



Annual Report 2003

Max Planck Institute of Cognitive NeuroScience Leipzig

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ANNUAL REPORT 2003

PREFACE

2003 was a milestone for the future of our institute. Founded in 1994, it will now, after a decade of rapid scientific developments, merge into a larger institute, one more visible on an international scale. Its new name reads: **Max Planck Institute for Human Cognitive and Brain Sciences**. By approval of the Senate of the Max Planck Society (MPS), the new center is realized by bringing together the prestigious Max Planck Institute of Psychological Research (Munich) and the Max Planck Institute of Cognitive Neuroscience (Leipzig).

The MPS anticipates that this concentration of resources will facilitate a scientific synergy that is certain to have a pronounced impact upon the national and international cognitive and neurosciences communities.

From January 2004 on, Prof. Wolfgang Prinz, presently director of the Munich institute, will become a member of the board of directors at the new institute. Until the end of 2006, when the Munich institute will move to Leipzig, we will have branches located in both Munich and Leipzig.

To house the new center, an annexe will be built on a plot that adjoins the present site of the Leipzig institute, providing unique conditions for joint interdisciplinary research into the behavioral and neurobiological bases of human cognition.

Research will address human cognitive and cerebral processes, with particular emphasis given to language, music, action, and executive functions. Presently, we are on the way to extending the neuroimaging domain by a directorship in the field of NMR-physics.

In this context we should mention that in 2003 another 3-Tesla magnetic resonance tomograph (TRIO, Siemens) was delivered which one day will replace the 'old' 3-Tesla NMR system (Bruker) which has now been working for more than 7 years.

Angela D. Friederici D. Yves von Cramon Leipzig, February 2004

















Siemens MAGNETOM Trio

The 3T cryo-cooled magnet is 2 meters long, weighs approximately 10 tonnes, and has a 60 cm-wide bore for the patient. A whole-body gradient system can generate a maximum gradient amplitude of 40 mT/m along each of the 3 Cartesian axes with a minimum rise time of 200 μ s. Eight parallel RF receive channels can be operated simultaneously. Standard and custom-made pulse sequences permit all kinds of anatomic, functional, and metabolic investigations.

PREFACE

1	ORGANIZATION OF THE INSTITUTE		9	
2	RESEARCH		17	
	2.1	NEUROCOGNITION OF LANGUAGE PROCESSING	17	
	2.2	NEUROCOGNITION OF LANGUAGE LEARNING	41	
	2.3	NEUROCOGNITION OF MUSIC	57	
	2.4	NEUROCOGNITION OF PROSODY	65	
	2.5	CLINICAL AND EXPERIMENTAL NEUROPSYCHOLOGY	79	
	2.6	FUNCTIONAL NEUROANATOMY OF THE FRONTAL LOBE	107	
	2.7	NUCLEAR MAGNETIC RESONANCE	127	
	2.8	MATHEMATICAL METHODS IN FMRI	141	
	2.9	MEG AND EEG: SIGNAL ANALYSIS AND MODELING	149	
3	OTHE	ER ACTIVITIES	163	
4	DEGR	REES AND AWARDS	183	
5	PUBL	ICATIONS	185	
6	INDE	X OF NAMES	227	

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2

NEUROCOGNITION OF LANGUAGE PROCESSING 2.1

The research in this group continued to specify the neural network underlying language processing in its different functional subcomponents and in their relative time course of activation.

The *functional neuroanatomy* of the inferior frontal gyrus has repeatedly been reported to support different aspects of language processing, both in production and comprehension. Different portions of it may serve different functions, as some of our fMRI studies suggest. It was demonstrated that the superior portion of the left BA 44 (Broca's area) is involved in phonological processing (2.1.1), and that the inferior tip of BA 44 activates as a function of access to grammatical gender (2.1.2). The superior portion of Broca's area (BA 44) together with parietal regions display an activation increase when syntactic ambiguous regions are processed, suggesting a functional relation to syntactic working memory (2.1.3). This functional neuroanatomy of BA 44 was demonstrated in a study crossing syntactic complexity and working memory load (2.1.4). An adjacent area in the inferior frontal gyrus, namely BA 45, was shown to be involved in lexical-semantic processes, though to different degrees, as a function of task demands (2.1.5). Moreover, bilateral activation in the inferior frontal gyrus was found for the processing of spoken word whose emotional meaning did not coincide with the emotional meaning value of the processo (2.1.6).

The *timing aspects* of syntactic, semantic, and prosodic processes were studied in a number of experiments. To test the notion of primacy of local structure building of syntactic processes over other processes as assumed by Friederici (2002), the multiple-response speed-accuracy trade-off (SAT) technique was used in one experiment. This method revealed that word category information necessary for local structure building is processed prior to subject-verb agreement information supporting the model (2.1.7). In an ERP study conducted in French, investigating the processing of local phrase structure violations and semantic violations in separate sentences and in doubly violated sentences provided additional support for a syntax-first model (2.1.8).

The processing of syntactic reanalyses of object-initial sentences was investigated for case marked sentences (2.1.9), and for sentences containing ambiguous noun-phrase and a disambiguating sentence final verb (2.1.10). The latter study indicates principled differences between reanalyses towards accusative- and dative-initial structures and the former was able to demonstrate that licensing of non-canonical structures is a late,

rather than an immediate process. The comprehension of temporarily ambiguous sentences has been found to vary interindividually, and to depend in part on the subject's working memory capacity (2.1.11). A new approach to classify interindividual differences was undertaken with the analysis of individual alpha frequency (IAF). It was demonstrated that different IAF based groups differed systematically in processing ambiguous sentences independent of whether the ambiguity was syntactic- or sentence-level semantic (2.1.12).

Two ERP studies evaluated the role and interplay of phonological, morphological, and semantic and syntactic aspects for lexical processes. One study investigated the appreciation of phonological, morphological, and semantic cues for the processing of syntactic gender in German (2.1.13). Another study found that prosodic cues are used to functionally differentiate between plural morphemes and linking element in compounds, even though they are identical in their graphemic form (2.1.14).

Three studies focus on auditory aspects of processing investigating the brain basis of binaurally and monaurally perceived sounds (2.1.15), differences in processing pitch information in speakers of a tonal and non-tonal language (2.1.16), and the effect of reduced acoustic input due to cochlear implant on the processing of language (2.1.17).

Last but not least, some studies follow a line of research investigating the processing of gestures, that is either gestures that carry a meaning in themselves, or gestures which are tool-related. An N400, a component known to reflect semantic processes, was observed when a tool was wielded by a hand mismatched the target object (2.1.18). The processing of meaningful gestures compared to meaningless gestures also elicited an N400 (2.1.19). Using similar items, an MEG study (see section 2.9) identified the underlying neural network of meaningful gesture recognition, suggesting a marked right hemispheric predominance.

2.1.1

Heim, S. & Friederici, A.D.

The time course of brain activity during phonological processing in a frontotemporal network

Neuroimaging studies (Burton et al., 2000; Thierry et al., 1999; Zatorre et al., 1996) provide evidence for the involvement of a left-lateralized fronto-temporal network activated during phonological processing in language comprehension, consisting of the superior portion of BA 44 (Broca's area) and the posterior portion of the superior temporal gyrus (pSTG, Wernicke's area). In this network, the peak of the BOLD response in Wernicke's area precedes that in Broca's area by approximately 3 seconds. Recently, we were able to demonstrate that in language production the same network is activated (Heim, Opitz, Müller & Friederici, 2003; cf. Figure 1). Here, we analyzed the time course of the BOLD signal in left Broca's and Wernicke's area. Our results reveal that, although the same network is involved in production and comprehension, the temporal dynamics is reversed (Figure 2). In production, there is a primacy of activation in Broca's compared to Wernicke's area. This effect is of the same size as in comprehension (i.e.,

approximately 3 seconds). The results can be interpreted with respect to the functionality of the different regions within the shared network, with Wernicke's area being the sound form store and Broca's area a processor necessary to extract relevant phonological information from that store.



Figure 1. Statistical parametric maps (SPM{z}) of the activations in the conjunction analysis representing phonological processing, superimposed onto a high-resolution 3D MDEFT scan of a representative individual brain. The colored scale bars indicate the activation strength. The displayed sections were taken at x=-47 (sagittal) and z=26 (axial) in Talairach coordinate space.



Figure 2. Time-to-peak of the modelled BOLD response in a 10-second time-window as a function of region and task.

Strategies modulate brain activation in metalinguistic decision tasks: The inferior frontal gyrus in focus

2.1.2

Heim, S. & Friederici, A.D.

Research investigating the neural correlates of grammatical gender processing has provided contradictory evidence with respect to activation in the left inferior frontal gyrus (IFG). Whereas Friederici, Opitz & von Cramon (2000) and Heim, Opitz & Friederici (2003) observed activation in the inferior tip of the left BA 44 for judgments of word class, word category, and grammatical gender in German, Miceli et al. (2002) reported the involvement of the superior portion of Broca's area (BA 44/45) for grammatical gender judgments in Italian. However, the subjects in the Miceli study reported a verbalization strategy to solve the task, i.e., they silently produced the definite determiner of the Italian nouns. As Heim et al. (2002) demonstrated, the overt production of determiners is related to activation comparable to that in the Miceli study.

In the present event-related fMRI experiment, we sought to resolve this controversy by taking into account different processing strategies reported by the subjects in a posthoc interview (i.e., silent production of the definite determiner or direct access to the gender information). The participants performed two tasks, a gender judgement of German nouns and a non-lexical baseline task. Depending on the strategy, we observed different patterns of activation in the left IFG. Direct access to gender information yielded activation in the inferior tip of BA 44, whereas the verbalization strategy produced activation in the superior portion of BA 44, BA 45/46, and the fronto-median wall (Figure 3). Thus, our results confirm the hypothesis that syntactical processing is really related to activation in the inferior tip of BA 44, whereas verbalization strategies may alter the activation or recruit different or additional brain regions.



Figure 3. Statistical parametric maps (SPM $\{z\}$) of the activations in the contrast GEN–BASE for the total sample (left column), the verbalizers (middle column), and the non-verbalizers (right column), superimposed onto a high-resolution 3D MDEFT scan of a representative individual brain.

2.1.3 Neural correlates of syntactic ambiguity in sentence comprehension for low and high span readers

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Syntactically ambiguous sentences have been found to be difficult to process, in particular for individuals with low working memory capacity (e.g., Friederici et al., 1998; MacDonald et al., 1992). The current study used fMRI to investigate the neural basis of this effect in the processing of written sentences. Participants with high and with low working memory capacity read sentences with either a short or long region of temporary syntactic ambiguity while being scanned.

A distributed left-dominant network in the perisylvian region was identified to support sentence processing. Within this network, only the superior portion of Broca's area (BA

44) and a parietal region showed an activation increase as a function of the length of the syntactically ambiguous region in the sentence. An interaction of working memory span, length of the syntactic ambiguity, and sentence complexity was seen only in one area, i.e., in the superior portion of BA 44 (see Figure 4). In this area, the activation increase for syntactically more complex sentences only became significant under longer regions of ambiguity, and for low span readers only. This finding suggests that neural activity in BA 44 increases during sentence comprehension when processing demands increase, be it due to syntactic processing demands or by an interaction with the individually available working memory capacity.



Figure 4. Interaction of working memory span, length of ambiguity, and sentence complexity found in the superior portion of BA 44. Brain area shown displays the activation seen during processing of the critical sentence region. The brain region showing the significant interaction effect is indicated.

Shared neural substrates for syntax and verbal working memory

There is an ongoing debate in the neuropsychology of language whether sentence processing and verbal working memory make use of the same cognitive resources (Just & Carpenter, 1992) or whether these two aspects of language rely upon separate cognitive resources (Waters & Caplan, 1999). This debate hinges on the question of whether or not an interaction between verbal memory load and the processing difficulty of sentences varying in their structural complexity can be found in behavioral measures. The question of whether or not syntax and verbal working memory interact is, however, also relevant at the neural level. If one assumes that shared cognitive resources are involved in two distinct cognitive processes, it is expected that these two processes should also draw upon the same brain areas (e.g., Friston, 1999). In the present study (see Figure 5A) using functional magnetic resonance imaging, we demonstrated that such an interaction is seen in the haemodynamic responses elicited in one brain area that is implicated in both domains, namely the pars opercularis of the left inferior frontal gyrus – i.e., Broca's area (Figure 5B). In this brain area, more activation for complex compared to simple sentences is seen only under conditions of low additional working memory load, activation is equally high for the different sentence condition when additional working memory load is high. This finding suggests that Broca's area provides cognitive mechanisms, which subserve both sentence comprehension and verbal working memory maintenance.

2.1.4

Fiebach, C.J. & Friederici, A.D.



Figure 5. (A) Experimental design of the present study. Participants memorized either one or six letters, while they read easy or complex German sentences. After reading the sentences, participants performed either a sentence comprehension task or a memory task. (B) Interaction of memory load and syntactic complexity elicited in the left inferior frontal gyrus (p<.001).

2.1.5 The role of the left inferior frontal cortex during semantic priming: Evidence from implicit and explicit semantic priming tasks

Kotz, S.A.¹, Fiebach, C.J.¹, Cappa, S.F.² & Friederici, A.D.¹

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While several imaging studies have suggested that BA 45 of the left inferior frontal cortex (IFG) is involved in semantic processing, only a few studies have explored to which degree the activation within this region varies as a function of task demands when processing semantic information. For example, Roskies et al. (2001) have shown that left inferior frontal activation can scale as a function of task demand. Thompson-Schill and colleagues (1997; 1999) reported modulation of this area during selection of semantic information. Recently, Kotz et al. (2002) have argued that BA 45 is engaged during auditory semantic priming in a lexical decision task.

In order to test the role of the inferior frontal cortex during auditory semantic priming, we tested semantic priming as a secondary process under more (semantic categorization) or less (animacy judgment) demanding task conditions. To this end, the same stimulus material as in the previous reported auditory primed lexical decision task (Kotz et al., 2002) was used. Subjects responded either to targets that were "eatable" or "drinkable"



Figure 6. Displayed on the left side of the graph is in sagittal view (x=-39) the activation pattern for semantic priming (unrelated > related) in the semantic categorization task and on the left side of the graph also in sagittal view (x=-37) the activation pattern for semantic priming in the animacy judgment task.

(semantic categorization) or to animate targets (animacy judgment). The semantic priming effect in each task was calculated for the non-targets only.

Results reveal that the activation in the left inferior frontal cortex due to semantic priming varies as a function of task demands. While semantic priming is largest in the lexical decision task and smaller but overall comparable in the animacy judgment task, semantic priming in the semantic categorization task was strongly reduced.

This direct comparison of semantic priming as a secondary process in an implicit and an explicit semantic task shows that activation of the left IFG is more enhanced in implicit semantic tasks than in explicit semantic tasks.

Gender differences in the activation of inferior frontal cortex during emotional speech perception

Previous event-related potential studies (Schirmer & Kotz, 2003; Schirmer, Kotz & Friederici, 2002) indicate that emotional prosody influences word processing and that this influence is mandatory in women, but not in men. The present experiment was set out to investigate the brain regions that mediate the influence of emotional prosody on word processing. To this end, male and female participants listened to positive and negative words that were spoken with happy or angry prosody. Hence, emotional prosody and word valence were either congruous or incongruous. Functional magnetic resonance imaging (fMRI) was performed, while participants listened to emotionally congruous and incongruous speech evaluating the emotional valence of either prosody or word meaning. An fMRI contrast between congruous and incongruous presentations was



Figure 7. This figure illustrates the contrast between congruous (i.e., positive words spoken with happy prosody, negative words spoken with angry prosody) and incongruous presentations (i.e., positive words spoken with angry prosody). This contrast revealed bilateral activity in the inferior frontal gyrus (IFG) in women only. A comparison between men and women revealed significant gender differences with respect to the effect in the left IFG.

2.1.6

Schirmer, A., Zysset, S., Kotz, S.A. & von Cramon, D.Y. conducted to identify the structures that mediate the interaction of emotional prosody and word valence. This contrast revealed increased activity in the bilateral inferior frontal gyrus (IFG) for incongruous as compared to congruous trials. With respect to the left IFG, this activity was significantly larger in women than in men. Moreover, the congruence effect was significant in women whereas it only appeared as a tendency in men (see Figure 7). As the left IFG (i.e., BA 44/45) has been repeatedly implicated in semantic processing, these findings are taken as evidence that semantic processing in women is more susceptible to influences from emotional prosody than is semantic processing in men. Moreover, the present data suggest that the left IFG mediates increased semantic processing demands imposed by an incongruence between emotional prosody and word valence.

2.1.7 On the primacy of word category information: Direct time course evidence

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Event-related potential (ERP) measures have provided convincing support for models of language comprehension assuming an initial stage of (post-phonological) processing drawing exclusively upon word category information (Friederici, 2002). The present study employed the multiple-response speed-accuracy trade-off (SAT) technique to compare the time course of ungrammaticality detection for word category (1a) and agreement violations (1b). The corresponding grammatical control conditions are shown in (1c).

- (1) a. *Das ist die Sauce, die du Verfeinerung. *This is the sauce that you as refinement.*
 - b. *Das ist die Sauce, die der Koch verfeinerst. *This is the sauce that the chef refine*_{25G}.
 - c. Das ist die Sauce, die der Koch/du verfeinert/verfeinerst. This is the sauce that the chef/you refines_{3SG}/refine_{2SG}.

SAT functions for the two violation types are shown in Figure 8. Visual inspection suggests that the word category violation rises to terminal (asymptotic) accuracy more quickly than the agreement violation. This impression was confirmed by the fitting of the data to an exponential approach to a limit (d'(t) = $\lambda [1-e^{-\beta(t-\delta)}]$ for t> δ , 0 otherwise) which provides three crucial parameters: asymptotic accuracy (λ), rate of rise (β) and intercept, i.e., departure from chance performance (δ). The β and δ parameters collectively characterize the dynamics of the function, i.e., the speed of processing. Indeed, the data were best fit by a model assuming an earlier intercept for the word category condition, thereby yielding an estimated dynamics difference ($1/\beta+\delta$) of 360 ms between the two violation types, which cannot be explained in terms of length

differences (estimated dynamics difference due to length: 110 ms). These findings thus provide strong converging support for an initial stage of (post-phonological) comprehension, in which only word category information is drawn upon.



Figure 8. SAT functions for word category vs. agreement violations.

The functional interplay between syntax and semantics: ERPs evidence from spoken French

The present study focuses on the functional interplay between the syntactic (i.e., phrase structure information) and lexical-semantic (i.e., selectional restriction information) processes during the comprehension of spoken French sentences by using event-related brain potentials (ERP) as the dependent variable. ERPs were continuously recorded while 20 native speakers of French listened to either correct or semantically and/or syntactically incorrect French sentences (i.e., violation paradigm). Participants performed an off-line judgment of grammaticality at the acoustic offset of each sentence. Doubly semantically and syntactically anomalous sentences [e.g., Le fauteuil qui est dans la <u>dort</u> (The garniture which is in the is sleeping)] provide a critical test for investigating the functional interplay between syntactic and lexical-semantic processes. Following the Helmholtz's superposition principle, an interaction of these processes should be attested by ERP effects in the doubly anomalous sentences (i.e., combined condition) that do not approximate the summation of the ERP effects of each type of anomaly in isolation from other. The ERP data showed that violations of the selectional restriction information (i.e., semantic condition) elicited an N400 component. A triphasic "anterior negativity (AN)-N400-P600" sequence was found in both the syntactic and the combined conditions. The absence of difference between the N400 effect in the syntactic and in the combined conditions indicates that the N400 found in the combined condition did not reflect a problem of lexical-semantic integration (see Figure 9). This triphasic AN-N400-P600 sequence was replicated in a second experiment by using a different pool of 80 critical French sentences. In sum, the present data suggest that semantic and syntactic processes do not interact during the processing of spoken French sentences. However, we cannot conclude that these processes are totally independent as phrase

2.1.8

Isel, F., Hahne, A. & Friederici, A.D.

structure violations were able to *block* subsequent lexical-semantic integration. This unidirectional influence gives strong support to syntax-first models, which postulate that a correct phrase structure is a *precondition* for lexical-semantic integration process to take place.



- Correct condition --- Combined condition --- Semantic condition

Figure 9. Grand average ERPs for the correct, semantic, syntactic, and combined conditions. Negative voltage is plotted up.

2.1.9 Scrambling as an interface phenomenon

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One of the most hotly debated topics in German syntax concerns the nature of the trigger for clause-medial argument order variation ("scrambling"; cf. 1b), if, indeed, there is one. While some researchers have proposed that scrambling is licensed (triggered) via the interaction between the syntax and other domains (e.g., phonology) (e.g., Büring & Gutiérrez-Bravo, 2001), others have assumed that scrambling occurs where the syntax does not forbid it (e.g., Haider & Rosengren, 2003). From the latter perspective, scrambling is non-triggered, but may be exploited at the grammatical interfaces where required.

