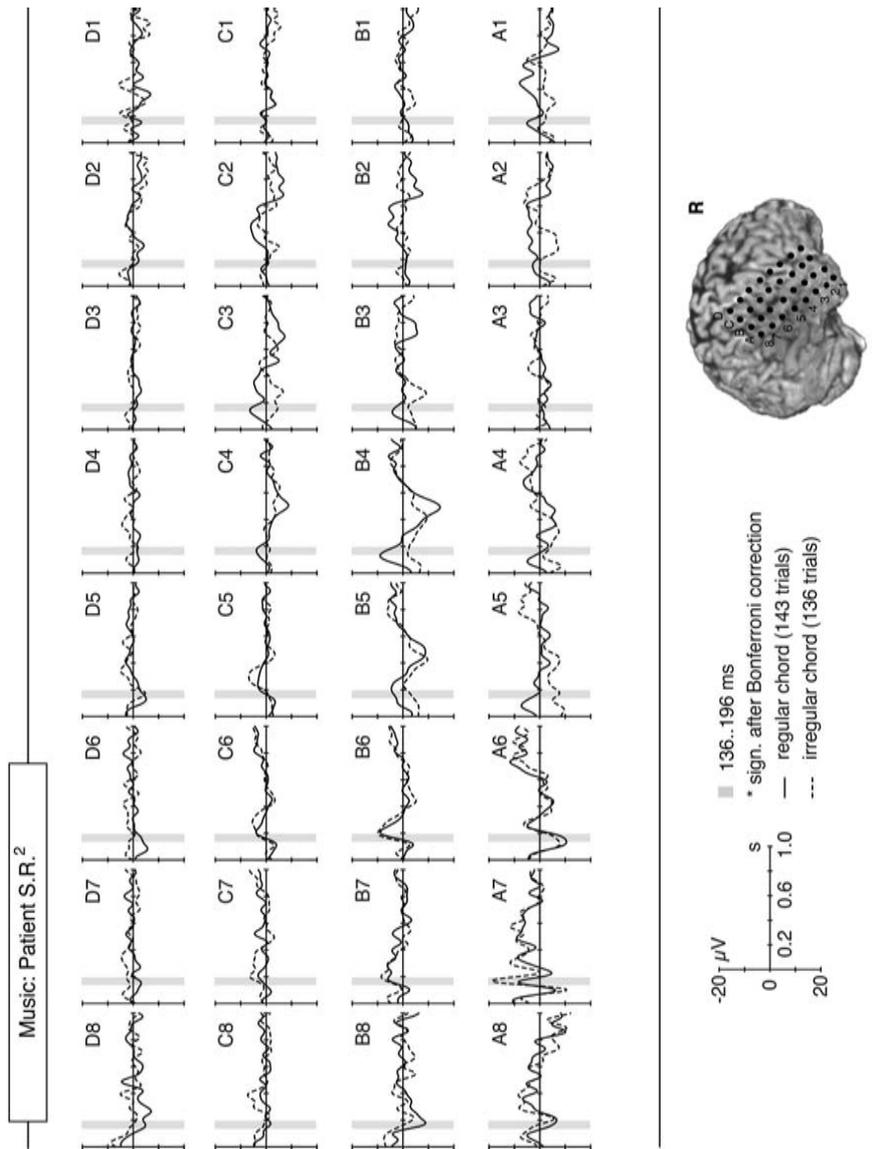


Figure B.18: ERPs of patient S.R.² in the music experiment

Table B.1: Localisation and statistical values of the electrodes showing early effects following phrase structure violations in language. Bold font indicates significant effects after Bonferroni correction. Coordinates refer to the stereotactic space of the Montreal Neurological Institute (MNI; Evans et al., 1994; Mazziotta et al., 1995). BA: Brodman area, IFG: inferior frontal gyrus, STG: superior temporal gyrus, MTG: middle temporal gyrus, ITG: inferior temporal gyrus, STS: superior temporal sulcus, SMG: supramarginal gyrus, SF: Sylvian fissure.