- (1) a. Canonical argument order (NOMINATIVE-ACCUSATIVE)
 ... dass <u>der Kanzler</u> den Präsidenten begrüßte.
 ... that [the chancellor]_{NOM} [the president]_{ACC} greeted
 - ' ... that the chancellor greeted the president.'

- b. Scrambled argument order (ACCUSATIVE-NOMINATIVE)
 - ... dass den Kanzler der Präsident begrüßte.
 - ... that [the chancellor]_{ACC} [the president]_{NOM} greeted
 - ' ... that the president greeted the chancellor.'

The two approaches differ in their predictions regarding language comprehension. Assuming immediate licensing (in a suitable context), scrambling (1b) should not engender additional processing cost in comparison to the canonical argument order (1a) at the position of the scrambled argument. Licensing at the interface, by contrast, predicts that there should be an initial penalty for scrambled orders, which is reduced at a later processing stage.

These predictions were pitted against one another in an ERP study involving contrastive (context-induced) readings of the scrambled argument. While contextual support increased the acceptability of the object-initial sentences (as measured via a behavioral task), a local processing penalty in the form of a negativity at the position of the fronted object remained (Figure 10). It thus appears that the licensing of scrambled structures is a late, rather than an immediate process, thereby supporting models assuming interface-based licensing.



Figure 10. Grand average ERPs at the position of the critical first argument (onset at the vertical bar) for subject- (solid line) vs. object-initial (dash-dotted line) sentences in a contrastive context. Negativity is plotted upwards.

2.1.10 Qualitative differences in syntactic reanalysis: Accusative vs. dative case

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Syntactic reanalysis mechanisms have typically been associated with the P600 eventrelated potential (ERP) component in the psycholinguistic literature. However, recent findings have shown that, under certain circumstances, the reanalysis of syntactic function ambiguities in German engenders an N400 (Bornkessel, 2002; Schlesewsky & Bornkessel, in press). Notably, this effect arises when the reanalysis entails a revision towards a dative-initial word order (rather than towards an accusative-initial order as in most previous studies).

The conclusions to be drawn from previous comparisons between reanalyses eliciting a P600 and those eliciting an N400 effect are constrained by two factors: all were undertaken across experiments and involve sentences of slightly differing structure. The present study therefore aimed to compare the two reanalysis types within a single experiment and in identical sentence structures. Examples of the critical sentence types are shown in (1a) and (1b) for accusative and dative verbs, respectively.

- (1) a. ... dass Dietmar Tänzerinnen <u>besucht/besuchen</u>, obwohl that Dietmar_{NOM/ACC/DAT.SG} dancers_{NOM/ACC/DAT.PL} visit_{SG}/visit_{PL}, although ...
 - b. ... dass Dietmar Tänzerinnen <u>dankt/danken</u>. ... that Dietmar_{NOM/ACC/DAT.SG} dancers_{NOM/ACC/DAT.PL} thank_{SG}/thank_{PL}, although ...

ERP responses at the position of the critical verbs (underlined) are shown in Figure 11. As is evident from the figure, reanalysis engendered by an accusative verb elicits a P600 effect (Panel A), whereas reanalysis engendered by a dative verb is reflected in an



Figure 11. Grand average ERPs for object-initial (dash-dotted line) vs. subject-initial (solid line) sentences at the position of the disambiguating verb (onset at the vertical bar) for accusative (A) and dative (B) verbs. Negativity is plotted upwards. The topographical maps show the distribution of the effects (object-initial – subject-initial).

N400 effect (Panel B). These findings therefore indicate that the qualitative differences between reanalyses towards accusative- and dative-initial structures previously reported are indeed principled differences between the two construction types, rather than epiphenomena of other types of cross-experiment variation.

Individual differences in the 'lexicon context' trade-off in lexical ambiguity resolution during sentence processing: Inhibiting working memory

2.1.11

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The experiment assessed the relation between inhibitory mechanisms underlying working memory (WM) and the influence of internal cognitive trade off between lexicon and context factors in sentence processing (see Perfetti & Hart, 2001). It has been suggested that whereas high span persons take lexicon information more into account than contextual information, low span persons show the opposite effect. The current experiment followed the basic design of Gunter et al. (2003). Participants with high and low WM-span were presented with experimental sentences. They were shown sentences that began with an ambiguous noun, and the meaning of this word was cued three words later by another noun. The cueing was then followed by a verb. In half of the cases the verb disambiguated the meaning of the homonym to the expected meaning (i.e., congruent with the disambiguation-cue), and in the other half, the verb did not disambiguate the meaning (i.e., subjects had to switch meanings). In contrast to Gunter et al.'s (2003) original experiment, the filler items were unambiguous. It was expected that manipulating the global experimental setting would emphasize the influence of the lexical factor on WM-content. Because less ambiguous information was presented in the current study, less disambiguation on the basis of sentential context was necessary, thus making it less valid information for choosing which meaning would be needed at



Figure 12. ERPs for the noun position where the disambiguation-cue was given. The solid line shows the ERPs elicited by the dominant cueing, whereas the dashed line shows the subordinate cueing. The left panel presents the data of the 15 low span participants, and the right panel of the 15 high span participants.

29

the cue-position of the experimental sentences (i.e., the content of WM). As predicted, the ERP-data at the cue position indicated that both high and low span subjects took lexicon information into account. Both groups showed a smaller N400 component for cueing toward the dominant meaning, suggesting that this meaning was active in WM. In contrast, in the original experiment only the high span subjects manifested this effect.

2.1.12 Individual alpha frequency reflects interindividual differences in language comprehension

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The influence of interindividual differences in verbal working memory capacity on language comprehension remains controversial not only due to conflicting experimental findings, but also in view of the difficulty associated with determining which measure should be used in participant classification. We propose that an electrophysiological measure, individual alpha frequency (IAF), may be a suitable means of classifying interindividual differences in sentence processing. Interindividual differences in IAF have been shown to correlate with performance on memory tasks and speed of information processing (cf. Klimesch, 1999).

In two experiments using event-related brain potentials (ERPs), IAF-based participant groups differed systematically with regard to the processing of ambiguous sentences



Figure 13. Grand average ERPs for unambiguous (solid line) vs. ambiguous (dash-dotted line) sentences (grammatical function ambiguity) throughout the ambiguous region for participants with a low (A) and a high IAF (B).

Figure 14. Grand average ERPs for unambiguous (solid line) vs. ambiguous (dash-dotted line) sentences (quantifier scope ambiguity) throughout the ambiguous region for participants with a low (A) and a high IAF (B).

such that the low IAF group showed a sustained positivity in the ambiguous region, while the high IAF group did not. These interindividual differences were independent of whether the ambiguity was syntactic (Figure 13) or sentence-level semantic (Figure 14). Moreover, they were reliable only when participants were classified according to IAF, but not in classifications based on reading span, speed of processing (reaction time) or accuracy of processing (error rate).

Phonological, derivational-morphological, and semantic aspects of grammatical gender processing in German

Controversial evidence in event-related potential studies has lead to a new discussion about lexical and/or semantic processing of grammatical gender information. At the sentence level, Gunter et al. (2000) postulated rapid and highly automatic lexical processing of gender information manifested in a left anterior negativity (LAN) followed by a positivity around 600 ms (P600). At the word level, Hofmann et al. (2002) showed an N400 effect reflecting lexical-semantic processing. One can state that the processing of grammatical gender information is more lexical or more syntactic dependent on the level of processing. Only the sentence level appears to induce syntactic rule application. Levelt et al. (1999) proposed that conceptual and syntactic features of a noun are stored in the mental lexicon. Therefore, a differentiation between both levels in the narrowest

2.1.13

Hofmann, J., Friederici, A.D. & Kotz, S.A.



Figure 15. Displayed are the scalp distributions of difference waves of the phonological, derivational-morphological, and semantic condition at the proposed gender processing stages. Negativity is colored in blue, positivity in red. sense is not necessary. An interesting question though is whether phonological gender cues can trigger gender processing as reflected in the LAN component already at the word level.

The current experiment investigated grammatical gender information at the word level with different gender information categories (phonological – PHON [phonologically marked with single phonemes], derivational-morphological – MORPH [phonologically marked with whole syllables and carrying categorical-semantic information] and semantic – SEM [carrying only categorical-semantic information]). ERPs were recorded from 64 electrodes. An N400 congruency effect (300-500 ms) for incongruent versus congruent items was observed for all gender information categories. An additional analysis collapsing across congruency showed a LAN (300-400 ms) for PHON in contrast to MORPH, and an early negativity (300-400 ms) for PHON and MORPH as compared to SEM. These negativities may reflect processing of phonological gender information cues (in PHON and MORPH), which in turn may activate a syntactic rule system to facilitate lexical access. An N400 effect was revealed for PHON vs. MORPH and SEM. As both morphological and semantic categories contain categorical-semantic information, this effect might reflect facilitated lexical-semantic processing. In addition, a late negativity (800-1100 ms) for PHON and MORPH vs. SEM may reflect postlexical matching between phonological gender cues and lexical grammatical gender.

2.1.14The processing of German noun compounds:Prosody disambiguates linking elements and plural morphemes

Köster, D., Gunter, T.C. & Friederici, A.D.

In this study, we investigated the role of prosody during the morphosyntactic processing of compounds. It was claimed that linking elements are plural morphemes (Wiese, 1996), and this idea was tested in an event-related brain potential (ERP) study. If the claim is correct, number incongruent linking elements of compound constituents should elicit the same effects as incorrect (irregular) plural morphemes of single nouns, i.e., an N400 effect (Clahsen, 1999; Weyerts et al., 1997). It was proposed by Isel, Gunter and Friederici (2003) that the prosodic cue duration is used to differentiate between compound constituents and single nouns. For the present experiment, the prosody was (naturally) varied between compound and single noun prosody. Compound constituents and single nouns were found to differ in duration, and in fundamental frequency after 75-100 ms. During the experiment, subjects heard indefinite determiners followed by a word that was produced either as an initial compound constituent or as a single noun. The number agreement between the determiner and the word was experimentally manipulated, and had to be judged by subjects. An appropriate experimental design made sure that there was no bias for interpreting the stimuli as compounds or single nouns. The results showed an N400 effect for stimuli with a single noun prosody that was preponderant over the left hemisphere. For the compound prosody there was no effect in the same time window or earlier (see Figure 16). Hence, it is argued that linking elements are functionally distinct from plural morphemes. The results also suggest that the prosodic cues change the morphosyntactic processing of compounds in comparison with single nouns; linking elements are not interpreted as plural morphemes as it is done for single

nouns. In contrast to the N400 effect for single nouns, there was a later effect under the compound prosody. It appeared after about 1,100 ms, but showed a different scalp distribution (right-anterior). Hence, the late effect is suggested to reflect a different cognitive process and shows that it is possible to interpret linking elements numerically.



number congruent
 number incongruent

Figure 16. The ERPs for number congruent (solid line) and incongruent (dashed line) single nouns (A) and compound constituents (B1) at four selected electrodes. A negativity between 600 and 900 ms was elicited by incongruent single nouns, but not by compound constituents. (B2) an extended plot of two right hemispheric electrodes for compound constituents which shows the late right-anterior effect for incongruent compound constituents. Horizontal arrows indicate the average word length.

Hierarchical processing and activation asymmetry in the human auditory brainstem, thalamus, and cortex

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Horizontal sound localization relies on the extraction of binaural acoustic cues by integration of the signals from the two ears at the level of the brainstem. It is commonly assumed that binaural integration involves both facilitatory and inhibitory interactions between the inputs from the two cochleae. The present study was aimed at detecting the sites of these two types of binaural interaction in the human brainstem using fMRI and a binaural difference (BD) paradigm in which the responses to binaural sounds. For compared with the sum of the responses to the corresponding monaural sounds. For comparison, the experiment also included a motion paradigm similar to those used in previous fMRI studies of auditory spatial processing. The BD contrast revealed a significant binaural suppression of the BOLD effect from the level of the inferior colliculus (IC) up to the primary auditory cortex (see Figure 17). The data suggest that the suppression of the BOLD effect neural inhibition at a level below the IC, the only possible candidate being the superior olivary complex. By contrast, no facilitatory binaural responses were observed. The absence of any evidence for

2.1.15

Schönwiesner, M.^{1, 2}, Krumbholz, K.³, Fink, G.R.^{3, 4}, Rübsamen, R.², Zilles, K.³ & von Cramon, D.Y.¹ facilitation is unexpected, given current models of interaural temporal processing, and thus asks for a revision of the underlying concepts. Contrary to the BD contrast, the motion contrast yielded no significant activation, neither in the brainstem nor in the primary auditory cortex, suggesting that motion processing 'starts' in non-primary auditory cortex in humans.

We also report evidence of a hemispherical asymmetry in the activation strength of the auditory brainstem, thalamus and cortex in response to monaural stimulation (Figure 18). The monaural left and right ear stimulation resulted in a strong activation of the ipsilateral cochlear nucleus (CN), whereas the activation pattern in the higher structures was asymmetric. The inferior colliculus (IC), medial geniculate body (MGB), and auditory cortex (AC) of the left hemisphere responded stronger to the (contralateral) right ear stimulation and less strong to the (ipsilateral) left ear stimulation than the respective structures of the right hemisphere. In the right hemisphere, no such activation difference was observed. We speculate that this reflects a corticofugal modulation of the activation of the subcortical auditory structures via the massive back-projections of the auditory cortex to MGB and IC.







Figure 18. The percentage signal changes in the left- and right-side auditory structures in response to sounds presented monaurally to the left and right ear. CN cochlear nucleus, IC inferior colliculus, MGB medial geniculate body, AC auditory cortex, l left, r right.

Processing of pitch and lexical tone in speakers of tonal and non-tonal languages 2.1.16

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Differences in pre-attentive processing of lexical tone in native speakers of a tonal language (Cantonese) and speakers of a non-tonal language (German) were explored in both, a behavioral and an ERP experiment. An easy frequency contrast (tone 1 vs. tone 2) and a difficult frequency contrast (tone 5 vs. tone 6) were presented in a mismatch paradigm (see Figure 19). All stimuli consisted of the syllable /gi:/ which is a phonologically legal pseudo-word in German as well as in Cantonese (Furthermore, it does not constitute a word in English or Mandarin, which some of the participants were fluent in). Blocks of speech stimuli and blocks of sinusoidal sounds, which had the same pitch contour as the speech stimuli were presented.



Figure 19. The F0-contour of the stimuli used for the easy (left panel) and the difficult (right panel) contrast. All stimuli were spoken by the same female native speaker.

Twenty native German speakers, students of the University of Leipzig (10 male), and twenty native Cantonese speakers, students of the Chinese University of Hong Kong (10 male), participated in the behavioral experiment. The Cantonese participants had an advantage for a same-different judgment of the stimuli (see Table 1).

% Errors/RT	speech easy	speech hard	sound easy	sound hard
Cantonese Germans	6.4 [921] 5.8 [968]	13.8 [1103] 19.0 [1110]	6.4 [898] 5.0 [942]	17.7 [1090] 22.2 [1100]
Mean	6.1 [945]	15.9 [1107]	5.7 [921]	20 [1096]

Table 1. Percentage correct and with the brackets RT as found for both speaker groups in the samedifferent judgment task which had to be carried out in the behavioral experiment.

The ERP experiment, carried out on 16 German and 16 Cantonese native speakers, showed two time windows of MMN-activity which can be related to pitch processing (early time window) and contour processing (later time window). The ERPs also showed

that the Cantonese participants processed the tone information more effectively than the Germans, but group performance was similar for sinusoidal sounds. Speakers of a tonal language probably use very early and subtle parameters when processing speech information in their language.

2.1.17 Auditory processing of argument structure violations in cochlear implant users

Wolf, A. & supported by DFG

Hahne, A.

The present study investigated the processing of verb argument structure information in cochlear implant (CI) users, i.e., patients whose profound hearing loss is corrected by a direct electric stimulation of the cochlear nerve. Hearing in these patients can be restored with a proven record of success. However, as cochlear implants can provide only a reduced acoustic signal, speech understanding in CI users never reaches the same level as in normal hearers.

In a previous experiment, we demonstrated for postlingually deafened CI users that the degraded acoustic input can result in changes in auditory sentence processing with respect to syntactic phrase structure information. For the processing of this syntactic information type, we observed for the patients an N400-like negativity instead of an ERP-correlate for syntactic processing (P600) which we interpreted in terms of a semantically based comprehension strategy in CI patients. However, the critical syntactic violation in that experiment was acoustically not very salient. Therefore, the question arose whether we could find a P600 as a correlate of syntactic processing with acoustically more prominent syntactic information in CI users. Argument structure information, where the relevant syntactic information is stored in the lexical entry of the verb, provides an interesting possibility for looking at this.

Thus, in a further experiment we presented sentences containing an argument structure violation as well as correct sentences. Previous studies have shown a biphasic ERP-pattern (an N400 followed by a P600) for this type of violation (e.g., Frisch, Hahne &



Figure 20. Grand average ERPs for 16 CI users and 16 age-matched normal-hearing controls.
Friederici, in press), which we could replicate for our normal-hearing control group. In contrast, for the group of postlingually deafened CI users, we found only an N400, but no P600. This was true although behavioral data from an additional correctness judgment task revealed better error detection for the argument structure violations compared to the previously tested phrase structure violations. The current findings suggest that changes in auditory sentence comprehension can also affect processing of acoustically more prominent syntactic information, namely argument structure. The lack of a P600 as correlate of syntactic processing indicates that CI users focus less on syntactic information. Instead, they seem to rely more on semantic information.

Conceptual and structural relations in action comprehension

2.1.18

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A perceived action can only be understood when all of its elements (effectors, instruments, tools, target objects) are related to one another. These relations can be established on the basis of two types of information, namely functional knowledge about the elements, and their spatial configuration. The present study investigated the neurophysiological correlates of how these relations are built up. Participants were presented with two consecutive frames. One showed a hand wielding an instrument, and the other a potential target object of the action. The participants judged whether instrument and target matched or not. Two types of mismatch were possible. First, the spatial features of target object and instrument could not match (e.g., different orientation of screwdriver and screw). Second, a functional mismatch happened when the instrument would usually not be used on the target object (e.g., applying a screwdriver to a keyhole). To assess whether processing depends on the type of stimulus, the order in which both frames were presented was varied (instrument precedes target object or vice versa). Event-related potentials (ERPs) were recorded time-locked to the presentation of the second stimulus. As such, they reflect integration of objects (with preceding actions) in one case, and that of actions (with preceding target objects) in the other. The processing of function gave rise to an N400-like effect in both experiments. The spatial integration of objects and effectors were associated with right and left lateralized negativities of similar latency, respectively. The results provide evidence for two separate processes establishing spatial and functional relations during action comprehension.



Figure 21. Examples for the stimuli used in the experiment.

Bach, P.¹, Gunter, T.C.², Knoblich, G.¹, Prinz, W.¹ & Friederici, A.D.²



Figure 22. Evoked potentials and scalp distributions for the two types of mismatch in both experiments.

2.1.19 Emblem priming during a crossmodal language processing task: ERP-evidence

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In an earlier experiment, presented in the annual report of 2002, it was shown that meaningful hand postures, called emblems (e.g., the 'thumbs-up' gesture), give rise to a smaller N400 component than meaningless hand postures. This fits well with ERP data of language studies comparing words with non-words. Although suggestive for the role of such hand postures in communication, further research was clearly needed. Therefore, we devised a cross-modal priming task in which two word German utterances were followed 200 ms later by a visually presented emblem that either fit or did not fit the utterance. Expectancy for a certain emblem was between 60% and 100% (mean 80%; i.e., the utterance 'Well done' combined with 'Thumbs-up' had an expectancy of 100%). After the presentation of the emblem, subjects were asked to judge whether or not the spoken words and the emblem belonged together. No feedback was given. ERPs were measured during emblem processing.

The ERPs for 'correctly' answered trials showed a frontally distributed N400, which was largest when the emblem and utterance did not fit. This result is in accordance with ERP studies on semantic picture processing. If a picture does not fit a context, it will

elicit a larger N400 than when it fits. Interestingly, the ERPs for 'errors' showed a comparable pattern related to subjective fit/non-fit (i.e., the rating showed that the emblem should fit, the subject judged that it did not, and vise versa). A large centrally distributed N400 showed up for subjective non-fits compared to fits. Although the difference in scalp distribution still needs further exploration, the data suggest that indeed semantic priming of emblems is possible, thereby pinpointing their semantic properties during communication.



Figure 23. Time course of the N400 effect between 300 and 500 ms in 50 ms steps. The upper panel presents the data of the 'correctly' answered items. The lower panel represents the N400 effect elicited during 'errors'.

This year's research on language learning again investigated first and second language learning.

First language learning was investigated within a larger research context provided by a research group founded by the German Research Foundation (DFG) in which 200 infants are followed up longitudinally from birth on. About 50 infants came from families with risk for Specific Language Impairment (SLI). In the Annual Report 2002, it was reported that 4-month-old infants are able to distinguish two-syllable pseudowords with stress on the first syllable from those with stress on the second syllable. Using the same stimulus material, it was demonstrated that 5-month-old infants without risk for SLI display a mismatch response for the item with stress on the first syllable, whereas no such pattern was observed for 5-month-old infants with risk for SLI, suggesting that this paradigm can be used as an early diagnostic tool (2.2.1). The infants' ability to process prosodic information at the phrasal level was investigated in 8.5-month-old infants. It was demonstrated that processing of intonational phrase boundaries is already present in infants at this age (2.2.2). The infants' lexical knowledge and its underlying neural mechanisms were studied in a picture-word matching paradigm. Infants at the age of 19 months show a clear N400 component when a spoken basic level word does not match the object displayed in the picture presented (2.2.3). The final analysis of data from a series of experiments mentioned in earlier Annual Reports on lexicalsemantic and phrase structure building processes in children between the age of 6 to 13 years was completed. The combined data revealed that an N400 at the sentence level was present by the age of 6 years, but that syntax-related ERP components, in particular the ELAN, was not. The ELAN, reflecting early structure building processes, is observable at the age of 7 years with a decreasing latency as the age increases (Hahne, Eckstein & Friederici, submitted). The childrens' way of processing object-experienced verbs was evaluated in 11-year-old children. Children at this age demonstrate a reanalysis ERP effect, similar to adults, although with a delayed onset and prolonged duration indicating that these children do use case information for establishing a thematic hierarchy between arguments (2.2.4).

Second language learning was studied in a miniature language system as well as in full-blown language systems. In a miniature language consisting of a subset of rules of Japanese we investigated syntactic and thematic processes. Native speakers of Japanese and German-Japanese learners were tested in a violation paradigm involving a word category violation, a case violation, and a classifier violation. The ERP patterns of L2 learners resembled those of natives in the late time window (P600), but not in the earlier time windows (ELAN, N400). The findings indicate that automatic syntactic and thematic processes are not easily established in late L2 learning, even when the number of rules to be learned is small (see 2.2.5 and 2.2.6). A number of additional studies

investigated lexical processes. A first experiment focussed on the processing of nounverb ambiguous words in sentential context (2.2.7). A second series of experiments investigated the processing of words that are orthographically identical in L1 and L2, but different in meaning, using ERP (2.2.8) and fMRI (2.2.9). A third study examined L1 homonyms and their influence on L2 processing using behavioral and ERP measures (2.2.10), and, as a fourth one, interlingual homographs and their influence on L2 processing (2.2.11). The combined data indicate that L1 influences lexical processing of L2, both on the word form and on the semantic level.

2.2.1 Impaired stress pattern discrimination in infants at-risk for SLI

Weber, C., Hahne, A., Friedrich, M. & Friederici, A.D. Within the prosodic bootstrapping account it is assumed that infants acquire information about possible word boundaries in their native language through stress cues provided by the speech signal. Using a typical electrophysiological standard-oddball design it was shown that German 5-month-olds (n=23, 12 male) are able to discriminate a deviant trochaic two-syllable pseudoword (/ba:ba/) when presented among iambic standards (/ baba:/), but not vice versa (cf. Weber et al., in press). Applying the same experimental design here, we examined whether a matched subgroup of the 5-month-olds' sample as well as 5-month-old infants at-risk for Specific Language Impairment (SLI) also displayed better discrimination abilities for the trochaic item.

CVCV-pseudowords of the same total length (750 ms) were presented (standard: p=5/6, deviant: p=1/6) within two experimental runs: In the first condition, the frequently occurring iambic pseudoword /baba:/ was occasionally replaced by the trochaic deviant item /ba:ba/. In the second condition, the trochaic item /ba:ba/ functioned as the standard, whereas the iambic pseudoword /baba:/ took the deviant position.

The subgroup of infants without risk for SLI (n=6, 6 male) showed the same mismatch response (MMR) pattern as the sample examined elsewhere, i.e., these infants displayed a negative MMR for the trochaic, but not for the iambic item (Figure 1). No hemispheric



Figure 1. Left. Grand average difference waves (deviant minus standard) for the trochaic pseudoword in infants at-risk (dotted line) and infants not-at-risk for SLI (solid line). Right. Grand average difference waves (deviant minus standard) for the iambic pseudoword in infants at-risk (dotted line) and infants not-at-risk for SLI (solid line).

differences were found. In contrast, infants at-risk (n=6, 6 male) did not show a MMR to either the trochaic or the iambic item (Figure 1). Separate peak analysis for frontocentral sites revealed significant differences in MMN amplitude between groups at C3. Taken together, this result points to reduced discrimination ability for the language specific trochaic stress pattern in 5-month-old infants at risk for SLI as compared to infants without risk.

Prosodic sentence processing in infants

In a recent study conducted in adults, a specific component, the Closure Positive Shift (CPS, Steinhauer et al., 1999) was found in correlation to an intonational phrase boundary (IPh) in the listeners' event-related potential (ERP). Since then, the CPS was replicated as a reliable ERP component. Therefore, in the present study it was used to examine prosodic sentence processing in German infants as young as 8.5 months (n=39). Additionally, adult controls were tested (n=20, mean age 23,4 years).

Single sentences were auditorily presented. Two experimental conditions were constructed: The first condition (Condition A) contained only one IPh whereas the second condition (Condition B) comprised of two IPhs. As expected, the adult ERP pattern varied as a function of sentence type: Whereas sentences presented in Condition A evoked only one CPS, sentences presented in Condition B elicited two CPSs (Figure 2, right).

For the condition with one IPh-boundary (Condition A), a positive maximum around 3500 ms was seen in 8.5-month-olds (Figure 2, left). However, its latency was longer than the one observed in adults for the same condition (at about 2700 ms). For the condition with two IPh-boundaries (Condition B), infants at the age of 8.5 months displayed a first positive maximum at about 2000 ms, i.e., 400 ms later than in adults.



Figure 2. Left. Grand average ERPs for the 8.5-month-olds (n=39) in Condition A (grey line) and Condition B (black line). Condition B displays a positive maximum at about 2000 ms. Right. Grand average ERPs for the adults (n=20) in Condition A (grey line) and Condition B (black line). Condition A shows one positive shift starting around 2000 ms. Condition B displays a first positive maximum at about 1600 ms and a second one at about 3200 ms.

2.2.2

Weber, C., Pannekamp, A. & Friederici, A.D. In sum, this data suggest that prosodic processing of intonational phrase boundaries is already present in infants as young as 8.5 months. However, it seems to be slower than in adults.

2.2.3 N400 in 19-month-old infants: Processing words in picture contexts

Friedrich, M. & Friederici, A.D.

In the present study, we investigated whether the mechanisms indexed by the N400 are already existent in 19-month-old infants. Using a picture-word-matching design we recorded the infant's ERP response to slowly spoken words from basic level categories. During the experimental session, infants were looking at sequentially presented pictures while words were simultaneously acoustically presented, either congruous or incongruous to the picture. The ERPs averaged across a group of 55 infants revealed a long lasting negative incongruency effect when comparing the responses to incongruous and congruous words. Two distinct brain regions, a left parietal and an anterior one, displayed an N400-like response. Moreover, the N400 semantic incongruency effect was preceded by an early phonological-lexical priming effect, i.e., a more negative going response, at fronto-lateral electrode sites for congruous than for incongruous words. The results suggest that both lexical expectations facilitating early phonological processing and mechanisms of semantic priming facilitating integration into semantic context, are already present during early language acquisition. The strong involvement



Figure 3. ERP responses of 19-month-old infants on slowly spoken words during picture-word-matching. Grand average ERPs of (A) all infants, (B) low comprehension group, and (C) high comprehension group. Black lines for congruous and red lines for incongruous words. (D) Spatial distribution of the infant's difference wave between incongruous and congruous words within consecutive time windows of 200 ms duration.

of anterior brain regions in the N400 semantic incongruity effect seems to reflect the important part of image-specific semantic processing at that age. The specific comprehension abilities of the infants /high versus low comprehension group) are reflected in strength, latency, and hemispheric differences of the N400 incongruity effect. Spatio-temporal differences in that effect, thus, indicate changes in the cerebral organization correlated with the infant's behavioral development.

Thematic reanalysis in children and adults

A crucial aspect of language acquisition lies in disentangling the relationship between morpho-syntactic and interpretive properties of an utterance. German is optimally suited to an examination of this process, since argument interpretation in this language is not governed by linear order or agreement, but rather by morphological case marking (cf. Schlesewsky & Bornkessel, in press). Thus, the adult comprehension system exploits the knowledge that causers or agents of an action typically bear nominative, casually affected arguments bear accusative, and arguments somewhere in between are marked with dative case. However, it remains unclear whether children also use case information for on-line thematic interpretation. To examine this question, we conducted an ERP (event-related brain potentials) experiment comparing verb-final sentences with active (1) and object-experiencer verbs (2). The former require a 'canonical' assignment of thematic relations with the nominative argument outranking the dative. The latter, by contrast, have been shown to engender a 'thematic reanalysis' in the form of an early positivity because the dative experiencer 'non-canonically' outranks the nominative (Bornkessel, Schlesewsky & Friederici, 2003).

- (1) Dass [der Zauberer]_{NOM} [den Zwergen]_{DAT} dankt, weiß doch jeder.
 'Everybody knows that the wizard thanks the dwarfs'
- (2) Dass [der Zauberer]_{NOM} [den Zwergen]_{DAT} **gefällt**, weiß doch jeder. '*Everybody knows that the the wizard is appealing to the dwarfs*'

In adults, the revision of the thematic hierarchy required by the object-experiencer verbs is reflected in an early positivity (Figure 4, top). The present findings are, therefore, a replication in the auditory modality of previous findings with visual stimulus



Figure 4. ERPs elicited by active (black) and object-experiencer verbs (red), separately for adults (upper row) and children (lower row).

2.2.4

Leuckefeld, K., Bornkessel, I. & Friederici, A.D. presentation. Eleven-year-old children show a similar effect, albeit with a delayed onset and a prolonged duration (Figure 4, bottom). Thus, school-aged children do use case information for establishing a thematic hierarchy between arguments, even though the corresponding revision process is not yet as fast and automatic as in adults.

2.2.5 ERP correlates of syntactic and thematic processing in a miniature language. Part I: Japanese native speakers

Müller, J.¹, Hahne, A.¹, Fujii, Y.² & Friederici, A.D.¹

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In our study we aimed to specify ERP patterns related to syntactic and thematic processing in Japanese native speakers. Therefore, we extracted a miniature language (MINI-NIHONGO) from Japanese that consisted of only 16 elements that could be combined in sentences. The basic sentence structure is illustrated in the following example meaning "two pigeons are jumping over two cats".

s T	NP _[Nom.]	NP _[Acc.]	VP
	Ichi wa no hato ga	ni hiki no neko o	tobikoeru tokoro desu.
	One unit of pigeon _[Nom.]	<i>two units of cat_[Acc.]</i>	<i>jump over take place</i> .
	NP _[Acc.]	NP _[Nom.]	VP
	Ni hiki no neko o	ichi wa no hato ga	tobikoeru tokoro desu.
	Two units of cat _[Acc.]	one unit of pigeon _[Nom.]	jump over take place.

The rationale of the miniature language paradigm was to create a system which would allow the comparison of native Japanese speakers' syntactic processing with syntactic processing in German participants before and after training. In MINI-NIHONGO, three different violation conditions could be created. In the word category violation, a verb occurred at a position where a noun was expected. The case violation consisted of a double nominative, indicated by an incorrect case marking postposition. In the classifier violation, the numeral classifier did not agree with its head noun. Correct and incorrect sentences were presented auditorily and the participants had to give a correctness judgment after each sentence. We observed differential ERP patterns for each condition (see Figure 5).

The case and word category violation both elicited a P600. In the word category violation the P600 was preceded by a broadly distributed early negativity (100-300 ms) with an anterior maximum, in the case violation by an N400. The classifier violation led only to a left anterior negativity. In the word category violation, processing of prosodic characteristics and incorrect word category information probably contributed both to the early negativity. The P600 for this condition reflects later syntactic repair processes. Similarly, the P600 in the case violation condition indicates probably rather structural repair processes, while the N400 in this condition no P600 was observed, which is

probably due to the fact that sentences containing incorrectly classified nouns are still interpretable in Japanese. The left anterior negativity in this condition underlines the syntactic nature of classifier agreement processing.



Figure 5. ERPs of word category violation, case violation, and classifier agreement violation in native speakers of Japanese.

ERP correlates of syntactic and thematic processing in a miniature language. Part II: Before and after training

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Previous studies of rule-processing in artificial sequences (Hoen & Dominey, 2000) or languages (Friederici, Steinhauer & Pfeifer, 2002) have found ERP components (anterior negativities) which were very similar to ERPs found for syntactic processing in natural languages. This finding is surprising as it is known from studies on second language processing that syntax related ERP components, specifically ELAN or LAN effects, are typically not present in late second language learners. In the present study, we used a miniature language system (MINI-NIHONGO, cf. Part I) in order to test if the findings from artificial language learning generalize to natural language learning. We tested if the ERP components that we have observed for syntactic and thematic processing in Japanese native speakers (cf. Part I) could be acquired in a short and intensive training. Participants underwent twice the same experiment as described in Part I, once before and once after an extensive training period that comprised up to 10 hours. The after-training measurement was conducted only when a high proficiency criterion was reached.

2.2.6

Müller, J.¹, Hahne, A.¹, Fujii, Y.² & Friederici, A.D.¹



Figure 6. ERPs of word category violation, case violation, and classifier agreement violation in learners before training.



Figure 7. ERPs of word category violation, case violation, and classifier agreement violation in learners after training.

Although no differences between correct and incorrect sentences were expected before training, we observed an early, broadly distributed negativity in the word category violation condition (see Figure 6). The other conditions did not yield any differences.

After training (see Figure 7), similarly to Japanese native speakers, a large P600 occurred in the case and the word category violation condition. The word category violation led additionally to an early negativity, which did not have the anterior distribution observed for the Japanese native speakers. Other effects that have been present in the native Japanese group, namely the N400 for the case violation condition and the left anterior negativity for the classifier violation condition, could not be found in the trained subjects despite their high behavioral performance. These findings suggest that rather automatic syntactic and thematic processes are not easily established in the late acquisition of a natural language.

Native and L2 processing of homonyms in context – An ERP study

We compare native speaker English and late L2 German-English learner processing of same syntactic category (noun-nouns, e.g., *sentence*) or mixed category (noun verbs e.g., trip) homonyms in sentences with a combined reaction time (RT)/event-related brain potential (ERP) lexical decision experiment (stimulus onset asynchronies [SOAs]: 200 and 500 ms). At the 200 ms SOA, overall RT and ERP priming in the N400 time window was observed in both natives and learners, indicating multiple access for both ambiguity types (see Figures 8 and 9). At the 500 ms SOA, RTs revealed that both groups deactivated contextually inappropriate meanings. In contrast, the ERP data reflecting the brain responses registered prior to behavioral responses showed that learners had not yet deactivated inappropriate meanings (Figure 10), while native speakers had (Figure 11). In addition, for contextually appropriate meanings, native speakers showed a difference in the distribution of effects for mixed category (frontal) versus same category (central) ambiguities (compare distribution maps in Figure 11). Results suggest that when processing same and mixed syntactic category homonyms in sentences, advanced L2 learners show native-like multiple access followed by deactivation of inappropriate meanings, but learners take longer to use sentence context to select the appropriate meaning and are less sensitive to differences in ambiguity type.



Figure 8. L2 learners show multiples access: N400 priming of both contextually appropriate and inappropriate meanings can be observed at the early SOA of 200 ms.

2.2.7

Elston-Güttler, K.E. & Friederici, A.D.



Figure 9. Native speakers show the usual pattern of multiples access at a short SOA of 200 ms: N400 priming of both contextually appropriate and inappropriate meanings can be observed.



Figure 10. L2 learners still show N400 priming of both contextually appropriate and inappropriate meanings at the 500 ms SOA.



Figure 11. Native speakers show N400 priming of contextually appropriate meanings only at the 500 ms SOA.

An ERP study on L2 concreteness effects: The role of proficiency

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In an ERP experiment, two groups of German-English second language learners (high and low proficiency) were tested in L1 (German) and L2 (English) with concrete and abstract words that either maximally overlapped (cognates) in orthography or not (noncognates). Cognates and non-cognates were translation equivalents in L1 and L2. Participants decided whether a visually presented word was an abstract or a concrete word. Language presentation was realized in blocks and counterbalanced across subjects. Results reveal an N400 concreteness effect in high and low proficient L2 speakers in German. In English, highly proficient L2 learners showed a similar N400 concreteness effect as in German, however, the latency of the effect was prolonged. In comparison to highly proficient L2 learners, less proficient L2 learners showed a reduced and a latency delayed N400 concreteness effect in English relative to German. The current data imply that L2 concreteness effects vary as a function of L2 proficiency. Facilitated processing of concrete targets in L2 was demonstrated when these targets share orthographic and semantic similarities in L1 and L2 in highly proficient L2 learners.



Figure 12. Different waves display the concreteness effect for highly proficient L2 (A) learners of English and less proficient L2 learners (B) in German (black solid line) and in English (black dashed line) with a baseline (-200 ms) to stimulus onset up to 800 ms post-stimulus onset.

2.2.8

Kotz, S.A.¹ & Hernandez, A.E.²

2.2.9 Is a maus a mouse: the influence of cognate status on concreteness judgments

Kotz, S.A.¹, Hernandez, A.E.² & Friederici, A.D.¹ ¹ Max Planck Institute of Cognitive Neuroscience ² Department of Psychology, University of Houston, Houston, TX, USA

In an fMRI experiment late high proficient German-English second language learners were tested in L1 (German) and L2 (English) with concrete and abstract words that showed maximal overlap (cognates) in orthography or not (non-cognates). Cognates and non-cognates were translation equivalents in L1 and L2. Participants decided whether a visually presented word was an abstract or a concrete word. Results revealed a graded language difference in neural activity with abstract non-cognates showing the most activation differences across languages, and concrete cognates showing the least differences. In English, abstract non-cognates showed increased right hemisphere activity in the superior parietal region, the precentral gyrus, the hippocampus, and the SMA, bilaterally. In German, judgments lead to increased activity in the posterior cingulate. Smaller differences were observed when comparing abstract cognates across languages. In particular, differences were only detected in the superior parietal region, the medial SMA, and the cerebellum in English, and in the inferior frontal sulcus in German. For concrete items, the difference across languages was further reduced. Concrete noncognates showed increased activity in the precuneus in English, and the superior temporal gyrus and the superior parietal lobule in German. Concrete cognates showed increased activity in the inferior parietal lobule and in the precuneus in English. Taken together, our results show that the amount of differential neural activity across languages depends on orthographic and semantic overlap. This is consistent with the view that items which have the least semantic and orthographic overlap in a late learned second language might require the use of neural structures involved in memory retrieval.



Figure 13. Displayed in a right sagittal view (x=16) is an example of the L2 activation for abstract non-cognates > concrete non-cognates in the abstract/concrete task.

2.2.10 Language control: Translated L1 homonyms and their influence on L2 processing – An ERP study

Paulmann, S., Elston-Güttler, K.E. & Kotz, S.A.

One test to explore language control in L2 is the use of translated L1 homonyms, which has received little attention in the bilingual literature. This word type allows to test whether a common translation in the L1 is activated during L2 processing and thus allows further insight into bilingual lexical-semantic processing. The main aim of the current study was to test how controlled homonym recognition is in the L2. We conducted an English semantic priming lexical decision ERP experiment with learners of English (L1 = German) divided into high and low proficiency groups (20 each). Reaction times (RTs) and event-related potentials (ERPs) were measured on targets (e.g., *clap*) that were preceded by translated homonyms or unrelated primes (*gossip/house*). Two types of homonyms were used in the experiment: homonyms (HOM) such as *clap/gossip* (German translation = KLATSCHEN) and semantic extensions (CSE) such as *duty/inch* (German translation = ZOLL; however, *duty* is ambiguous in English, too). We predicted that if L1 influences L2 processing, *clap* should prime/ interfere with *gossip* due to a possible L1-L2 translational link. Also, if it is true that high L2 proficiency is near-native like, one could expect that low proficiency L2 learners show more priming/interference than high proficient L2 learners, due to more reliance on the L1 lexicon for low proficient L2 learners.

The behavioral results reveal a significant inhibitory effect in both groups and for both homonym types. ERPs in the low proficiency group show an "N200" priming effect for the HOM word type and a reversed effect in the same time window for CSEs, potentially indicating interference (see Figure 14). Overall, the results indicate that there is an interaction between pairs such as *clap* and *gossip*. The prediction that the low proficiency group would show more priming/interference (because they rely more on the L1) was not confirmed in the RT data. The "N200" effect suggests a lexical-translational link at the word form level. Since effects were mainly interference effects, this may suggest that translations are competitors at the word form (early ERP effect for CSEs) and at the semantic level (later RT interference effects). Taken together, the results of the experiment support the view that L1 influences L2 lexical processing at both the word form and lexical-semantic level.