Patient (Time window)	Elec-trode	Polarity	Region	BA	x	y	z	T-value	p-value
<i>Left Hemisphere Electrodes</i>									
K.H. (136..216 ms)	B7	neg.	MTG, anterior	21	-58	-4	-18	-2.415	< .017
	C4	pos.	Precentral Gyrus	6	-62	-5	12	3.251	< .004
	C5	pos.	STG, anterior	22	-60	-2	3	5.034	< .001
	C7	neg.	Temporal pole	38	-55	6	-15	-2.082	< .040
	D4	pos.	Precentral Gyrus	6	-61	3	17	2.043	< .044
G.M. (160..240 ms)	C6	neg.	MTG, middle	21	-61	-26	-3	-3.209	< .002
	C7	neg.	MTG, posterior	21	-61	-36	4	-4.390	< .001
S.R. ¹ (106..186 ms)	A4	neg.	Temporal Pole	38	-53	12	-8	-4.537	< .001
	A6	pos.	Precentral Gyrus	6	-61	7	11	2.732	< .007
	B4	neg.	STG, anterior	22	-55	3	-13	-3.851	< .001
	B5	neg.	STG, anterior	22	-59	1	-4	-3.925	< .001
	B6	pos.	STG, anterior	22	-63	-2	5	11.186	< .001
	B7	pos.	Postcentral Gyrus	1/2/3	-64	-6	16	4.935	< .001

Patient (Time window)	Elec- trode	Polarity	Region	BA	x	y	z	T-value	p-value
M.S. (220..300 ms)	C1	neg.	ITG, anterior	20	-40	1	-44	-3.201	< .002
	C4	neg.	MTG, anterior	21	-56	-6	-18	-4.184	< .001
	C5	neg.	STG, anterior	22	-62	-8	-9	-2.949	< .004
	C7	pos.	STG, posterior	22	-66	-15	11	16.006	< .001
	C8	pos.	SMG, anterior	40	-65	-19	20	4.209	< .001
	D5	neg.	MTG, middle	21	-63	-19	-14	-2.581	< .011
	D7	pos.	STG, posterior	22	-67	-25	6	6.724	< .001
	D8	pos.	STG, posertior	22	-68	-28	16	4.527	< .001
W.O. (110..170 ms)	A4	neg.	Precentral Gyrus	6	-65	1	13	-2.045	< .043
	A7	pos.	SMG, anterior	40	-68	-22	35	2.251	< .026
	B2	neg.	Temporal Pole	38	-55	10	-10	-3.294	< .002
	B3	neg.	SF, anterior	-	-61	3	-2	-1.983	< .050
	B4	pos.	SF, anterior	-	-66	-4	4	5.784	< .001
	B6	pos.	SMG, anterior	40	-69	-21	20	3.251	< .002
	B7	pos.	SMG, anterior	40	-69	-29	27	3.062	< .003
	D6	pos.	STG, posterior	22	-70	-32	0	2.399	< .018
D8	neg.	Angular Gyrus	39	-66	-49	14	-2.129	< .035	
W.O. (110..170 ms)	A1	pos.	IFG, pars triangularis	45	-44	30	-10	2.045	< .043
	A2	pos.	IFG, pars triangularis	45	-51	24	-4	2.110	< .037
	B5	neg.	SF, middle	-	-65	-6	3	-2.702	< .008