Figure 14. This illustration shows ERPs elicited by critical targets at FZ electrodes. Waveforms show the average for related (blue) and unrelated (red) targets from 200 ms prior to stimulus onset up to 800 ms post-stimulus onset.

2.2.11

Paulmann, S. Elston-Güttler, K.E. & Kotz, S.A.

Language control: Interlingual homographs and their influence on L2 processing – An ERP study

We investigated the processing of lexical ambiguity to test L1 influence on L2 lexicalsemantic processing. We conducted an English (L2) semantic priming lexical decision ERP experiment with learners of English (L1 = German) divided into high and low proficiency groups (20 each). Reaction times (RTs) and event-related potentials (ERPs) were measured on targets (e.g., *boss*) that were preceded by interlingual homographs or unrelated primes (*chef/house*). Related targets were language-inappropriate translational equivalents in L1. To explore the possible effect of "natural language context" (in how far are language context cues needed/used), we presented a film in either German (L1inappropriate language) or English (L2-appropriate language) prior to the experimental run. If lexical access engages both L1 and L2 lexicons, we predicted that priming of a "false friend" would be obtained. Furthermore, according to the "Language Mode Framework" (Grosjean, 2001), one could assume to find stronger priming effects when an English film precedes the experiment.

RTs revealed a priming effect in the high proficiency group (primed by the German movie version) and a priming effect in the low proficiency group (primed by the English movie version). In addition, there was a block effect in the low proficiency group (primed by the German movie version), i.e., related pairs were responded to slower in the first half of the experiment than in the second. ERPs showed an N400 effect in the high proficiency group (irrespective of the movie version) in the first half of the experiment (see Figure 15A). The low proficiency group showed a trend towards an N400 effect in the second half, but not in the first half (see Figure 15B). Overall, the results indicate that ERP word priming effects vary as a function of proficiency. Also, both proficiency groups showed interlingual homograph-translation semantic priming effects. These effects confirm previous results (Beauvillain & Grainger, 1987; Dijkstra et al., 1999), but extend these findings to uni-lingual context priming in L2. Furthermore, the obtained results support the view that initial parallel activation of both, the L1 and L2 lexicon, upon presentation of an interlingual homograph occurs, challenging the selective access view. The implications of the Language Mode Framework by Grosjean (2001) cannot be confirmed, as priming into a specific language mode does not account for the current ERP data. Taken together, the results of both experiments support the view that L1 influences L2 lexical processing. In particular, the data imply that L2 learners are not able to consciously suppress L1 influence.





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Figure 15. These illustrations show ERPs elicited by critical targets at FZ electrodes (see difference maps for a whole head display of all measured electrodes). Waveforms show the average for related (blue) and unrelated (red) targets from 100 ms prior to stimulus onset up to 800 ms post-stimulus onset.

With the beginning of 2003, the group 'Neurocognition of Music' became an Independent Junior Research Group, enabling us to considerably intensify our investigations on how and where the human brain processes music. Main foci of the group are (a) neural correlates of processing structure and meaning in music, (b) functional neuroanatomy of auditory sensory memory and working memory for pitch, (c) investigation of emotion with music, (d) developmental aspects of music processing, (e) interactions between music and language processing, and (f) transfer-effects of musical training on language development in children.

This year, we developed new experimental designs to investigate the processing of musical structure: One study investigated electrophysiological correlates elicited by music-syntactically irregular chord functions when these chord functions did not represent a physical deviance, and when these irregular chord functions were in-key chord functions (2.3.1). The irregular chord functions elicited an early right anterior negativity (ERAN) showing that the ERAN can be elicited even without the presence of a physical deviance, and even by in-key chord functions. Another study examined the influence of short-term experience on the processing of musical structure (2.3.2) revealing that the ERAN is slightly influenced by short-term experience. A new focus of our group was the investigation of musical meaning using sentences and musical excerpts that prime a target word (2.3.3). The N400 elicited by the target words indicated that musical information can prime the meaning of a word, even when participants are nonmusicians who are naively presented with the musical excerpts. Another EEG study continued our research on music and emotion using spectral analysis of EEG data to uncover neural correlates of emotion processing (2.3.4), a complementary study was conducted using fMRI (2.3.5). Converging evidence from both experiments suggests that left-frontal cortical regions are active when listening to pleasant music.

In cooperation with the MEG group, the processing of musical phrase boundaries was investigated, revealing that the closure positive shift (CPS) that has been described for the processing of phrase boundaries in language experiments can also be elicited during the perception of music (see 2.9.11).

2.3.1 The ERAN can be elicited by (irregular) in-key chord functions

Koelsch, S. & Jentschke, S.

The present study utilizes music-theoretically described regularities of major-minor tonal music to investigate neural mechanisms underlying abstract auditory information processing. In previous studies, which used Neapolitan sixth chords as music-structural violation, Neapolitan chords not only represented a structural violation, but also a slight physical deviation (the Neapolitan chords introduced out-of-key notes). Thus, it could not be determined whether an ERAN can be elicited without the presence of a physical deviance. Therefore, an experiment with two blocks was run with 24 subjects, using a new musical paradigm: In one experimental block (a) tonic chords and (b) dominantto-dominants (DDs) were presented equiprobably at the end of a five-chord sequence. In another block, the same sequences were presented, except that DDs were replaced by (c) supertonics (STs). Both DDs and STs are functionally irregular chord functions when presented at the end of a harmonic sequence. DDs represent both a functional and a tonal violation, STs represent a functional violation only (STs are in-key chords, they do not contain out-of-key notes, and they cannot be detected as irregular on a purely physical basis). Participants (non-musicians and amateur-musicians) ignored the harmonic dimension of the musical stimulus and were asked to detect infrequently presented timbre deviants.

In both blocks, the functionally irregular chords (DDs and STs) elicited negative electric brain responses: An ERAN (maximal around 200 ms) and an N5 (maximal around 500 ms). Results indicate that ERAN and N5 can be elicited by in-key chord functions, that is, even in the absence of any physical irregularity. Thus, the ERAN elicited in the present study reflects purely music-structural processing. In an additional behavioral study, participants were asked to differentiate regular from irregular sequence endings (the group of subjects was independent from the ERP group). Participants (nonmusicians and amateur musicians) had about 80% correct responses. The behavioral data indicate that the brain responses measured in the ERP experiment were elicited by structural violations that can be detected well above chance level, but that are not clearly salient to the participants (subjects performed well below 100%-accuracy).



Figure 1. Examples of the chord sequences terminated by (A) a regular tonic chord, (B) an irregular dominant-to-dominant and (C) an irregular supertonic.



Figure 2. ERPs elicited by the regular and irregular chords (recorded at frontal electrodes): DDs compared to tonic chords (upper row), and STs compared to tonic chords (bottom row). The thick solid line indicates the ERPs elicited by the (regular) tonic chords, the dotted line depicts the ERPs elicited by the irregular chords (DDs and STs), and the thin solid line shows the difference between the two conditions.

Effects of the duration of an experimental session on music-structural processing

In our previous experiments, harmonically inappropriate chords elicited an early right anterior negativity (ERAN) reflecting the processing of complex musical regularities that have been described by the theory of harmony. In those experiments, fairly short block-durations were used to avoid a possible habituation of subjects to the irregular chords. Therefore, it remains unclear whether the ERAN is affected by the repeated presentation of irregular chords during the course of a longer experimental session. Participants presumably establish a representation of irregular sequence-endings when such endings are repeatedly presented. That is when an unexpected chord is repeatedly presented, participants might begin to expect the irregular chords. Consequently, the ERAN elicited by irregular chords should decrease in amplitude, because the ERAN is taken to reflect the violation of a musical sound-expectancy. The question of how the ERAN is affected by the duration of an experimental session sheds light on how processing of highly abstract auditory information processing is modified by shortterm experience.

In this experiment chord sequences were presented (see Figure 1 of section 2.3.1) that ended either (a) on a (regular) tonic chord or (c) on a (slightly irregular) supertonic. Note, that supertonics are in-key chords, that is, they do not contain out-of-key notes and cannot be detected simply on the basis of a physical irregularity. The experimental session had a duration of approximately 120 min (672 sequences per condition). Subjects (n=20) were watching a silent movie with subtitles under the instruction to ignore the harmonic dimension of the musical stimulus, and to detect infrequently occurring deviant instrumental timbres.

Compared to tonic chords, supertonics elicited a clear ERAN (peaking around 180 ms) with right-anterior scalp distribution. When dividing the data into 12 sub-blocks, the

2.3.2

Koelsch, S. & Jentschke, S. ERAN decreased in amplitude with increasing duration of the experimental session. As in previous experiments, the ERAN was followed by an N5 (peaking around 550 ms). In contrast to the ERAN, the mean amplitude of the N5 virtually did not change across the session. For the ERAN as well as for the N5 the differences of the regular and the slightly irregular chord endings were significant. Results indicate that the ERAN is influenced by musical short-term experience. The amplitude-decrease of the ERAN was moderate, justifying experimental paradigms in which large trial numbers are needed per subject to increase the SNR of individual data sets.



Figure 3. ERPs elicited by the slightly irregular chords compared to the regular chords, recorded at frontal electrodes. The thick solid line indicates the ERPs elicited by tonic chords, the dotted line depicts ERPs of supertonics and the thin solid line shows the difference between the two conditions.

2.3.3 Music, language, and meaning: Brain signatures of semantic processing

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Meaning is a key feature of language. Whether music can activate brain mechanisms related to the processing of meaning information has remained an unanswered question, and most linguists would reject the notion that music can transfer particular semantic concepts. The purpose of this study was to compare the processing of meaning information in language and music, investigating the semantic priming effect as indexed by behavioral measures and by the N400. Subjects listened to short musical excerpts or sentences that either did or did not prime a target word (target words were either concrete or abstract nouns, e.g., king, cellar, reality, wideness). Musical excerpts were recorded from commercially available CDs. Behavioral data indicate that subjects with no special musical training who are naively presented with particular musical excerpts similarly associated the musical excerpts with particular words. The ERP results reveal that target words, which are preceded by meaningfully unrelated musical primes compared to words, preceded by related musical primes elicited an N400 effect. This N400 priming effect did not differ between language and music with respect to time-course, strength, and neural generators. Thus, results demonstrate that the perception of musical and linguistic primes can have similar effects on the processes of semantic analysis during the perception of a target word. Musical primes presumably transferred meaning when they (a) were reminiscent to the sound or the quality of an object (e.g., low tones

associated with *basement*), (b) resembled prosodic or gestural cues (e.g., sigh), or (c) elicited stylistic associations (e.g., a church anthem priming the word *devotion*). Both, behavioral and ERP results, indicate that musical information is capable of priming representations of meaningful concepts, that is, that music can "tell" considerably more than previously believed.



Figure 4.

Music and emotion: Electrophysiological differences in the processing of pleasant and unpleasant music

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Music is a powerful tool in the investigation of emotion. The purpose of the present study was to investigate oscillations during the processing of pleasant and unpleasant music. Subjects were presented with consonant musical excerpts and their manipulated (dissonant) counterparts to induce pleasant and unpleasant emotions. Participants kept their eyes closed during the whole experiment, tapped the metre of the music with their right index finger and were asked to rate how (un)pleasant they felt after each musical piece. Furthermore, the experiment comprised silence periods to enregister a baseline condition.

Behavioral data show that participants felt rather pleasant during the presentation of consonant musical excerpts, while dissonant pieces mainly induced unpleasant emotions. Contrasting music vs. rest, data show correlates of auditory processing and motor activity: We found an overall delta synchronization during the listening condition presumably reflecting relaxation of participants. Furthermore, power spectra show a frontal theta synchronization presumably reflecting the processing of musical structure, general attention, or encoding and retrieval of the musical excerpts. In addition, a frontal beta desynchronization occurred during the listening condition, possibly reflecting precentral activity already found in a previous fMRI study (Koelsch et al., submitted). Motor activity due to the finger tapping was reflected by left central alpha and beta desynchronization and a right parietal alpha synchronization (see Pfurtscheller & Lopes da Silva,

2.3.4

Sammler, D.^{1, 2}, Koelsch, S.¹ & Grigutsch, M.¹ 1999). Contrasting the processing of pleasant and unpleasant musical excerpts, we found left frontal power differences within the delta and the upper alpha band. During listening to dissonant pieces, delta power was significantly greater and upper alpha power was significantly smaller than during the processing of consonant pieces. No differences in motor related frequency bands (beta) could be found.

Results show that the application of spectral analysis can contribute to the investigation of music perception and motor activity. Concerning the investigation of emotional processing, a divergence between different methods (behavioral, fMRI and spectral analysis of EEG data) was found. Further studies should be conducted to illuminate the importance of frontal left delta and alpha in the processing of emotions.





Figure 5. Delta/theta synchronization and beta desynchronization during the listening condition compared to the resting condition.

Figure 6. Alpha desynchronization over the left hand area and alpha synchronization over right parietal leads reflecting motor activity (music contrasted to rest).



Figure 7. Pleasant vs. unpleasant music processing. Delta power is significantly higher for unpleasant pieces, whereas upper alpha power is significantly greater for pleasant musical excerpts. No differences in motor related frequency bands (beta) could be found.

2.3.5 Investigating emotion with music

Fritz, T. & Koelsch, S. The present study investigates neural correlates of emotion using consonant instrumental dance tunes (recorded from commercially available CDs) and their manipulated, dissonant counterparts. In previous behavioral studies, the consonant tunes had been rated as "pleasant", the dissonant counterparts had been rated as "unpleasant". A previous fMRI study using these pleasant and unpleasant stimuli revealed an activation of the rolandic operculum in the left hemisphere for the contrast pleasant vs. unpleasant music. The rolandic operculum comprises the representation of the larynx, i.e., of a vocal tract articulator that is involved in vocalization. This finding suggested that the subjects coded vocal sound production (without subsequent actual movement) while hearing

the original "pleasant" tunes. Such an activation of a motor effector without actual movement is reminiscent of mechanisms of perception-action mediation described for the auditory modality in monkeys and the visual modality in both monkeys and humans. It was not possible to specify whether the lack of activation while listening to the dissonant tunes was due to the fact that they were perceived as "unpleasant" or because it is more difficult to sing along with them.

In the present study, the consonant and dissonant stimuli from the previous study were used, and additionally two additional stimulus types were employed: A reversed version of the consonant tunes as well as a reversed version of the dissonant tunes. The reversed stimuli had the same frequency spectrum as the initial tunes, but less meaningful structure.

To present the auditory stimuli in the absence of scanner noise, a sparse temporal sampling design was used.



Figure 8. (A) contrast pleasant vs. unpleasant (z>4.7), (B) contrast pleasant vs. unpleasant reversed (z>4.5)

One finding was that, as expected, contrasting the "pleasant" versus the "unpleasant" condition revealed an activation in the left rolandic operculum (Figure 8A) replicating our previous findings. A similar activation occurs when contrasting the "pleasant" versus the "unpleasant reversed" condition (which had been rated behaviourally as even more unpleasant than the "unpleasant" condition) (Figure 8B).

The data, thus, replicate our previous findings, and also show an activation of the rolandic operculum when contrasting the pleasant stimuli with an additional unpleasant condition. Furthermore, it reveals that the rolandic operculum is activated within the first second after the onsets of the pleasant stimuli. In monkeys, the postcentral aspect of the rolandic operculum is closely interconnected with the monkey motor cortex, thus, it is plausible to assume that the activation of the rolandic operculum replicated in the present study might subserve motor readiness.

With the year 2003, the Independent Junior Research Group 'Neurocognition of Prosody' completed its 4th year of existence. As in previous years, we furthered our understanding of the influence of prosody on auditory language processing and its interaction with lexical semantics, syntax, information structure, and sentential semantics. In close collaboration with our music-processing group, we also investigated the communalities and differences between speech and music processing on different levels, that is, on the level of single syllables or notes, as well as on the level of a prosodic or musical phrase. These studies, together with the studies carried out in the last three years, brought us significantly nearer to our primary goal, namely the identification of the brain basis of prosody. We have formulated a preliminary model of prosodic functions regarding the relative contribution of the two hemispheres (Friederici & Alter, in press).

Prosody on the sentence level. A new Ph.D. project started this year investigating the influence of minimal attachment structures on auditory sentence processing in bilinguals (2.4.1). A new paradigm has been developed that makes it possible to disentangle syntactic, semantic, and prosodic information with regard to the processing of prosodic phrases (2.4.2). The investigation of the interaction between informational structure, syntax, and prosodic information has been expanded to experiments demonstrating the influence of pitch (2.4.3), sentence length (2.4.4), and task parameters (2.4.5). A new project investigated the relationship of focus particles (e.g., "sogar"/even), focus accents, and semantic scope in a sentential context (2.4.6). A study compared the lateralization of hummed and normally spoken sentence materials in an fMRI measurement (2.4.7). A project started this year scrutinizing the interplay between prosodic contours, topicalization, and semantics. A study was conducted in collaboration with the University of Marseilles investigating the interaction between semantic and prosodic information in statements and interrogations (2.4.8).

Prosody on the single word/single syllable level. An innovative cross-modal word-fragment priming paradigm was developed to investigate the impact of pitch information and its relation to word stress in collaboration with the University of Konstanz (2.4.9). A project done in collaboration with the University of Leipzig investigated the impact of pitch information on the processing of artificial vowels (2.4.10).

Processing of affect and the evolutionary perspective. A Ph.D. project has started on the differentiation of affective and linguistic prosody in patients supervised by Sonja Kotz and Kai Alter. In a different new project, the influence of affective prosody on language processing is investigated comparing affectively spoken words and affect bursts in collaboration with the University of Tübingen. A third Ph.D. project in this domain started this year comparing the processing of human and non-human sounds.

Processing of speech and music. In an fMRI experiment using bi-syllabic speech- and music-like items, communalities and differences between music and speech processing were reported (2.4.11). Another study investigated the neural correlates of phrasal segmentation in music and compared it to the neural correlates of phrasal segmentation in normal speech (see 2.9.11).

Further activities. Our group organized an international workshop 'Syntax and Beyond' in collaboration with the University of Nijmegen and the University of Leipzig discussing new results and methods in sentence and prosody processing. Members of the group also contributed to the distribution of knowledge with regard to prosodic processing and experimental methods by diverse teaching activities. Kai Alter gave a one-day tutorial on 'The application of neurophysiological methods in research on prosody' at the workshop on 'Intonation and tones' at the University of Oxford in April 2003. Ulrike Toepel gave an in-house lecture on the use of software for speech recordings and speech analysis. André Szameitat gave a lecture on the use of Latex. Anja Ischebeck gave an in-house lecture on the use of data evaluation software for the analysis of a variety of experimental and corpus data. She also gave a three-day intensive course at the University of Innsbruck about fMRI data analysis in July 2003, and, also at the University of Innsbruck, a tutorial on experimental design in event-related fMRI at the "Dritter Österreichischer fMRI Workshop" in December 2003.

2.4.1

On the influence of preposition type on prosodic phrasing: An ERP investigation of relative clause attachment

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Current research in sentence processing suggests that even in silent reading, prosodic principles influence parsing decisions. Besides phrase length, the nature of the lexical elements involved affects prosodic phrasing (e.g., Lovric, 2003). The present EEG study examined visual processing of relative clause attachment ambiguities:

- **A.** Holger kannte die **Kolleginnen** \emptyset der <u>Juristin</u> die lange im Büro **waren** / <u>war</u>. Holger knew the colleagues_{pl} of-the judge_{se} who long in-the office were_{pl}
- B. Holger kannte die Kolleginnen bei der Juristin die lange im Büro waren / war.
- C. Holger kannte die Kolleginnen von der Juristin die lange im Büro waren / war.

We used a 2x3-factorial design: Factor 1 was forced attachment site (high or low via number agreement of the finite verb with either DP1 or DP2). Factor 2 was choice of preposition (*null* (the Genitives in A) vs. thematic preposition *bei* (B) vs. non-thematic preposition *von* (C)). A set of 46 sentences per condition was tested. While former studies (e.g., Hemforth, 2000) found a general high attachment preference for German Genitives, a low attachment preference for the items comparable to those in B has also



Figure 1.

been reported. The *von*-DPs were of special interest as they express the same semantic relation as the genitives, but might introduce a distinct prosodic pattern to the sentences.

Interestingly, participants did not exhibit clear attachment preferences for the Genitives: No significant differences for **A** forced high vs. forced low could be observed. In contrast, we found a preference for low attachment with both the **B** and **C** items, indicated by a fronto-centrally distributed positivity between 300 and 1.000 ms after the onset of the critical verb. The difference observed can be explained by a prosodic preference for the sentences containing a preposition (thematic or non-thematic) to lower attachment preferences.

Prosody-driven sentence processing: An ERP study

Spoken language generally provides various levels of information for the interpretation of the incoming speech stream. In a study with four experiments, we focused on the processing of prosodic phrasing, especially on its interplay with phonemic, semantic, and syntactic information.

An event-related brain potential (ERP) paradigm was chosen to record the electrophysiological responses to the processing of sentences containing differing amounts of linguistic information. The constant factor in all experiments was the presence of major intonational boundaries. To elaborate the online perception of these input-structuring boundaries, the Closure Positive Shift (CPS) has been manifested as a reliable and replicable ERP component. It has convincingly been shown to correlate to major intonational phrasing in spoken language. However, to define this component as exclusively relying on the prosodic information in the speech stream, it is necessary to systematically vary the linguistic content of the stimulus material. This was done by creating quasi-natural sentence material with decreasing semantic, syntactic, and phonemic information, i.e., jabberwocky sentences (in which all content words were replaced by meaningless words), pseudo word sentences (in which all function and all content words are replaced by meaningless words), and delexicalized sentences (hummed intonation contour of a sentence removing all segmental content). The stimulus material in all four experiments is additionally separated into two sentence conditions. A first

2.4.2

Pannekamp, A., Toepel, U., Alter, K., Hahne, A. & Friederici, A.D. condition (Condition A) contains only one major intonational boundary, whereas the second one (Condition B) contains two. Twenty to twenty-two volunteers took part in every experiment and were auditorily presented with the varying materials.

In all experimental variations, Condition A evokes one positive shift, whereas Condition B exhibits two. Thus, a CPS was identified in all sentence types in correlation to the perception of their major intonational boundaries (Figure 2) and regardless of the overall linguistic content of the materials. The independence of the evocation of the CPS thus indicates that this event-related component is driven purely by prosody.



Figure 2. Grand average ERPs for the four experimental variations illustrated at CZ. In all sentence types, Condition A (dotted line) evokes one CPS whereas Condition B (solid line) exhibits two.

2.4.3 Perception of intonational phrase boundaries in speech with flattened pitch

Hruska, C., Steinhauer, K., Alter, K. & Friederici, A.D.

In speech processing, listeners use intonational phrase boundaries for an immediate evaluation of the syntactic structure of sentences. An intonational phrase boundary can be marked by different prosodic cues such as pre-boundary lengthening, pause and boundary tone. While the last cue is based on the fundamental frequency, the other cues rely on the durational structure. The perception of intonational phrase boundaries has been shown so far when listeners get the full prosodic cues as well as after the pause removal. In all auditory experiments, the event of an intonational phrase boundary elicited the Closure Positive Shift (CPS) in the event-related brain potentials, regardless of pause removal.

In the present study, we evaluated the perception of sentences with full prosodic parameters in comparison to a flattened pitch contour (PRAAT; Boersma & Weeninck, 2001) using the paradigm of Steinhauer et al. (1999). This acoustic manipulation leaves the durational structure and the amplitude envelope unaffected.

Spoken sentences differed in their underlying syntactic structure (intransitive/transitive and cross spliced version). Acoustically unmanipulated and pitch flattened versions were presented. Participants had to judge the prosodic appropriateness of the sentence prosody after each given trial, regardless of the artificial sounding of the pitch flattened sentences. The behavioral data suggest no general effect of the pitch flattening procedure. Cross-spliced sentences were highly rejected by listeners, whereas intransitive and transitive conditions were mostly accepted. Moreover, the pitch-flattened conditions were even accepted when two prosodic cues (pitch and pause) had been removed.

In the event-related brain potentials, the CPS was measurable at each intonational phrase boundary in unmanipulated sentences as well as in pitch flattened versions (Figure 3). Nevertheless, in the condition where the pause and the pitch variation were removed, the CPS latency was shortened. Furthermore, the pitch flattening leads to a sustained fronto-central, right lateralized negativity in the ERPs (Figure 4).



Figure 3. Grand averages ERPs for transitive sentences (solid lines), the transitive condition without pause insertion (dashed lines), and cross-spliced conditions (dotted lines).



Figure 4. Evoked potentials of normal conditions (solid lines), of pitch-flattened conditions (dotted line), and the difference wave (red line). The topographical maps indicate the right lateralized effect of listerener's perception due to pitch-flattened sentences.

Thus, the ERPs give an insight into sentence processing in the absence of prosodic cues, which is not possible in offline measurements. The unnatural monotonous sentence melody leads to an additional brain activation, which was also reported in a related fMRI study as an effect of reanalysis/repair of pitch information by Meyer and colleagues (2003). Nevertheless, the durational structure (pre-boundary lengthening) can be used as reliable prosodic cue to identify syntactically based IPh-boundaries.

2.4.4 Influences of sentence length on the syntactic structure analysis

Hruska, C., Alter, K. & Friederici, A.D. In spoken language prosodic boundaries (intonational phrase boundaries) are helpful markers for the immediate analysis of the underlying syntactic structure (Nespor & Vogel, 1984; Selkirk, 1986). The perception of these intonational phrase boundaries is detectable by ERP measurements and reflected by a posterior positivity at prosodic boundaries (Steinhauer et al., 1999).

To examine the usage of prosodic cues in relation to syntactic structure in dependence of the sentence length, we presented short sentence material analogous to the material of Steinhauer et al. (1999; without the conjunctional phrase; vertical lines in the following examples denote intonational phrase boundaries).

intransitive:	Peter verspricht Anna zu arbeiten und das Büro zu putzen.		
	(Peter promises Anna to work and to clean the office.)		
transitive:	Peter verspricht Anna zu entlasten und das Büro zu putzen. (Peter promises to support Anna and to clean the office.)		
cross-spliced:	Peter verspricht Anna zu arbeiten und das Büro zu putzen. (Peter promises to support Anna and to clean the office.)		

Acoustic analyses show significant effects on duration, pause and fundamental frequency at expected fragments between the conditions. Sets of the three sentence conditions (intransitive, transitive and cross spliced) were then presented auditorily.

The analysis of behavioral data shows a clear disapproval of the cross-spliced condition, whereas the intransitive and transitive conditions were highly accepted. In the ERP measurements we detected a broadly distributed negativity at the intonational phrase boundaries in the transitive and the cross-spliced conditions. The CPS occurred only in a small time window at posterior-occipital electrodes (Figure 5).

Comparisons of initially prosodic equivalent conditions (transitive and cross-spliced condition) at the critical constituent show only the N400-effect (see Figure 6). However, the expected ERP-pattern of the syntax-prosody mismatch, the P600 component, cannot be detected. Additional analyses of subgroups sorting the participants by reading span or gender also fails to prove any differences.

In short sentences, the perception of intonational phrase boundaries are reflected by a broad distributed negativity, whereas in long sentences a prominent posterior positivity, the CPS, occurs in the ERPs. Unexpected syntactical continuations after initial prosodic structure building leads to aggravated lexical/semantic integration. Moreover, the reanalysis of the syntax-prosody mismatch seems not to be necessary in short sentences.



Figure 5. Grand-averages ERPs for transitive (blue lines), intransitive (green lines), and cross-spliced sentences (red lines). For the transitive condition, a broadly distributed negativity elicits, following by the expected posterior CPS.



Figure 6. Evoked brain potentials and topographical map of the N400-effect in the syntax-prosodymismatch condition of short sentences.

2.4.5 ERP effects in the perception of contextually embedded sentences

Hruska, C., Alter, K. & Friederici, A.D. Many studies examine the processing of speech. Nevertheless, it is less investigated so far how context information influences speech perception. In dialogue sequences, the prior contextual information can direct listener's perception of new information. The focus can be established by Wh-questions. The subsequent focused information is highlighted by word variation or prominent pitch accents in German.

Regarding the latter aspect, results of previous studies utilizing ERPs show the existence of two main effects in the perception of contextually embedded sentences: First, a frontally distributed negativity (expectancy negativity; EN) before/at the position of the focused information, and second, a posterior positivity (closure positive shift, CPS) after perceiving the focused information. The frontal distribution of the EN led us to hypothesize that it is related to memory and, therefore, the interval between context and answer sentences plays a role in the evocation of the EN.

We conducted a study with varying lengths of the question answer interval (QAI). Dialogue sequences were presented auditorily in two different QAIs (1500 ms vs. 3000 ms) in a pseudo-randomized order. In the ERPs, the EN and the CPS are both shown in the answer sentences at the positions described above. Moreover, the longer QAI leads to an enhanced EN effect, whereas the posterior CPS was not affected by the QAI variation.

Our findings suggest that frontal effects are indeed modulated by maintaining previously encountered information in the phonological working memory storage, whereas the posterior CPS is not influenced by this aspect. Furthermore, the latter result can be interpreted as evidence against the equality of the P3b component and the CPS.



Figure 7. Grand average ERPs for short and long question-answer interval (QAI).
Focus on focus: An ERP study on the processing of default and shifted accents in2.4.6German

In linguistic theory, it is assumed that focus particles like "even", "only" and "also" prototypically assign narrow focus, accent and semantic scope to the constituent following the particle. Although this seems to be the default assignment in German, too, the focus particle "sogar" (even) may also be associated with a preceding accentuated constituent. In the present ERP study, we investigated the interaction of the effects induced by the focus particle "sogar" (local prosodic structure) and the effects of global prosodic structure. The global prosodic structure was manipulated via accent on the right adjacent (default reading, Condition 1) or sentence initial word (Condition 2), no (= missing, Condition 3) accent, or double (= superfluous, Condition 4) accent.

The materials were as follows (capital letters indicate accent):

- 1) Peter verspricht sogar ANNA zu arbeiten und das Büro zu putzen. (*Peter promises even Anna to work and the office to clean*).
- 2) PETER verspricht sogar Anna zu arbeiten und das Büro zu putzen.
- 3) Peter verspricht sogar Anna zu arbeiten und das Büro zu putzen.
- 4) PETER verspricht sogar ANNA zu arbeiten und das Büro zu putzen.



Figure 8. Mean ERPs for two constituents (1st NP: Peter; 2nd NP: Anna) at two midline electrode sites (FZ, CZ) as a function of presence (solid lines) or absence (dashed lines) of prosodic accent. Left column: Effects on the 1st NP. Right column: Effects on the second constituent as a function of presence (solid arrows) or absence (dashed arrows) of prosodic accent on the first constituent.

Heim, S., Stolterfoht, B., Gunter, T.C. & Alter, K.

The results show that, independently of the presence or absence of a preceding accent, the focus particle "sogar" requires the presence of an accent on the right adjacent word (local prosodic structure). These accents evoke a fronto-central negativity around 400 ms, which is not modulated by the presence or absence of a preceding accent. Later, however, the ERP is influenced depending on whether the accent was correct, missing, or superfluous (global prosodic structure). Accents on sentence-initial words are processed with delay. This seems to be the result of the relational character of prosodic structure which needs the following word(s) to decide whether the first word bears a narrow focus accent or not. Thus, the data show that global prosodic structure is relational, but can locally be overridden by focus particles and their default assignment of focus, accent and scope to the right adjacent constituent.

2.4.7 Processing normal and hummed speech

Ischebeck, A., Alter, K. & Friederici, A.D. Natural speech contains not only segmental information essential to the understanding of the syntactic and semantic content of an utterance, but also prosodic cues, which convey, among others, information about phrase boundaries. When a naturally spoken sentence is hummed by a speaker, it retains its global intonational contour while all segmental information is lost. Investigating the communalities and differences between the activation patterns observed for normally spoken and hummed sentence materials during an fMRI measurement can, therefore, shed some light on the processing of the prosodic and segmental information contained in natural speech. Hummed sentences as well as normally spoken sentences activated the superior temporal gyrus including the primary and secondary auditory cortex bilaterally. Normally spoken sentences additionally activated regions in the posterior region of the left superior temporal gyrus, the thalamus and the cerebellum (Figure 9). It has been proposed that the two hemispheres are specialized with regard to different aspects of the auditory signal (e.g., Poeppel, 2001; Zatorre & Belin, 2001). Some evidence has been reported for a right hemispheric



Figure 9. Top row: Activation of the superior temporal gyrus bilaterally for normal and hummed speech materials, for contrasts against baseline and between activation conditions. Bottom row: A voxelwise laterality test reveals that the auditory processing of normal and hummed language is predominantly left lateralized.

specialization for intonational or sentence prosody (Gandour et al., 2003). It can therefore be assumed that the right hemisphere might be more involved in listening to hummed speech as compared to normal speech. However, a voxel-wise test of laterality revealed that normal speech as well as hummed speech is predominantly processed in the left hemisphere (Figure 9). This might indicate that the left hemisphere dominates the processing of speech and speech-like materials, whereas the right hemisphere might become more active when other materials, such as music and environmental sounds, are presented.

Brain potentials during semantic and prosodic processing in French

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The present experiment was aimed at investigating the on-line processing of semantic and prosodic information. We recorded the event-related brain potentials (ERPs) to semantically and/or prosodically congruous and incongruous sentences that were presented aurally to study the time course of semantic and prosodic processing, and to determine whether these two processes are independent or interactive. The prosodic mismatch was produced by cross-splicing the beginning of statements with the end of questions, and vice-versa. Subjects had to decide whether the sentences were semantically or prosodically congruous in two different attention conditions. Results showed that a right centro-parietal negative component (N400) was associated with





Figure 10. ERPs to prosodically congruous (P+) and incongruous (*P) sentences are presented separately for semantically congruous and incongruous sentences in the prosody attention task. ERPs are illustrated for 10 lateral electrodes. The prosodic mismatch effect (P800) is clearly larger for semantically incongruous than semantically congruous sentences.

2.4.8

Astésano, C.¹, Besson, M.¹ & Alter, K.² semantic mismatch, and a left temporo-parietal positive component (P800) was associated with prosodic mismatch. Thus, these two electrophysiological markers of semantic and prosodic processing differed in their polarity, latency and scalp distribution. These differences may indicate that the two processes stem from different underlying generators. However, the finding that the P800 elicited by prosodic mismatch was larger when the sentences were semantically incongruous than congruous suggests that the two processes may be interactive.

2.4.9 The first syllable determines lexical activation in spoken word recognition: ERP evidence

Friedrich, C.K., Alter, K. & Friederici, A.D.

Lexical decisions to visual target words can be modulated by preceding spoken or visual word onset fragments. Responses to words that match the fragment (e.g., in the prime target pair kon - Konto [account]) are faster than responses to unrelated controls (e.g., *kon* - *Salto* [somersault]). The behavioral facilitation is reliably accompanied by a reduced positive going ERP deflection, named the P350, and a reduced amplitude of the N400. The P350 effect has been related to activation of modality-independent lexical representations, whereas the N400 priming effect seems to reflect later strategic mechanisms (Friedrich, Kotz, Friederici & Gunter, in press). In the present two experiments, we tested effects for targets that partially mismatch spoken monosyllabic fragments. In Experiment 1, partially mismatching targets deviated in syllable nucleus (e.g., in the prime - target pair kon - Kante [edge]), in Experiment 2 they deviated in the position of the syllable boundary (e.g., kan. - Kanz.ler [chancellor], dots indicate the syllable boundary). In both experiments, responses were faster to partially mismatching words than to controls. However, P350 and N400 effects were differently sensitive to partial mismatch. Amplitudes of the P350 did not differ for partially mismatching words and controls. In contrast, the N400 paralleled the reaction times, showing a reduced



Figure 11. Reaction times in ms (above) and ERPs (below) elicited in word fragment priming. Syllable nucleus mismatch was tested in Experiment 1 (left), syllable boundary mismatch was tested in Experiment 2 (right). Across both experiments, there was no reduction of the amplitude of the P350 for mismatch, whereas N400 amplitude and reaction times were reduced for that condition.

amplitude for partially mismatching words as compared to controls. The P350 effect reveals that only lexical representations, which completely match the first syllable of the spoken input, receive activation. Both the behavioral facilitation and the N400 priming effect for partially mismatching word appear to be correlates of late integration processes.

Pre-attentive vowel categorization from dynamic speech stimuli

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Speech is normally perceived without effort. Understanding speakers of different pitch of voice and timbre requires the construction of phonetic representations while abstracting from specific sound features. From static input, categorical phonetic information is comprehended pre-attentively, that is even in the absence of intentional selection. Here, we investigate whether phonemes are pre-attentively constructed from more realistic dynamic speech input varying in fundamental frequency and intensity, even while the auditory stimuli are being ignored. The mismatch negativity (MMN) component of the event-related brain potential, an index of auditory sensory memory-based detection of stimuli deviating from a regularity in a sequence of auditory stimuli, was employed. Tokens of /a/ and /i/ vowels varying in pitch of voice and amplitude envelope were presented in oddball and separate control blocks. Participants ignored the sounds while watching a subtitled silent movie. MMN was observed for tokens of



FZ

LM

ΤuV

Control Tones



Figure 12. Event-related brain potentials (ERPs, left column) and ERP difference waves (right column). Phonemes /a/ and /i/ and control tones. In the /a/ and /i/ phoneme dddball conditions mismatch negativity (MMN) was elicited. In the control tones oddball condition no MMN was observed. Physically identical stimuli contributed to the ERPs of each respective stimulus class. MMNs were computed by subtracting identical phonemes of the control condition (dashed) and also the standard condition (dotted) from deviant phonemes. Average peak latencies of the negativity effects in the phoneme conditions were 119 ms after stimulus onset at frontal and 125 ms at mastoid leads.

2.4.10

Jacobsen, T.¹, Schröger, E.¹ & Alter, K.²

FZ

LM

the /a/ and /i/ vowels varying in pitch of voice and amplitude envelope when they occurred infrequently among the respective other vowel. The speech perception system pre-attentively extracted the language information, despite the enormous variation in the speech-irrelevant sound input. Capacity-limited attentional resources are not employed and thus left free to operate on higher level language comprehension processes, necessary for fast, reliable message construction.

2.4.11 Neurocognitive comparison between speech and music sound processing: ERP and fMRI experiments

Tervaniemi, M.¹, Szameitat, A.J.², Kruck, S.², De Baene, W.³, Alter, K.², Schröger, E.⁴ & Friederici, A.D.²

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Sound frequency, duration, and intensity are key elements in carrying prosodic and musical information. Our aims were to compare the neurocognition of speech and music sounds, and to determine the relative importance of the above mentioned features.

The subjects were presented with pseudowords and music sound patterns of matched duration, intensity, and fundamental frequency. As rarely occurring "deviants", pseudowords and music patterns with acoustically matched pitch, duration, and intensity changes were employed. In addition, all additive combinations of those changes were included (ERP study). The subjects watched a silent video (ERP: Ignore), performed a target detection task (ERP: Attend), or categorized the sounds as speech or music (fMRI). The change-specific MMN component was modulated by the deviating sound parameter, the number of deviated parameters, and the sound type (music vs. speech). Moreover, N2b was influenced by the subjects' musical expertise, deviated sound parameter, and marginally also by the sound type. Up to some extent, fMRI dissociated the brain areas involved in speech vs. music processing (Figure 13). Taken together, these results support the existence of (at least partially) modular music- and speech-specific systems in neurocognition of auditory information.



Figure 13. The direct comparison of speech and music sound conditions illustrates cortical areas activated more strongly by speech than music sounds (yellow) and vice versa (music > speech; blue). While music processing is associated with areas of the superior temporal gyrus, speech processing is associated with areas of the superior temporal sulcus.

During the last year the projects of the CNPS group exploited all techniques and methodological achievements available in our institute to further characterize the pathological state of diffuse and focal brain disease. Most clinical projects evolved through the close linkage between the Day Clinic of Cognitive Neurology at the University of Leipzig and the Max Planck Institute.

In 2003, the Day Clinic treated 227 patients. 145 (64%) of the current patients participated in clinical research projects. Moreover, 125 former patients were taking part in actual studies. Our database now consists of a pool of more than 980 patients with brain injuries of various etiologies. Thus, each patient, characterized by a detailed analysis of medical history, neuropsychological and linguistic profile, helped with his/her contribution to a better insight into the basic understanding of cognitive neurology.

CNPS research centered around four major topics: (1) the neural correlates of syntactic and error processing in patients with focal lesions as assessed by event-related brain potentials (ERP); (2) the assessment of cerebrovascular reactivity and its physiological cofactors in patients and healthy controls based on the fMRI BOLD response; (3) the circadian variability and aging effects assessed by standardized functional near-infrared spectroscopy protocols (fNIRS); and (4) the substrate of interhemispheric transfer and auditory and visual processing.

Clinical ERP-studies. The different ERP correlates of error processing were determined in two patients groups with basal ganglia and lateral frontal cortex lesions (2.5.1). The functional role of the left anterior temporal lobe in automatic syntactic processing was defined in 2.5.2.

Cofactors and variability of fMRI BOLD signal changes. Several projects addressed the robustness of fMRI defined cerebrovascular reactivity (CR) in terms of intra- and intersession reproducibility (2.5.3), analyzed the temporal dynamics of hyper- and hypocapnia (2.5.4), related the global CR values to a focal activation paradigm in poststroke patients (2.5.5), and studied pharmacological effects on cerebral hemodynamics applying β -adrenergic blockade (2.5.6).

Standard analysis of fNIRS in normal aging and reproducibility studies. The general linear model and a spatially resolved spectral analysis was implemented for standard evaluation of fNIRS data (2.5.7). In a combined fNIRS and fMRI study, this analysis procedure was used to further study the underlying physiology of the undershoot of the BOLD signal (2.5.8). Further projects addressed the decline of low frequency oscillations associated with normal aging (2.5.9) and the circadian dynamics of the fNIRS response (2.5.10).