Patient (Time window)	Elec- trode	Polarity	Region	BA	x	y	z	T-value	p-value
S.G. (110..190 ms)	B6	neg.	SF, middle	-	-68	-14	10	-2.299	< .023
	A3	neg.	Precentral Gyrus	6	-59	3	5	-4.755	< .001
	A4	neg.	Precentral Gyrus	6	-62	-5	12	-4.731	< .001
	A5	neg.	Postcentral Gyrus	1/2/3	-63	-14	17	-5.154	< .001
	A7	neg.	SMG, anterior	40	-60	-33	25	-3.478	< .001
	A8	neg.	SMG, posterior	40	-59	-42	30	-8.346	< .001
	B2	pos.	Temporal Pole	38	-56	8	-8	2.140	< .034
	B3	neg.	STG, anterior	22	-59	0	-4	-4.375	< .001
	B4	pos.	STG, anterior	22	-62	-9	2	6.257	< .001
	B5	neg.	STG, middle	22	-63	-18	7	-5.153	< .001
B6	pos.	STG, middle	22	-61	-27	11	4.584	< .001	
B7	pos.	STG, posterior	22	-59	-37	15	2.227	< .028	
B8	pos.	SMG, posterior	40	-58	-46	20	5.327	< .001	
C6	pos.	MTG, posterior	21	-60	-32	1	2.617	< .010	
D8	pos.	MTG, posterior	21	-57	-56	-1	2.237	< .027	
<i>Right Hemisphere Electrodes</i>									
K.R. (174..254 ms)	PR1	neg.	IFG, pars triangularis	45	56	25	3	-2.968	< .004
	PR2	neg.	IFG, pars opercularis	44	60	16	10	-2.353	< .020
	PR4	neg.	Precentral Gyrus	6	64	0	20	-2.520	< .013
	PR5	neg.	Postcentral Gyrus	1/2/3	65	-9	26	-2.244	< .026

Patient (Time window)	Elec- trode	Polarity	Region	BA	x	y	z	T-value	p-value
B.N. (194..274 ms)	FTR2	neg.	STG, anterior	22	65	-2	-7	-4.294	<.001
	FTR4	pos.	STG, posterior	22	67	-21	7	3.822	<.001
	TR1	pos.	ITG, posterior	20	50	-7	-41	2.504	<.013
	TR2	pos.	ITG, posterior	20	57	-11	-34	2.718	<.008
	A6	neg.	MTG, middle	21	68	-19	-12	-3.066	<.003
	A8	neg.	STG, posterior	22	68	-34	7	-6.041	<.001
	B4	neg.	MTG, anterior	21	57	2	-23	-2.700	<.008
	B5	neg.	MTG, anterior	21	63	-4	-14	-6.654	<.001
	B6	neg.	MTG, middle	21	65	-11	-6	-3.965	<.001
	B8	pos.	STG, posterior	22	68	-26	14	2.891	<.005
	C4	neg.	Temporal Pole	38	55	11	-16	-2.547	<.012
	C5	neg.	STG, anterior	22	61	5	-8	-3.277	<.002
	C8	pos.	Postcentral Gyrus	1/2/3	67	-17	21	2.648	<.009
	D3	pos.	Temporal Pole	38	45	23	-16	2.548	<.012
D6	pos.	Precentral Gyrus	6	62	8	8	7.247	<.001	
D7	pos.	Precentral Gyrus	6	65	0	20	6.240	<.001	
D8	pos.	Postcentral Gyrus	1/2/3	65	-9	28	4.250	<.001	
S.R. ² (178..258 ms)	A6	neg.	STG, middle	22	61	-24	2	-7.377	<.001
	A7	neg.	STG, posterior	22	63	-31	10	-9.828	<.001
	A8	neg.	STG, posterior	22	65	-38	19	-2.565	<.011
	B4	pos.	STG, anterior	22	53	-2	-7	5.051	<.001

Patient (Time window)	Elec-trode	Polarity	Region	BA	<i>x</i>	<i>y</i>	<i>z</i>	<i>T</i> -value	<i>p</i> -value
B5		pos.	STG, posterior	22	55	-10	1	4.977	< .001
B8		pos.	SMG, posterior	40	62	-32	27	2.182	< .030
C1		pos.	Temporal Pole	38	37	24	-20	2.594	< .011
C4		pos.	STG, anterior	22	51	5	4	5.063	< .001

Table B.2: Localisation and statistical values of the electrodes showing early effects following irregular chords in music. Bold font indicates significant effects after Bonferroni correction. Coordinates refer to the stereotactic space of the Montreal Neurological Institute (MNI; Evans et al., 1994; Mazziotta et al., 1995). BA: Brodman area, IFG: inferior frontal gyrus, STG: superior temporal gyrus, MTG: middle temporal gyrus, STS: superior temporal sulcus, SMG: supramarginal gyrus.