Neuro-morphometry in clinical applications. A comparative analysis of morphometric findings across MR scanners – essential for the design of mulicenter studies - was undertaken in 2.5.11 and a method for a variable resolution analysis of the cortical surface developed in 2.5.12. Clinical morphometric applications included cortical thickness and ventricular size evaluation in normal aging 2.5.13, as well as in patients with severe head trauma (2.5.14), and on a structural level in patients with diffuse axonal injury (2.5.15). Neurosurgical applications applying brain shift models focused on patients undergoing interventional MRI-guided stereotactic biopsies (2.5.16) and patients with hydrocephalus (2.5.17).

Experimental neuropsychology. The functional importance of the auditory cortex was addressed in 2.5.18 including patients with left auditory cortex damage, while the neural correlates of visual dimension and response changes were localized in left frontopolar cortex based on a fMRI study in normal controls (2.5.19). The role of the orbitofrontal and hippocampal paralimbic belts for auditory target detection was revealed in a dichotic listening task (2.5.20). Finally, we report a fMRI study on normal participants which was carried out to investigate differences in object picture versus word-related visual processing (2.5.21). A study on interhemispheric resource sharing (2.5.22) gave an impressive example of the usefulness of relating computational models to behavioral and imaging data.

2.5.1

Lesions of the basal ganglia and the lateral frontal cortex differentially interfere with error processing

Ullsperger, M. & von Cramon, D.Y.

Recent models of performance monitoring suggest that the error-related negativity (ERN) is based on dopaminergic reinforcement signals resulting from errors in reward prediction. They further assume that the basal ganglia (BG) play an important role in determining errors in reward prediction and thus in error detection. The frontolateral cortex (FLC) has also been shown to be highly important for error detection as lesions in this region lead to a disruption of the ERN. It was proposed that the lesions of FLC interfere with the updating of task rules thus, resulting in disturbed representations of the required response.

In the present set of experiments we investigated the behavioral and electrophysiological correlates of error processing in patients with circumscribed brain lesions in the basal ganglia (BG group, n=8) and in the FLC (FL group, n=7) while they performed a flanker task. Participants were requested to correct errors by immediately pressing the correct response button.

Both lesion types led to abolition of the ERN (Figure 1). Interestingly, corrective behavior did not differ between the BG group and controls, whereas the FL group corrected less errors and needed more time for error correction (Figure 2). Moreover, only in the FL group were response times for errors not shorter for hits, suggesting that in these patients errors were not due to premature responses, but rather to high uncertainty.

BG as well as FLC lesions similarly altered the event-related potential (ERP) correlates of error processing. Behaviorally, however, the groups showed large differences. The

BG group had no problems with error detection and correction, suggesting that BG lesions interfere with the generation of the ERN rather than with error processing itself. As the lesions were unilateral, it is conceivable that the error detection system could still compensate the deficits to the extent that behavior was normal. This suggests that ERPs provide a more fine-grained measure for lesion characterization. In contrast, unilateral FLC lesions seem to interfere with error processing to a larger degree, e.g., by disrupting the establishment of the correct response tendency.



Figure 1. Response-locked grand average waveforms at FCz for correct (blue) and incorrect (red) incompatible trials for patients (left) and controls (right). (A) Basal ganglia lesion group, (B) frontolateral cortex lesion group.



Figure 2. Immediate corrections. Mean correction rates (left) and correction times (right) for patients (red) and controls (blue). (A) Basal ganglia lesion group, (B) frontolateral cortex lesion group.

2.5.2

Kotz, S.A., von Cramon, D.Y & Friederici, A.D.

Differentiation of syntactic processes in the left and right anterior temporal lobe: Event-related brain potential evidence from lesion patients

In recent years neuropsychological (e.g., Donkers et al., 1994; Grossman et al., 1998) and functional neuroimaging studies (e.g., Friederici, 2002; Mazover et al., 1993; Meyer et al., 2000) have implicated the anterior temporal lobe as one of the neural substrates to engage in auditory sentence comprehension. In particular, it has been proposed that the comprehension of speech relies on syntactic processing (e.g., Friederici et al., 2003; Humphries et al., 2001). As previous event-related brain potential studies (ERPs) show, syntactic processing can be separated into automatic (rule-based) and controlled syntactic processes, which correlate with the early anterior negativity (ELAN) and the late centroparietal positivity (P600), respectively (e.g. Hahne & Friederici, 1999). Support for a neuronal differentiation of these processes comes from ERP lesion studies. While patients with left inferior frontal lesions show no deflection of the early anterior negativity (Friederici et al., 1999), patients with lesions and neurodegenerative changes of the basal ganglia show a modulation of the late positivity (Friederici et al., 2003; Frisch et al., 2003; Kotz et al., 2003). In addition, a recent MEG study (Friederici et al., 2000b) reported that the neural generator of the early anterior negativity is localized bilaterally, but left accentuated in the inferior frontal and anterior temporal regions. In order to complement the neural circuitry that is engaged in automatic and controlled syntactic processes we investigated auditory sentence comprehension in six patients with anterior temporal lobe (ATL) lesions, and five patients with right anterior temporal (ATR) lobe lesions as well as eleven controls.

Age-matched controls displayed the expected biphasic ERP pattern resulting from phrase structure violations: An early anterior negativity followed by a late centro-parietal positivity. Patients with ATL lesions showed no deflection of the early anterior negativity, but a P600, which was maximal at right centro-parietal electrodes. Patients with ATR lesions showed a left-accentuated early anterior negativity and a P600 with a maximal distribution over left centro-parietal electrodes.



Figure 3. Displayed are on the left side at selected electrodes the missing E(L)AN effect, but the P600 effect in the LAT patients and on the right side the E(L)AN and P600 effect in the RAT patients.

The current results reveal supporting evidence that the left anterior temporal lobe plays a functional role in automatic syntactic processes. In addition, the current data show that controlled syntactic processes also seem to be mediated by the left and the right anterior temporal lobe, respectively. We propose that the anterior temporal lobe might be part of a cortico-subcortical network engaged in syntactic processing during auditory sentence comprehension.

Reliability and reproducability of fMRI defined cerebral vasoreactivity

Functional MRI (fMRI) has been demonstrated to assess cerebrovascular reactivity (CR) in normal controls and patients (Hund-Georgiadis et al., 2003) using a hyperventilation task. The present study was designed to assess the inter- and intra-session reproducibility of this technique. Twenty-two healthy controls of two different age groups (G1: 26 ± 2 and G2: 57 ± 5) were included. Twelve subjects took part in inter-session examinations, intra-session hyperventilation scans were performed in 10 controls. The percentage signal change – normalized by endtidal CO2 values – was measured in various brain regions and the global fMRI signal decreases in response to hyperventilation mapped for each session.

Elderly controls showed significant qualitative and quantitative differences of the fMRIresponse to hyperventilation as compared to young participants: The volume of grey matter showing significant CR was reduced by 26% as compared to young controls (Figure 4). Moreover, time course analysis showed significant regional effects in frontal, parietal, occipital, and cerebellar brain regions.

High reproducibility of CR values was found for different intra-session scans. The time course analysis of the two recordings summarized for ROIs in all brain regions did not show significant differences (Figure 5A). Evaluation of inter-session recordings showed a slight decrease of signal changes during the second session without reaching statistical significance (Figure 5B).



Figure 4. Averaged BOLD signal decrease in response to hyper-ventilation for young (top) and elderly (bottom) controls. Age was identified as an important cofactor of fMRI-defined vasoreactivity. For better visualization a z-value > 5 was applied.

2.5.3

Hund-Georgiadis, M., Martin, E.M., Zysset, S. & von Cramon, D.Y. In sum, the hyperventilation protocol was demonstrated to generate reproducible and robust vasoreactivity maps, which are applicable in dynamic and follow-up studies. For group studies, age has been identified as an important and significant cofactor of fMRI-based CR-assessment.



Figure 5A. Time course analysis of the BOLD signal in response to hyperventilation: Robust and comparable results were gained from two different recordings within one session. The results are based on 20 intra-session scans of 10 subjects.



Figure 5B. Intersession-comparisons of the BOLD-signal in response to hyperventilation: The results are based on 24 inter-session recordings of 12 subjects. The data show a decrease of the BOLD-response during the second session without statistical significance.

The cerebral vascular response to hyper- and hypocapnia: A comparative fMRI study

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Functional magnetic resonance imaging (fMRI) has gained considerable importance in the non-invasive assessment of cerebral vasomotor reactivity (CR) to respiratory challenges. Hypercapnia produces vasodilatation and thereby increases CBF, whereas hypocapnia acts reversely; it induces vasoconstriction and thereby decreases CBV. The present study investigated the vascular CO, response in a combined hyper- and hypocapnia study design to contribute to a better understanding of the temporal and spatial dynamics of fMRI signal changes associated with respiratory stress.

Six healthy and trained subjects without any history of neurological disorders (all male, age 19-29 years, mean age 27.8 years) randomly performed a hyperventilation (HV) and a breath-holding task (BH) in the MR-scanner. Hypercapnia and hypocapnia related changes of the BOLD signal showed a significant different reversed effect only after 60 seconds of the corresponding breathing condition. During the first 20 seconds, a short peaking of the BOLD response was found in **both** respiration tasks. The fMRI response was significantly more enlarged during HV as opposed to BH (Figure 6/HV vs. BH: 801 ± 157 cm³ vs 543±150 cm³, p=.02). No significant regional preponderance of the BOLD response associated with effective hyper- or hypocapnia was found. Our findings clearly demonstrate that the vascular compensation of vasoactive stress - regardless whether hypercapnia or hypocapnia is addressed – does not occur as rapidly as widely assumed in healthy subjects. Clearly CO, induced changes evolved only about 60 seconds post onset of the respiration task and did not show a significant regional preponderance.



Figure 6. The averaged magnitude of the MR signal changes in response to HV and BH is displayed according to the time course analysis of the BOLD response in three intervals: Effective CO₂-changes were assessed only after 60 seconds of the breathing tasks and produced significantly different BOLD responses.

2.5.4

Hund-Georgiadis, M.¹, Zysset, $S.^{1}$, Naganawa, S.², Norris, D.G.³ & von Cramon, D.Y.¹

2.5.5 Impaired cerebrovascular reactivity and BOLD contrast in post-stroke patients

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Functional MRI is a widely-used neuroimaging technique based on BOLD contrast that reflects an incompletely understood coupling of neuronal activity and cerebral blood flow. Based on steady-state animal preparations and on healthy human volunteers, computation of signal changes in each voxel of the brain volume assumes a constant cerebrovascular reactivity (CVR) across regions. However, this assumption is questionable in the elderly and especially in patients with brain lesions or cerebrovascular diseases.

To evaluate the relationships between CVR and BOLD contrast in eloquent areas, eight patients with full recovery from middle cerebral artery (MCA) infarctions were investigated. In all patients, the primary motor cortices remained structurally intact. The patients' data were compared to results gained from eight age-matched controls during motor tapping tasks and a hyperventilation (HV) task determining CVR. The controls showed equal fMR signal changes (%SC) in primary motor cortices (M1), supplementary motor area (SMA), and dentate nucleus (CRB) of both hemispheres for all tasks. In the healthy hemisphere of patients, %SC were identical to controls in M1 and SMA for all tasks, but decreased in CRB for contralateral movements. In the affected hemisphere, %SC were decreased in M1 and SMA for both, hyperventilation and motor tasks (Figure 7). In sum, impaired CVR was identified as an important contributor of decreased %SC in eloquent areas adjacent to structural lesions in patients with MCA infarctions at chronic stage.



Figure 7. Group studies in controls (top row) and patients with right MCA infarction (n=8) (buttom row) during hyperventilation (HV), bimanual, unaffected hand, and affected hand movements. Decreased fMR activations in M1 and SMA of the affected hemisphere were observed in the patients group for all tasks.

Cerebral hemodynamic and cognitive function under ß-adrenergic blockade with esmolol

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The effects of β -adrenergic blockade on cerebral circulation and cognitive function are still a matter of debate. The modern β_1 -antagonist esmolol with its unique pharmacokinetic features (an onset of activity within 2 minutes after IV injection and a full recovery from β -blockade within 20 minutes) allow the performance of a variety of tasks in the presence or absence of β -blockade within a single experimental session conducted to explore possible drug effects on the human brain. Therefore, fMRI was employed to investigate esmolol's effects on cerebral blood flow, cerebral vasoreactivity, and cognitive functions in human volunteers. Accordingly, the BOLD signal was measured in ten healthy volunteers at rest, during a hyperventilation challenge, and



Figure 8. BOLD signal intensity time courses (averaged across all subjects) depicting drug effects in the brain after bolus injection of 1 mg kg⁻¹ esmolol over 2 minutes followed by an infusion with 150 μ g kg⁻¹ min⁻¹ for 2 minutes. The bolus injection period is indicated by the dark gray area, the following infusion period by the light grey area. Injection of the esmolol bolus caused an immediate BOLD signal increase in all of the selected regions. Vertical lines represent the standard error of mean.

2.5.6

Heinke, W.¹, Zysset, S.², Hund-Georgiadis, M.², Olthoff, D.¹ & von Cramon, D.Y.² during a cognitive task (color word matching Stroop task) in the presence and absence of β -blockade.

Our results demonstrate that esmolol decreased cardiac output during the different experimental conditions. This is indicated by the observed reduction in heart rate and blood pressure, and confirms the efficacy of the pharmacological intervention. Moreover, the bolus injection of esmolol was accompanied by an immediate BOLD signal increase in most of the investigated brain areas, suggesting a transient cerebral vasodilatation associated with the injection of the drug (Figure 8). We interpret this finding as autoregulatory response of cerebral blood vessels in order to compensate the sudden drop in cerebral perfusion pressure associated with acute β -blockade. The study further demonstrates that esmolol neither affects the BOLD signal increases or the reaction times while subjects were performing the Stroop task (Figure 9), nor does it affect the global BOLD signal decrease in response to hyperventilation, indicating that moderate intravenous β_1 -blockade does not affect cognitive performance or cerebral vasoreactivity.



Figure 9. Mean reaction time (\pm SE) and error rates for the Color-Word Matching Stroop task. Reaction times were averaged over all subjects. Reaction time and error rates remained unaffected by esmolol during both conditions (neutral, incongruent) of the color-word matching Stroop task.

2.5.7 Towards a standard analysis for functional near-infrared imaging

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Functional near-infrared spectroscopy (fNIRS) allows the monitoring of brain activation by measuring changes in the concentration of oxy- and deoxy-hemoglobin. Until now, no standardized approach for fNIRS data analysis has been established, although this has to be regarded as a precondition for future application. Hence, we applied the wellestablished general linear model to optical imaging data. Further, fNIRS data were analyzed in the frequency domain. Two visual tasks were investigated with optical topography: A checkerboard paradigm supposed to activate the primary and secondary visual cortex, and a paradigm consisting of moving colored stimuli (rotating 'L's) additionally involving the motion area V5. Analysis with the general linear model detected the activation focus in the primary and secondary visual cortex during the first paradigm (Figure 10). For the second paradigm, a second laterally localized activated brain region was found, most likely representing V5. Spatially resolved spectral analysis confirmed the results by showing maxima of power spectral density and coherence in the same respective brain regions (Figure 11). Moreover, it demonstrated a delay of the hemodynamic response in the motion area. In summary, the present study suggests that the general linear model and spatially resolved spectral analysis can be used as standard statistical approaches for optical imaging data, particularly because they are independent of the assumed differential pathlength factors.



Figure 10. Averaged Z-maps for visual stimulation overlaid onto an anatomical reference image: Stimulation vs. baseline during the checkerboard and rotating 'L's paradigm, and contrast between both paradigms. Z-maps are shown for oxy-, deoxy-, and total hemoglobin (Hb). Z-values were thresholded at Z=1.7, which corresponds to an alpha-level of 0.05.



Figure 11. Averaged power spectral density-, coherence-, and phase-maps for the stimulation frequency and deoxy-hemoglobin. Coherence and phase delay were calculated in relation to the medial activation focus. Phase delay is shown for a coherence above 50% only.

2.5.8 Investigating the post-stimulus undershoot of the BOLD signal – A simultaneous fMRI and fNIRS study

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Measuring the hemodynamic response with functional near-infrared spectroscopy (fNIRS) together with another imaging method may overcome limitations of singlemethod approaches. Accordingly, we applied fNIRS simultaneously with functional magnetic resonance imaging (fMRI) in 12 young subjects during an event-related visual stimulation task (Figure 12). A long intertrial interval of 60 s was chosen to include the prolonged post-stimulus undershoot of the blood-oxygenation level dependent (BOLD) signal. Further, depth penetration of near-infrared light was examined. The BOLD signal, oxy-, and total hemoglobin (Hb) increased, whereas deoxy-Hb decreased during visual stimulation (Figure 13). During the post-stimulus period, we found an undershoot of the BOLD signal, oxy-Hb, and an overshoot of deoxy-Hb. Total Hb as measured by fNIRS returned to baseline immediately after the end of stimulation. Taking into account that total Hb represents corpuscular blood volume only and is insensitive to plasmatic blood volume, results were consistent with the Balloon and Windkessel models assuming



Figure 12. Location of the fMRI slices and the two emitter-detector pairs for fNIRS. Highest correlation between oxy- and deoxy-Hb and the BOLD signal might be expected in the slice in the center of the banana-shaped near-infrared sampling volume (blue).



Figure 13. Concentration changes of oxy-, deoxy, total Hb, and cytochrome-c-oxidase (Cyt-Ox) as measured by fNIRS, and the BOLD signal as measured by fMRI. Visual stimulation started at 0 s and continued till 6 s. Mean±SD.

that blood volume returns later to baseline than blood flow after stimulus cessation. Moreover, data indicate the persistence of a high-level oxygen consumption after blood flow returned to baseline. Temporal changes in the BOLD signal were highly correlated with deoxy-Hb, with lower values for oxy-, and total Hb. Highest correlation between the BOLD signal and deoxy-Hb was found in a distance of 15 mm from the skin surface. These results were confirmed by simultaneous fNIRS/fMRI measurements during rest. In summary, results indicate that the post-stimulus undershoot of the BOLD signal is caused by a later return of blood volume than blood flow to baseline, and by a persisting high-level oxygen consumption after stimulus cessation.

2.5.9 Spontaneous low frequency oscillations decline in the aging brain

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It is well known that aging leads to a degeneration of the vascular system. Hence, one may hypothesize that spontaneous oscillations decrease in the cerebral microvasculature with aging. Accordingly, we investigated the age-dependency of spontaneous oscillations in the visual cortex during rest, and during functional activation. As an imaging method we applied functional near-infrared spectroscopy, because it is particularly sensitive to the microvasculature. Visual stimulation led to an increase of oxy-hemoglobin (Hb), total Hb, and a decrease of deoxy-Hb, without any influence of age. As illustrated in Figure 14, peaks of normalized power spectral density were detected for spontaneous low (0.07-0.11 Hz) and very low (0.01-0.05 Hz) frequency oscillations, with a higher amplitude for oxy- than deoxy-Hb. Spontaneous low frequency oscillations of oxy-,



Figure 14. Normalized power spectral density (PSD) in comparison between young and elderly subjects in the visual cortex during rest and stimulation with a checkerboard. The frequency range includes spontaneous very low and low frequency oscillations and the stimulation frequency (0.028 Hz). Hb hemoglobin, Cyt-Ox cytochrome-c-oxidase.

and deoxy-Hb declined strongly with aging during both rest and visual stimulation. Reduction of spontaneous low frequency oscillations might indicate a declining spontaneous activity in microvascular smooth muscle cells, in conjunction with an impaired cerebral autoregulation, and increased stiffness with aging. Our approach might be applied to diagnose large and small cerebral artery disease in the future.

Circadian variability is negligible in functional imaging studies

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The hemodynamic response is influenced by several factors such as the brain region, the task performed, or the day of measurement. Most of the functional imaging studies implicitly assume that variability of the hemodynamic response throughout a single day is negligible. Our aim was to formally test this assumption. Therefore, visual brain areas of eleven young subjects were stimulated six times throughout the day, from 08:00 until 18:00, with an event-related checkerboard paradigm. Concentration changes of oxygenated (oxy-Hb) and deoxygenated hemoglobin (deoxy-Hb) as well as cytochrome-c-oxidase were simultaneously monitored over the visual cortex by functional near-infrared spectroscopy (fNIRS). As illustrated in Figure 15, visual stimulation led to the typical hemodynamic response with a decrease of deoxy-Hb and a concomitant increase of oxy-Hb. Comparing the six measurements with repeated measures, ANOVA revealed that the factor time of day had no significant influence on the magnitude of the hemodynamic response. Furthermore, intraclass correlation coefficients (ICCs) were calculated as a measure of reliability for every chromophore. Deoxy-Hb (ICC=0.62) was the chromophore with the highest and oxy-Hb (ICC=0.27) the one with the lowest intraclass correlation coefficient. In conclusion, these findings support the common practice of ignoring circadian variability in functional imaging studies of young subjects.