Patient (Time window)	Elec- trode	Polarity	Region	BA	x	y	z	T-value	p-value
<i>Left Hemisphere Electrodes</i>									
K.R. (170..210 ms)	C3	neg.	Postcentral Gyrus	1/2/3	-63	-9	23	-1.970	< .050
	D6	neg.	IFG, pars opercularis	44	-56	10	1	-3.567	< .001
S.R. ¹ (182..222 ms)	A6	neg.	Precentral Gyrus	6	-61	7	11	-2.607	< .010
	C6	pos.	STG, posterior	22	-65	-11	1	3.430	< .001
	D7	neg.	STG, middle	22	-67	-25	6	-3.026	< .003
S.G. (184..224 ms)	A8	pos.	SMG, posterior	40	-59	-42	30	3.917	< .001
	B1	pos.	Temporal Pole	38	-50	15	-15	2.036	< .043
	C5	neg.	STS, middle	22	-62	-23	-3	-1.989	< .048
	C7	neg.	MTG, posterior	21	-58	-41	5	-2.671	< .009
<i>Right Hemisphere Electrodes</i>									
B.N. (146..206 ms)	A7	neg.	STG, middle	22	68	-26	-3	-4.632	< .001
	A8	pos.	STG, posterior	22	67	-34	7	2.164	< .032

Patient (Time window)	Elec- trode	Polarity	Region	BA	x	y	z	T-value	p-value
	B4	pos.	MTG, anterior	21	57	2	-23	2.670	< .009
	B5	pos.	MTG, anterior	21	63	-4	-14	2.662	< .009
	C5	pos.	STG, middle	22	61	5	-8	4.210	< .001
	C6	pos.	STG, middle	22	65	-2	1	2.896	< .005
	D1	pos.	Temporal Pole	38	36	28	-34	2.069	< .040
	D6	neg.	Precentral Gyrus	6	62	8	8	-6.122	< .001
S.R. ² (136..196 ms)	A7	neg.	STG, middle	22	63	-31	10	-3.244	< .002
	B5	pos.	STG, posterior	22	55	-10	1	2.393	< .018
	B8	neg.	SMG, posterior	40	62	-32	27	-2.194	< .030
	C3	pos.	STS, middle	-	48	11	-6	2.113	< .036
	C4	pos.	STS, middle	-	51	5	4	2.415	< .017

B.2 BSCD mapping

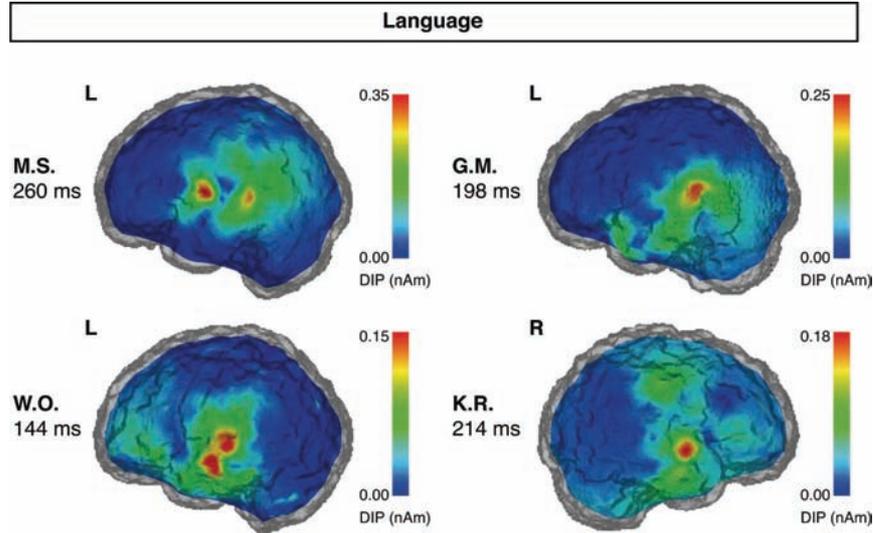


Figure B.19: Results of the BSCD mapping (Knösche et al., 1999) of the early effect elicited by phrase-structure violations in the language experiment in patients M.S., G.M., W.O., and K.R.