---- oxy-Hb ---- deoxy-Hb ---- cyt-ox

Figure 15. Time courses of oxygenated (oxy-Hb), deoxygenated hemoglobin (deoxy-Hb) and cytochrome-c-oxidase (cyt-ox) (insert). Visual stimulation (between arrows) elicited a hemodynamic response at each time of day. Average across 10 subjects and both sides. Note the different scaling of the y-axis on the insert.

2.5.10

Bücheler, M.M.¹, Schroeter, M.L.² & von Cramon, D.Y.^{1, 2}

2.5.11 On the replicability of morphometric findings across MR scanners

Tittgemeyer, M., Zysset, S., Mildner, T. & Möller, H.E. In neurobiological applications, morphometry aims to describe of brain structure from imaging modalities in terms of size, shape, and texture. Therewith, morphometry offers promising approaches for an 'in-vivo' characterization of many neurological or psychiatric pathologies. In addition to physiological alteration and methodological misuse, the error in morphometric measurements is primarily determined by the scanner protocol. In addition to starting up the new Siemens TRIO scanner, we were concerned to evaluate the within-scanner and between-scanner reliability of volumetric measurements on our two MR devices.

Three young healthy volunteers were scanned on three separate days using the two different systems. One 3D T1w scan was acquired with the Bruker system, and four 3D T1w scans were acquired consecutively on four different occasions on the TRIO system. The resulting datasets were analyzed by the same protocol with the identical image processing tools: To avoid bias in the matching procedure by extracranial tissue, the intracranial compartment was extracted first. Following signal normalisation and rigid body matching, image volumes were subtracted. The resulting difference image can be overlaid in colour to display the changes visually, while the actual difference in volume can be calculated as the integral of shift in the boundaries. The procedure revealed an average apparent volume loss of 2.5% for the supratentorial brain at between-scanner comparison (Figure 16) whereas the within-scanner reliability was excellent for all three subjects (Figure 17). To account for this effect, it was decided to avoid any interference of anatomical scans from different systems in any structural brain study.



Figure 16. Registration of scans taken at different scanners. Notice the perfect alignment of the scans made at the Bruker (left) and TRIO (middle) system. From the morphometric analysis an apparent tissue loss would be inferred (red color, right panel).



Figure 17. Registration of scans taken for the same subject one after another at the same scanner (TRIO). The difference images depict a perfect reliability for the supratentorial brain.

Towards determinants of cortex shape

At a macroscopic level, the shape of the human cortex is highly convoluted. The reason for its specific pattern is still under research. Numerous hypotheses were proposed that emphasize different causal and descriptive aspects of cortex growth and shape. The parameter space underlying cortical forming appears manifold: Parameters under discussion include geometric-, physics-, cellular-, genetic-, and neuronal based determinants. Whereas maybe all of these parameters contribute to the unique cortical forming as we can macroscopically observe it, a geometrical description appears to be sufficient for its shape. However, a general description about variants of cortical shape is still outstanding.

We facilitate spherical harmonic functions to quantitatively investigate shape determinants. By decomposing general shape in (analytic) basis functions, spherical harmonics make it possible to calculate spectra of form. As first step we implemented a tool to map the cortex segmented from high-resolution MRT images to mathematical representations with spherical harmonic basis functions. This method allows variable resolution analysis of the cortical surface. The spherical parametrization is translation-, rotation-, and scaling invariant. Form spectra given by the spherical harmonic basis functions can be used to compare different subjects in terms of sulcal and gyral patterns, from the initial elliptic shape with only one harmony to the final cortex shape (Figure 18). The analytical approximation can be used to classify and analyze inter-individual differences in form, but it also has the potential to infer the gyrification mechanism.



Figure 18. Approximation of brain surface by spherical harmonic functions with 1, 6, 11, 18, and 40 basis functions.

2.5.12

Hübsch, T., Tittgemeyer, M. & von Cramon, D.Y.

2.5.13

Preul, C., Hund-Georgiadis, M., Lohmann, G. & von Cramon, D.Y.

Cortical thickness and ventricular size throughout normal aging: A morphometric analysis of 525 brains

It is diversely discussed whether internal and external atrophy physiologically occur with advancing age or not. As long as there are no standard values, the radiologic evaluation of cranial MRIs in terms of atrophy largely depends on the radiologists' experience. In this study, 525 datasets from our database were retrospectively analyzed for cortical thickness and ventricular width. The cortical thickness as a marker of external atrophy was estimated using an automated algorithm. The ventricular width as a marker of internal atrophy was planimetrically assessed. The datasets were attributed to different decades of normal aging. Cortical thickness decreases significantly every other decade of normal aging (3.48 mm \pm 0.07 for teenage years to 3.22 mm \pm 0.12 for subjects aged 60-69) (Figure 19). The ventricular parameters scale up throughout normal aging, in particular the third ventricle (4.1 \pm 0.7 mm for teenage years to 7.7 \pm 2.74 for subjects aged 60-69) (Figure 20). External and internal atrophy are strongly related (*p*<.01, *r*=-0.583) and both correlate significantly with age (*r*=-0.69 and r=0.65). Moreover, the season of image acquisition was identified as a relevant cofactor of cortical thickness values (summer vs. winter, *p*<.05).

A strong correlation between cortical thickness reduction and ventricular enlargement with advancing age suggests that brain atrophy is a physiologic process that occurs with normal aging. The decrease of cortical thickness plateaus every other decade from teenage-life on, whereas the ventricular system scales up more constantly. Seasonal differences in cortical thickness with thicker cortices in winter times may be due to a relative hypohydration of the subjects in summer.



Figure 19. Total cortical thickness in mm (\pm SD) for a selected number of subjects for each age group (age group 1 covers the subjects aged 10-19, age-group 2 represents subjects 20-29 etc.). Note the plateaus of the values, every other decade with significant downscaling of the cortical thickness between groups 2 and 3, and between 4 and 5 (p<.05).



Figure 20. Ventricular indices and 3rd ventricular width for the same sample as in Figure 19. Values are given \pm SD. VBI = ventricular body index, AHI = anterior horn index, 3V = width of the third ventricle. Note the increasing standard deviation for the third ventricle with advancing age.

Morphometric changes in the chronic stage of traumatic brain injury

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The clinical outcome of patients with diffuse axonal injury (DAI) cannot be sufficiently explained by the amount and extent of structural lesions. The preferential location of the typical traumatic microbleeds is the border of the grey and white matter in the superior frontal region. If the microbleeds finally cause a deafferentation, a reduction of cortical thickness in this area and along the frontoparietal, projection is likely. We measured the regional cortical thickness along the superior frontal and intraparietal sulcus in 14 patients (age 19-43 years, mean 24.4 ± 6) with isolated DAI in the chronic stage (Glasgow outcome score 4-8, mean 5.5) and correlated it with the clinical outcome. 14 age- and gender-matched subjects (age 21-43 years, mean 24.9 ± 5.4) served as controls.

We found regional differences of cortical thickness values, which were significantly reduced along the superior frontal sulcus in patients as compared to controls, whereas parietal cortical thickness values did not differ significantly in between groups (Figures 21A and B).

In conclusion, the superior frontal cortex reacts to DAI-linked microbleeds in terms of a regional reduction of the thickness, most likely secondary to deafferentation. A correlation between the number of microbleeds and the clinical outcome with the cortical thickness reduction could not be substantiated in our sample. Future dynamic studies, including a larger sample of patients and different subgroups of DAI, will further enlighten the clinical relevance of this morphometric parameter.

2.5.14

Preul, C.¹, Scheid, R.², Hund-Georgiadis, M.¹, Lohmann, G.¹ & von Cramon, D.Y.^{1, 2}



Figure 21. (A) Regional cortical thickness along the superior frontal sulcus on both sides in patients versus controls. The reduction in the patients group is statistically significant (p<.05). Values given in mm ± standard error. (B) Regional cortical thickness along the intraparietal sulcus on both sides in patients versus controls. The reduction in the patients group is not statistically significant (p>.05).

2.5.15 T2*-weighted gradient echo imaging at 3 Tesla in the evaluation of diffuse axonal injury

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Diffuse axonal injury (DAI) is frequently accompanied by tissue tear haemorrhages. In order to examine whether high-field strength T2* GE-imaging in the chronic stage of TBI may have advantages in the evaluation of DAI, prospective MR-imaging of 66 patients (age range 17-57 years) on a 3 T system, 3-292 months (median 23.5 months) after TBI was performed. T1-, T2-, T2*-hypointense and T2-hyperintense foci of 1-15 mm diameter were registered in 10 brain regions by two readers separately. Foci, which appeared hypointense both on the T1- and T2- and/or on the T2*-scans, were defined as traumatic microbleeds (TMBs). In 46 subjects (69.7%) T2* GE revealed TMBs. Hyperintense foci on the T2-weighted scans were observed in only 15 patients (22.7%). T2*- showed significantly more TMBs (p=.000) than T1- and T2-weighted images. Interobserver agreement was strong (κ =0.79; τ =0.749; *p*=.000). In 14 subjects (21.2%), T2* GE revealed TMBs in the corpus callosum, whereas in only 2 subjects (3%) there were hyperintense callosal lesions on the T2-weighted scans. While there was a significant correlation between the total amount and callosal appearance of TMBs and the Glasgow Coma Scale (GCS) (p=.000), there was no correlation with the extended Glasgow Outcome Scale (GOS). In conclusion, T2* GE at high field strength proves to be a useful tool for the evaluation of DAI in the chronic stage of TBI. DAI-related brain lesions are mainly haemorrhagic. The relevance of DAI for long-term clinical outcome is uncertain.



Figure 22. TMBs in the posterior corpus callosum. Left: T2-weighted image; right: T2*-weighted image. Note the additional TMBs in the left side of the splenium and at the grey/white matter border of the frontal lobes, which are not visible on the T2-weighted images.



Figure 23. Frequency and site of TMBs according to 10 brain areas. Shown is the total number of TMBs in each brain area (front: frontal lobe; temp: temporal lobe; par: parietal lobe; occip: occipital lobe; cereb: cerebellum; bg: basal ganglia; thal: thalamus; cc: corpus callosum; mes: mesencephalon; bs: brain-stem).

Evaluation of brain shift in interventional MRI-guided stereotactic biopsies

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Deep brain stimulation (DBS) at the subthalamic nuclei offers a striking possibility to mitigate motor dysfunction in Parkinson disease (PD). It is based on the finding that increased neural activity in this structure leads to the main symptoms in PD. A bilateral electric stimulation of the nucleus subthalamicus (STN) or of the globus pallidus, pars interna (GPI), is a surgical option to relieve motor dysfunction, once the possibilities of medical treatment are exhausted.

For DBS, two electrodes are placed bilaterally into the STN or GPI by a stereotactically guided neurosurgical procedure. Stereotactic localization based on MRI is increasingly used to guide the neurosurgeon during biopsy with a desired accuracy of less than 1 mm. To achieve such a precise localization that is crucial for the success of the procedure, high-precision stereotactic frames are employed. Nevertheless, the accuracy of this kind of "static" image guided device decreases with increasing time of surgery. Loss of cerebrospinal fluid (due to suction and opening of the dura) through the admission

2.5.16

Tittgemeyer, M.¹, Winkler, D.², Preul, C.¹, Wollny, G.¹, Meixensberger, J.² & von Cramon, D.Y.¹ holes, the effect of gravity, and anethesiological agents cause an intraoperative displacement of brain tissue. This dynamic reconfiguration of brain structure during surgery is well known as "brain shift". It was so far expected not to drastically effect bioptic surgery.

In a collaborative study with the Department of Neurosurgery (NCH), we performed a retrospective deformation analysis of pre- and intraoperative MR images of a patient with advanced PD. The patient underwent the surgery to benefit from DBS at the STN. During surgery, we deduced a mean frontal brain shift of 13 mm and, surprisingly, a tissue displacement of still more than 2 mm in the region of the STN (Figure 24A and B). Suchlike, brain shift significantly influences the accuracy of stereotaxy. In consequence of the tissue displacement, electrodes had to be repositioned to fit the target point. For a successful and minimal treatment, it therefore seems to be essential to prevent the CSF loss as much as possible, or to algorithmically compensate for the brain shift effect, even in bioptic surgery approaches.



Figure 24. (A) Deformation analysis reveals tissue displacements in fronto- occipital direction. The maximum (frontal) brain shift is 13 mm. A shifting is still present at the diencephalon. (B) The average displacement at the subthalamic nucleus (STN) is 2 mm. To facilitate orientation, the admission channels of the biopsy needle are outlined (turquoise).

2.5.17

Preul, C.¹, Tittgemeyer, M.¹, Lindner, D.², Trantakis, C.², Meixensberger, J.² & von Cramon, D.Y.¹

intracranial pressure relief

Quantitative assessment of parenchymal and ventricular readjustment to

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The adaptation of the brain parenchyma and ventricular system to altered intracranial pressure is an important part of the evaluation of MR-images. In the treatment of hydrocephalus, for instance, these changes can be vital when comparing pre- and postoperative ventricular size. We introduced a new technique to demonstrate the dynamics of brain tissue adaptation in a patient with subacute triventricular hydrocephalus due to aqueductal stenosis (Figure 25A). The patient underwent an endoscopic ventriculocisternostomia of the third ventricle to bypass the aqueduct by deviating the CSF flow into the interpeduncular cistern (Figure 25B). 3D T1w volume datasets at 3 Tesla were obtained prior to surgery and thrice postoperatively: Immediately after surgery and after an interval of 3 months and 8 months. The images were then registered onto

one another. Offline analysis allowed the assessment of the temporally varying brain morphology using a 3D vector field from a nonlinear transformation. A statistical approach to this deformation led to a quantification of the local volume change at each voxel (Figure 26).

Extensive changes in terms of structural reconfiguration could be deduced in all parts of the ventricular system in the postoperative course in terms of a re-ascent of the third ventricular floor and a drop of the ventricular roof with most extensive changes in the early postoperative course (Figure 27). These findings give evidence for the mechanisms of brain reconfiguration after intracranial pressure relief and add valuable information to evaluate and comprehend success or failure of the intervention.



Figure 25. Triventricular hydrocephalus due to aqueductal stenosis (A). The postoperative condition 8 months after endocscopic 3rd ventriculostomia shows an extensive decrease of the ventricular size (B). T2-weighted midsagittal MRI at 3T.



Figure 26. Vector field analysis reveals a decrease of the ventricular system with most extensive changes at the third ventricular floor as indicated by the direction and length of the green vector arrows. Note the extensive alteration at the surgical approach in the right ventricular body.



Figure 27. Constant decrease of the ventricular system from early postoperative (T1) to late postoperative (T3) MRI-scan as compared to the preoperative condition (T0).

2.5.18 Improved directional discrimination after left auditory cortex damage

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The two main hypotheses about the functional importance of auditory cortex (AC) in directional hearing in humans suggest contralaterally dominant processing and/or a right-hemisphere lateralization. The contralateral dominance hypothesis was adopted from animal models of neural peak responses and impaired localization behavior after unilateral brain damage for the contralateral hemifield, and it is true for other sensory modalities in humans as well. A right-hemispheric specialization is known to exist at higher cortical levels in multimodal spatial processing in the parietal lobe. The role of AC or the impact of damage to its anatomical correlate Heschl's gyrus in sound localization have rarely been explicitly studied. We approached this issue by investigating directional discrimination in the horizontal plane in patients suffering from a Heschl's gyrus lesion or deafferentation (interruption of acoustic radiation and transcallosal fibers from contralateral AC). Minimal audible angles (MAAs) for low- and high-frequency noise bursts were measured as a function of reference direction applying an adaptive three-alternative forced-choice paradigm. In patients with left AC damage, spatial resolution was barely impaired when compared to the controls (Figure 28). Threshold elevations occurred only occasionally, predominantly in the right hemifield. In the left hemifield to the contrary, they were rarely observed, and performance was even better than in the control group. The asymmetry in the distribution of elevated thresholds gives evidence for the bilaterally organized perception of auditory space with contralateral accentuation. The improved performance observed after left AC damage, suggests that the cooperativity between the two cortices may not be purely complementary, but in part competitive. In case of left AC damage, the right hemisphere takes over, yielding a better than normal performance in the left hemifield, presumably due to the contralaterally dominant representation. Together with deficits in directional discrimination observed after right AC damage, our results support the notion of righthemisphere dominance in spatial hearing established at this level already.



Figure 28. Minimal audible angles (MAAs) in patients with left Heschl's Gyrus damage (red) and control group (grey) as a function of reference direction (negative: left; positive: right hemifield) for (A) low-frequency (0.25-1.2 kHz), and, (B) high-frequency (2-8 kHz) noise bursts.

Neural correlates of visual dimension changes and response changes

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We investigated the neural correlates of visual dimension changes and response changes with event-related fMRI. In a visual singleton feature search task, participants had to search for a color (red)- or motion (diagonally moving)-defined target presented among green horizontally moving distractor triangles, which pointed arbitrarily to the left or right. The pointing direction of the target triangle indicated the correct response, a compatible left or right key press. These compound stimuli enabled us to vary target dimension changes (from color to motion and v.v.) and response changes (from left to right button and v.v.) independently. We observed dimension change-related activation in occipital cortex and, separately, response-related activation in motor cortex. In addition, left frontopolar cortex activation was selectively increased during visual dimension changes. An interaction between visual dimension and response changes was observed in the preSMA, in the motor part of the cingulate gyrus, and in the posterior insula. We conclude that visual dimension and response changes lead to separate effects on sensory input and motor output areas. Left frontopolar cortex selectively supports visual dimension changes, but may both control attentional modulation of visual processing areas, facilitating dimension changes, and signal the presence of dimension changes to medial premotor areas, facilitating response changes.



Figure 29. Dimension change-related activation in left frontopolar cortex is independent of response changes.

2.5.19

Pollmann, S.¹, Weidner, R.¹, Müller, H.J.² & von Cramon, D.Y.^{1, 3}

2.5.20

Pollmann, S.¹, Lepsien, J.¹, Hugdahl, K.² & von Cramon, D.Y.^{1, 3}

Auditory target detection in dichotic listening involves the orbitofrontal and hippocampal paralimbic belts

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In dichotic listening, two similar, yet different stimuli are presented simultaneously to the left and right ear (Hugdahl, 1995). When two syllables are presented in this way, they seem to blend and discrimination of syllables presented to one ear is only possible with uncertainty. In this event-related fMRI study, we found that the orbitofrontal and paralimbic belts were involved in target detection in dichotic listening. The posterior orbital gyri bilaterally, the left amygdala, hippocampal formation, and the left pregenual paracingulate area (PPA) were activated more strongly during dichotic target detection than during correct rejection of target presence. The right posterior orbital gyrus also showed stronger activation during dichotic compared to diotic target detection. Further analyses showed that the BOLD responses in these areas, with the exception of the right hippocampal formation, varied rather with the subjective decision on target presence than with the physical target presence itself. The left PPA, amygdala and hippocampal formation responded differently to left and right ear target detection, suggesting their involvement in the right ear advantage observed in this task. The data show the importance of the orbitofrontal and hippocampal paralimbic belts for auditory stimulus decision processes based on ambivalent sensory information.



Figure 30. Detection of target CV-syllable, but also false alarms, leads to increased activation in the posterior orbital gyrus bilaterally. CD: correct detection; Miss: missed target; CR: correct rejection of target presence; FA: false alarms. Left hemisphere is on the left. Legend indicates Z-scores.

Object picture versus word-related activation in ventral occipital cortex

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To investigate effects of stimulus format on activation patterns in ventral occipital cortex, we used event-related fMRI to investigate the passive viewing of pictures showing buildings and faces, and reading the corresponding names of those pictures. Consistent with earlier findings, pictures of faces maximally activated a region in the fusiform gyrus, which has been termed the fusiform face area (FFA; Kanwisher et al., 1997), whereas pictures of buildings maximally activated a more anterior and medial region in the parahippocampal gyrus, previously called the parahippocampal place area (PPA; Epstein & Kanwisher, 1998; see Figure 1). For each building, we also presented a word denoting the type of building (castle, church, etc). Faces were taken from different nationalities, and the names of these nationalities were also presented as words. Matching pictures and words were presented to the participants before the experiment.

Analyzing the percent signal change in the FFA and PPA, we did not find any differences between words of the two categories: Words naming faces and buildings yielded comparable signal amplitudes in both, FFA and PPA. Signal amplitudes were as high as for the non-preferred picture conditions (see Figure 31). However, across categories, words presented in both hemifields yielded higher activations than objects in left fusiform gyrus, consistent with previous reports (Cohen et al., 2000; 2002), which may indicate that the words have at least been processed up to the level of the visual word form. Taken together, these results show that names of pictures did not automatically activate the corresponding object-selective areas.



Figure 31. Timecourses of the hemodynamic response to word- and picture-conditions for the four regions of interest (left and right FFA and PPA).

2.5.21

Reinholz, J. & Pollmann, S.