Table B.3: Results of the BSCD mapping. Coordinates indicate the localisation of the local maxima of sources underneath and in the close vicinity of the electrode grid. Their magnitudes are indicated in nAm or z -transformed with respect to the magnitude of all generators within the respective hemisphere. Only maxima with z -values > 1.00 are reported. Coordinates refer to the stereotactic space of the Montreal Neurological Institute (MNI; Evans et al., 1994; Mazziotta et al., 1995). BA: Brodman's area, m : mid, p : posterior, STG: superior temporal gyrus, MTG: middle temporal gyrus, ITG: inferior temporal gyrus, TP: temporal pole, STS: superior temporal sulcus, IFG: inferior frontal gyrus, p . tr.: pars triangularis, prec. g.: precentral gyrus, postc. g.: postcentral gyrus.

x	y	z	nAm	z-value	region	BA
<i>Left hemisphere</i>						
M.S.						
-61	-9	2	0.37	7.33	mSTG	22
-65	-38	0	0.31	6.08	pSTS	-
-61	-51	9	0.18	3.08	pSTS	-
G.M.						
-65	-35	7	0.24	6.68	pSTG	22

x	y	z	nAm	z-value	region	BA
-60	-23	-26	0.13	2.97	mITG	20
-56	-18	-32	0.12	2.61	mITG	20
-44	15	-28	0.11	2.43	TP	38
-49	16	-17	0.10	2.00	TP	38
-38	2	-41	0.08	1.30	TP	38
W.O.						
-62	-12	-19	0.18	6.41	mMTG	21
-67	-21	-9	0.16	5.68	mMTG	21
-60	-14	-25	0.15	5.53	mMTG	21
-64	-39	-24	0.09	2.73	pITG	20
-63	-10	-3	0.09	2.72	mSTG	22
-46	29	-12	0.07	2.06	IFG, p. tr.	47
-42	37	-10	0.06	1.72	IFG, p. tr.	47
<i>Right hemisphere</i>						
K.R.						
61	-7	-10	0.18	7.22	prec. g.	6
59	-11	-23	0.12	4.02	mMTG	21
60	-24	37	0.11	3.80	postc. g.	1/2/3
54	-18	-32	0.11	3.54	mITG	21
43	6	-37	0.06	1.25	TP	38
59	-3	17	0.06	1.12	prec. g.	6
51	27	0	0.06	1.07	IFG, p. tr.	45
23	7	-37	0.06	1.02	TP	38

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List of Abbreviations

GLM	General Linear Model
GTC	Generalized Tonic-Clonic Convulsions
HG	Heschl's Gyrus
ICA	Independent Component Analysis
iEEG	Intracranial EEG
IFG	Inferior Frontal Gyrus
IFL	Inferior Frontal Lobe
ILAE	International League Against Epilepsy
L-P-S	Leistungsprüfsystem
LFP	Local Field Potential
LPC	Late Positive Component
MEG	Magnetoencephalography
MIT	Melodic Intonation Therapy
MMN	Mismatch Negativity
MNI	Montreal Neurological Institute?
MNLS	Minimum-Norm Least-Squares
MRI	Magnetic Resonance Imaging
MTG	Middle Temporal Gyrus
PAC	Primary Auditory Cortex
PET	Positron Emission Tomography
PP	Planum Polare
PT	Planum Temporale

PTL	Posterior Temporal Lobe
RATN	Right Antero-Temporal Negativity
ROI	Region of Interest
SAC	Secondary Auditory Cortex
SEM	Standard Error of Mean
SF	Sylvian Fissure
SMG	Supramarginal Gyrus
SNR	Signal-to-Noise Ratio
SPECT	Single Photon Emission Computed Tomography
SPS	Simple Partial Seizures
SSIRH	Shared Syntactic Integration Resource Hypothesis
STG	Superior Temporal Gyrus
STM	Short Term Memory
STP	Superior Temporal Plane
STS	Superior Temporal Sulcus
tDCS	Transcranial Direct Current Stimulation
TL	Temporal Lobe
TLE	Temporal Lobe Epilepsy
TMS	Transcranial Magnetic Stimulation
vIPMC	Ventro-Lateral Premotor Cortex
VLSM	Voxel-Based Lesion-Symptom Mapping
WM	Working Memory
WMS	Wechsler Memory Scale

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- Koelsch, S., Schulze, K., Sammler, D., Fritz, T., Müller, K., & Gruber, O. (2008). Functional architecture of verbal and tonal working memory: An fMRI study. *Human Brain Mapping, in press*.
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Paper Both music and language are sequences of discrete elements that are organised according to “syntactic” rules. It has been proposed that syntactic processing in music and language shares cognitive and neural resources. The overlap of cognitive resources is supported by interactions and transfer effects between musical and linguistic syntax processing. The neural location of the shared operations is, however, not yet fully clarified.

The present dissertation investigated whether the inferior frontal gyrus (IFG) and the superior temporal gyrus (STG) represent anatomical convergence zones of syntax processing in music and language by means of event-related potentials (ERPs). The “Early Right Anterior Negativity” (ERAN) and the “Early Left Anterior Negativity” (ELAN) that are elicited by syntactic violations in chord progressions and sentences respectively were studied. Experiment 1 investigated whether lesions in brain regions that are essentially involved in the processing of linguistic syntax lead to parallel deficits in the processing of musical syntax. To this end, the ERAN was measured in two patient groups with lesions in the left IFG or the left anterior STG and compared with data of healthy controls. In Experiment 2, ERPs were recorded from subdural grid-electrodes, the electrocortical equivalents of the ERAN and ELAN were identified, and their generators were localised and compared by means of distributed source modelling.

The combined results indicate an overlap of musical and linguistic syntax processing within the left IFG as well as the STG in both hemispheres, thus, identifying these structures as anatomical correlate of shared syntactic processing components in music and language.

Referat Sowohl Musik als auch Sprache bestehen aus Einzelementen die gemäß “syntaktischer” Regeln angeordnet sind. Es wird angenommen, dass Syntaxverarbeitung in Musik und Sprache gemeinsame kognitive und neuronale Ressourcen nutzt. Die Überschneidung kognitiver Ressourcen wird durch Interaktions- und Transfereffekte zwischen musikalischer und sprachlicher Syntaxverarbeitung belegt. Die neuronale Lokalisation der gemeinsamen Operationen ist jedoch noch nicht vollständig geklärt.

Die vorliegende Dissertation untersuchte mittels ereigniskorrelierter Potenziale (EKPs), ob der Gyrus Frontalis Inferior (GFI) und der Gyrus Temporalis Superior (GTS) anatomische Schnittstellen der Syntaxverarbeitung in Musik und Sprache darstellen. Die “Early Right Anterior Negativity” (ERAN) und die “Early Left Anterior Negativity” (ELAN), die durch syntaktische Verletzungen in Akkordfolgen bzw. Sätzen ausgelöst werden, wurden untersucht. Experiment 1 ging der Frage nach, ob Läsionen in Hirnarealen, die grundlegend an der Verarbeitung sprachlicher Syntax beteiligt sind, zu vergleichbaren Defiziten in der musikalischen Syntaxverarbeitung führen. Dazu wurde die ERAN in zwei Patientengruppen mit Hirnläsionen im linken GFI oder dem linken anterioren GTS untersucht und mit Daten gesunder Kontrollprobanden verglichen. In Experiment 2 wurden EKPs von subduralen Gitterelektroden abgeleitet, die elektrokortikale Äquivalente der ERAN und ELAN bestimmt und deren Generatoren mit Hilfe verteilter Quellmodellierung lokalisiert und verglichen.

Zusammengefasst zeigen die Ergebnisse eine Überschneidung der musikalischen und sprachlichen Syntaxverarbeitung sowohl im linken GFI als auch im GTS beider Hemisphären, womit diese Strukturen als anatomisches Korrelat gemeinsamer syntaktischer Verarbeitungskomponenten in Musik und Sprache ausgewiesen werden können.

Selbstständigkeitserklärung

Hiermit erkläre ich, dass die vorliegende Arbeit ohne unzulässige Hilfe und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt wurde und dass die aus fremden Quellen direkt oder indirekt übernommenen Gedanken in der Arbeit als solche kenntlich gemacht worden sind.

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Leipzig, den 3. September 2008

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