2.5.22 Interhemispheric resource sharing: Comparison of fMRI data with connectionist modelling

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When stimuli have to be matched in a complex task (such as whether 2 letters have the same name), performance is better when stimuli are presented across the hemispheres of the brain, whereas for simpler tasks (such as whether 2 letters have the same shape), better performance is achieved when stimuli are presented unilaterally. We carried out an event-related fMRI study to investigate the neural substrate of this effect (Pollmann, Zaidel & von Cramon, 2003). In addition, we showed that the bilateral distribution advantage effect emerged spontaneously in a neural network model learning to solve simple and complex tasks with separate input layers and separate, but interconnected, resources in a hidden layer. Hidden layer activity changes during contra-, ipsi- and bilateral matches matched closely the fMRI signal changes in an area in the left lateral occiptal gyrus, which has been shown to support visual processing of letter shape. This is an example that relating computational models to behavioral and imaging data proves fruitful for understanding hemispheric processing and generating testable hypotheses.







Figure 33. Hidden layer activity in a connectionist model of letter name and shape matching follows closely the fMRI activation pattern in the same task in a letter processing area in left lateral occipital gyrus.

There are two main research strategies in cognitive neurosciences: The cognitive approach looks for the neural correlates of cognitive functions as described in psychology; the anatomical approach seeks the specific functional contributions of a specific brain area to different cognitive functions. Both strategies are combined in the working group 'Functional neuroanatomy of the frontal lobe'. Its focus is on the main frontal functions: Performance control and error monitoring, planning and prediction, decision-making and inference.

A series of studies investigated the neural correlates of anticipatory sequencing. Using the so-called serial prediction task paradigm, these studies focused especially on nonmotor functions of the lateral and the medial premotor cortex. To test whether stimulusdriven and memory-driven aspects are differently supported by lateral and medial premotor areas, a visual SPT paradigm was modified to draw particularly on memorybased sequencing (2.6.1). A further fMRI study sought to find out if the typical premotor correlates of object-specific and spatial prediction survive a pre-experimental sensorimotor training that assigns arbitrary finger responses to either of these stimulus properties (2.6.2). Based on the assumption of a premotor somatotopy that can be triggered by external cues, repetitive body part motion was presented to stimulate the premotor body representation in passive observers (2.6.3). Finally, repetitive TMS was employed to induce virtual lesions over dorsal premotor sites during a spatial SPT, either during early sequence encoding or during late sequence monitoring (2.6.4). Just as these results support the view that attentional perception has an impact on action, especially if stimuli are dynamically changing, it has also been stated that, conversely, action has an impact on perception. This latter view gained support by two fMRI experiments combining a visual identification instruction and a Go-Nogo-task (2.6.5).

Cognitive control requires the selection of task-relevant information, task coordination, interference control, and working memory. Previous fMRI findings have indicated that the inferior frontal junction area plays a crucial role in the implementation of these aspects of cognitive control. A series of fMRI studies mainly employed modified versions of task-switching paradigms to further tackle this issue. Two-dimensional task cues were used to provide congruent, incongruent, or neutral cueing situations; contrasting the former two with the neutral cueing, this study intended to identify the brain correlates of selection of task-relevant information (2.6.6). A direct testing of IFJ function in different cognitive control paradigms was pursued in a study that combined task-switching, Stroop and an n-back task within one experimental session (2.6.7). Different types of the switching paradigm, i.e., cueing and alternating runs, were combined in another fMRI study to explore specifically correlates of the internal generation of task sets (2.6.8). In a switching study focusing particularly on areas of verbal rehearsal, correlates of advance task preparation were investigated with respect to their comparability to verbal self-instruction (2.6.9).

The posterior frontomedian cortex is known to be engaged in error monitoring, an essential component in action control and optimization. The induction of error correction behavior in instruction-biased participants was investigated using different methods. First, an EEG study yielded a specific ERP correlate or error correction, the so-called Correction-related Negativity (2.6.10). In a parallel fMRI experiment, error correction was found to induce activation in two subareas of the frontomedian wall (2.6.11). And finally, heart rate changes were found to be associated with both corrected and uncorrected errors, pointing to a general motivational significance of errors (2.6.12). Converging evidence for posterior frontomedian contribution to decisional conflict comes also from a pseudo learning manipulation showing that activation in this area decreases with the decreasing frequency of negative feedback (2.6.13).

Focusing on more anterior portions of the frontomedian wall, another group of studies focused on text comprehension, especially with regard to coherence building and situation models. A typical feature of these paradigms is that the experimental stimulus does not tell the participant the correct response; rather, the system is also required to decide on own subjective reasons. The on-line updating of the situation model, i.e., a mental model of the general gist of a text, was investigated using an inconsistency paradigm that manipulated both emotional and temporal information (2.6.14). Inconsistency between two successively presented sentences was manipulated on a parametric scale to induce different strengths of coherence and, hence, search for coherence in a further fMRI study (2.6.15). A behavioral study tested a new stimulus material on verbal humor (2.6.16). Comparing jokes with non-joke texts that require linguistic revision, a behavioral study revealed that verbal humor is characterized not only by linguistic revision, but also by an affective reaction (2.6.5).

2.6.1

Schubotz, R.I. & von Cramon, D.Y.

Memory-driven versus stimulus-driven sequencing: Anterior and posterior premotor fields dissociated with fMRI

Serial prediction of perceptual events has been repeatedly found to engage premotor cortex (PM) in the absence of motor requirements supporting attentional functions in this area. The present fMRI study used a modified serial prediction task (SPT) to investigate whether mesial and lateral portions of this large brain region may support different sub-functions of this task. According to the canonical view on motor functions, mesial PM (pre-supplementary motor area, preSMA) serves memory-driven processes rather than sensory-driven ones, whereas the opposite is true for the lateral PM. Capitalizing on this dichotomy, the present study introduced a parametric manipulation that aimed to force memory-driven aspects, and hence SMA engagement, in serial prediction. To this end, we employed a visual object-SPT paradigm with 15 stimuli per trial consisting of five subsequent presentations of three-element sequences. Within the last 12 stimuli of each trial varying amounts of stimuli were masked by a non-informative stimulus. Since participants were provided with a flash-like pacing signal on each stimulus, they were able to keep track of the sequence, even if several successive stimuli were covered. Seven parametric levels were introduced, with zero to six covered elements
per trial, corresponding to 0%, 8.3%, 16.6%, 25%, 33.3%, 41.6% or 50% of covering. In addition, a serial match to sample task was employed. This task required remembering the first picture presented in a trial, but no sequence memory; this task was used to control for effort as well as for perceptual and response effects. According to our hypotheses, we expected lateral PM and preSMA to be engaged during SPT as compared to the control task. In addition, the BOLD response elicited within the preSMA was expected to co-vary positively with an increasing percentage of coverings per trial. Results revealed that both, lateral and mesial aspects, showed a main effect for the SPT as compared to the baseline task, and both also co-varied positively with increasing amount of coverings (parametric effect). However, premotor sites that were more engaged for increasing covering rates (depicted in Figure 1) were located anteriorly to those which showed only a main effect for SPT. Moreover, signal change analyses yielded that the anteriormost premotor fields responded also for the serial match to sample condition, as compared to null events. Results indicate an anterior-posterior gradient within the premotor cortex, with posterior parts being more specific for sequence prediction as compared to anterior parts, whereas the opposite is true for memorydriven processes. Future studies must test whether this points more generally to predictive/planning functions in posterior premotor areas and memory functions in anterior premotor areas, which these might share with adjacent prefrontal sites.



Figure 1. Premotor sites which were found to be specifically engaged in the serial prediction task (colored bars) as compared to the serial match to sample control task (white bars), and which additionally covaried positively with increasing percentages of masked items in a sequence (red corresponds to zero masking, purple to 50%). The middle panel shows considered sites on a white matter segmentation: superior and inferior ventral premotor cortex (sPMv, iPMv), dorsal premotor cortex (PMd) and supplementary motor area (SMA) (left hemisphere is shown on the left). Bar charts display percent signal change in corresponding areas.

2.6.2

Wolfensteller, U., Schubotz, R.I. & von Cramon, D.Y.

Motor significance overrides attentional modulation – Premotor cortex investigated with fMRI

The lateral premotor cortex is known to be modulated by attention to different stimulus properties. This has been suggested to reflect a representation of perceived stimuli according to a habitual pragmatic body map. We used functional magnetic resonance imaging (fMRI) to investigate whether an arbitrarily assigned motor significance for a particular stimulus property influences the premotor activation during a purely perceptual serial prediction task. To this end, subjects trained a sensorimotor mapping linking either four objects of different size or four spatial orientations to the four fingers of one hand. We employed a two by two mixed design with between-subject factor TRAINING (motor significant stimulus property object size vs. spatial orientation) and within-subject factor PROPERTY (attended stimulus property object size vs. spatial orientation). During the experiment, all subjects performed in both serial prediction of object sizes as well as of spatial orientations. Additionally, we introduced catch trials (11%) for the motor significant property, where subjects were required to reproduce the encoded sequence in order to test the sensorimotor mapping. In a first step, activation during encoding a sequence was contrasted with activation in control trials separately for sequences with and without motor significance. In the following, these contrasts were compared between subjects who were attending to object sizes, and subjects who were attending to spatial orientations. We expected attending to object sizes to elicit more ventral premotor



Figure 2. Results of second level *t*-tests (attending to objects vs. attending to spatial orientations) for trials with (lower panel) and without motor significance (upper panel) contrasted with the control task. Foci of maximal individual activation ($z \ge 3.1$) within premotor space during sequence encoding (light yellow = object sequences, light green = spatial sequences) contrasted with control task are plotted separately for trials with and without motor significance and left and right hemisphere, respectively. Group averaged mean locations with standard deviations are colored dark yellow (objects) and dark green (spatial orientations).

activation as compared to attending to spatial orientations which we expected to elicit more dorsal premotor activation (Schubotz & von Cramon, 2001).

Results showed that this pattern was present in trials without a motor significance, whereas it vanished in trials with a motor significance (Figure 2). These results were further confirmed by discriminant analyses on sagittal and axial location of individual activation peaks. Subjects attending to objects could be discriminated from subjects attending to spatial orientations on the basis of their axial location within the left hemisphere in trials without motor significance, while this was impossible in trials with motor significance. Moreover, the mean coordinate of maximal activation in trials with motor significance was located in a more dorsal part of the premotor cortex, regardless of whether subjects attended to object sizes or spatial orientations. Thus, an arbitrarily assigned motor significance influences premotor activation overriding the property specificity. This points to an extreme flexibility of premotor cortex in the adaptation to different task demands.

Distal and proximal body part movements dissociate premotor correlates in passive observers: Functional magnetic resonance imaging (fMRI) as a premotor body map

Apart from the well described primary motor and somatosensory somatotopy, the somatotopical organization of the human lateral premotor cortex (PM) is still a matter of debate. The aim of the present fMRI study was to investigate the premotor body map in a passive observer. Recent fMRI studies have revealed that the PM is engaged in perceptual anticipation as tested by the serial prediction task (SPT). This task requires participants to extract and predict repetitive sensory pattern within sequentially presented stimuli. The present study used selected sequences of human motion to investigate the response of different premotor sites in passive observers, and the possible correlation between the observed body part in motion and the observer's own motor system. In contrast to a recent study that employed goal-directed action of different motor effectors (Buccino et al., 2001), the present study hypothesized that even repetitive motion can trigger limb-specific premotor activation in the observer as long as the task requires predicting the motion pattern.

To investigate this issue, a visual SPT was employed showing repetitive senseless motion (flexion, extension, or rotation) of eight different body parts: mouth, fingers, wrist, arm, shoulder, foot, leg, and trunk. Within each trial, one of these motions was presented four times consecutively. Participants had to attend to the ongoing movement patterns and to indicate afterwards by a forced choice button press whether the last repetition of the presented motion was smoothly repeated or not. In the latter case, which occurred in half of all trials, the movement was slightly accelerated or decelerated. Trials of different conditions were presented in randomized order.

FMRI results revealed that the direct comparison between the single conditions (e.g., foot vs. hand) could not dissociate different premotor fields in the observers. However, the direct contrast between distal motions (collapsed across finger and mouth condition) and proximal motions (collapsed across arm, shoulder, leg, and trunk condition) yielded

2.6.3

Sakreida, K., Schubotz, R.I. & von Cramon, D.Y. distinct premotor activations. The prediction of distal motion resulted in activation of the ventrolateral premotor area (PMv), whereas prediction of proximal engaged the dorsolateral premotor region (PMd) (see Figure 3). These findings confirm the assumption of a premotor body map for predictive perceptual tasks, which is not as fine-grained as the primary motor or somatosensory one.



Figure 3. Group averaged activation maps of the direct contrast between distal (finger plus mouth) vs. proximal (arm plus shoulder plus leg plus trunk) motion (left brain is left). The Z-values were thresholded at Z=3.1.

Repetitive transcranial magnetic stimulation (rTMS) over dorsal premotor

2.6.4

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areas interferes with visuospatial attention

The present study used repetitive transcranial magnetic stimulation (rTMS) to investigate virtual lesions in the dorsal premotor cortex (PMd) during a non-motor task. In a series of fMRI studies, this brain region has been demonstrated to be significantly engaged during the serial prediction task (SPT) in which subjects are required to predict upcoming perceptual events on the basis of sequentially regular patterns. These findings suggest that the premotor cortex contributes also to functions that are not directly related to motor output, as already proposed in monkeys.

To further clarify this assumption, we employed a visuospatial SPT, which is known to engage the PMd bilaterally around the crossing of the superior frontal sulcus and the superior precentral sulcus. Using a three by two design, rTMS was applied either targeting the right PMd, the left PMd, or a sham position in the vicinity of the occipital pole (factor SITE), and either during the early sequence encoding phase or during the late sequence deviant monitoring phase (factor TIME). In addition, we employed a non-predictive visual baseline task, which was expected not to be impaired by any stimulation and which controlled for perceptual and response effects. Twelve healthy young volunteers (4 female, mean age 25.1 years) participated in the study. All participants underwent a careful clinical screening to exclude enhanced risk for seizures, and the

experimental protocol was approved by a local ethics committee. Stimulation sites were determined by the following procedure. Using a standard 10-20-EEG cap, several areas on the scalp were marked by surveying relative distances between CZ and FCZ. Liquid-filled tablets were applied on these positions before subjects underwent an anatomical MRI scan (see Figure 4, left panel). Subsequently, the estimated stimulation sites over the right and the left target area in the PMd were slightly corrected on the basis of the anatomical MRI pictures. Immediately afterwards, participants performed in the rTMS experiment.

Performance was assessed by the absolute difference of error scores between the SPT and the neutral baseline task. As a result, we found a significant SITE by TIME interaction (F[1.4, 15.2]=4.2, p<.049). Single t-tests revealed that this interaction was caused by two effects (see Figure 4, right panel). First, early stimulation over the right PMd resulted in a behavioral impairment as compared to early stimulation over the left PMd [t(11)=2.7, p<.02]. Second, within the left hemisphere, performance was worse after late stimulation as compared to early stimulation [t(11)=2.9, p<.013]. Findings confirm that rTMS interference over PMd can cause behavioral impairments in a serial prediction task. Moreover, the specific effects suggest different functional roles of the right and the left PMd in the encoding and the deviant monitoring in perceptual sequences, respectively.



Figure 4. Stimulation sites (red: left dorsal premotor cortex, yellow: right dorsal premotor cortex) are shown on an individual brain (right panel). The lower panel shows the liquid-filled markers attached on the skull surface corresponding to the target areas, which are shown on the same brain on the upper panel. Bar charts show the error scores for the different stimulation conditions; significant *t*-tests are indicated by asterisks.

2.6.5

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Where action impairs visual identification - Action-induced blindness in an event-related fMRI study

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Behavioral studies revealed an impact of action on visual perception. If participants are engaged in a motor task, they proved to be worse at identifying a visual stimulus (actioninduced blindness effect; Müsseler & Wühr, 2002). In two event-related fMRI experiments, healthy participants had to accomplish a visual identification task combined with a Go-Nogo-task. Thus, we were able to investigate the influence of a motor response on visual identification. Three different stimulus onset asynchronies (SOAs) were used, providing different overlaps between the motor task and the visual task. We compared visually identical trials with and without a concurrently-performed motor response. Behavioral data revealed an impairment of visual identification in Go trials compared

to Nogo trials. This discrepancy is most pronounced at short SOAs, i.e., when the motor task and the visual identification task processing overlap to a great extent. FMRI results (Figure 5 and 6) showed an action-dependent BOLD response modulation in the extrastriate visual areas V3/V3A and, additionally, V4 in Experiment 2. Thus, results demonstrated that the planning of an action has modulatory effects in brain areas concerned with early processes in visual encoding, resulting in an identification impairment.

NOGO vs. GO (z > 3.1)



Figure 5. Experiment 1: The visual task required to identify masked left- or right-pointing arrows. Averaged contrast images of Nogo trials vs. Go trials with the SOA of 200 ms. Red blobs indicate a stronger activation in Nogo trials than in Go trials and blue blobs indicate stronger Go activations. Nogo activations: Along the transverse occipital sulcus (V3A) and in the right cuneus (V3). Go activations: In the left sensorimotor cortex and frontal eye fields, SMA proper, thalamus and cerebellum.



Figure 6. Experiment 2: We hypothesized that the extrastriate area where the BOLD modulation can be observed is stimulus-dependent, e.g., with color as relevant stimulus dimension the modulation should occur in a color processing brain area. Therefore, we changed the visual task: Participants had to identify masked red or green rings. The Go-Nogo-task remained the same as in Experiment 1. By adding color as stimulus dimension, an additional Go-Nogo-discrepancy appears in the color sensitive area V4.

The selection of task-relevant information: A functional MRI study

In our daily life it is permanently necessary to distinguish relevant from irrelevant information in order to determine the adequate behavior in a specific situation. The aim of the present study was to investigate the neural substrate underlying the selection of task-relevant information using functional MRI. We devised a new paradigm in which participants had to switch between two different number judgment tasks, which were instructed by task cues. The task cues had two dimensions (form and color). In half of the experimental blocks the color dimension was relevant, and in half of the blocks the form dimension was relevant. The congruency of both cue dimensions was manipulated within the blocks. In congruent trials, both cue dimensions indicated the same task. In incongruent trials, both dimensions indicated different tasks and in neutral trials only the relevant dimension indicated a task. When comparing trials in which both cue dimensions carried a task information (incongruent and congruent trials) with trials in which only the relevant cue dimension carried a task information (neutral trials), we found an activation in the middle portion of the left inferior frontal sulcus and in the left intraparietal sulcus (Figure 7). These findings suggest that these cortical areas are involved in the selection of task-relevant information. While some authors have pointed to the role of the lateral prefrontal cortex in cognitive control, the present experiment provides deeper insights into the understanding of this region.

2.6.6

Brass, M. & von Cramon, D.Y.



Figure 7. Cortical activation (z>3.1) for the contrast of incongruent and congruent trials versus neutral trials.

2.6.7

Derrfuss, J., Brass, M. & von Cramon, D.Y.

Cognitive control in the posterior frontolateral cortex: Evidence from common activations in task coordination, interference control, and working memory

Cognitive control has often been associated with activations of mid-dorsolateral prefrontal cortex. However, recent evidence highlights the importance of a more posterior frontolateral area around the junction of the inferior frontal sulcus and the inferior precentral sulcus (the inferior frontal junction area, IFJ). In the present experiment, we investigated the involvement of the IFJ in a task-switching paradigm, a manual Stroop task, and a verbal n-back task in a within-session within-group design. After computing contrasts for the individual tasks, the resulting *z* maps were overlaid to identify areas commonly activated by these tasks. We also averaged the group *z* maps from the three tasks and masked the resulting average *z* map by the overlap of all tasks to be able to



Figure 8. (A) Common activation at the peak coordinate in the left inferior frontal junction (x=-38, y=2, z=32). Voxels that were identified by the conjunction analysis are depicted in red.(B) Result of the conjunction analysis in the present study (red outline) in comparison to the significant activation found in the study by Brass and von Cramon (blue outline).

identify peak coordinates in regions revealed by the conjunction analysis. Common activations were found in the IFJ, in the pre-SMA extending into mesial BA 8, in the middle frontal gyrus bordering the inferior frontal sulcus, in the anterior insula, and in parietal and thalamic regions. Figure 8A shows the overlap at the peak coordinate in the left IFJ (x=-38, y=2, z=32). To display the similarity of IFJ activations in the current study and the study of Brass and von Cramon (Annual Report 2002, section 2.6.5), Figure 8B depicts the result of the conjunction analysis in the present study in comparison to the significant activation found in the study by Brass and von Cramon. Our results indicate the existence of a network of prefrontal, parietal, and subcortical regions mediating cognitive control in task coordination, interference control, and working memory. In particular, they provide further evidence for our assumption that in the frontolateral cortex not only the mid-dorsolateral region, but also the IFJ plays an important role in cognitive control.

Neuronal correlates of endogenous control in task-switching: An investigation with fMRI

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It is widely acknowledged that the prefrontal cortex (PFC) plays a major role for goaldirected behavior. For this, endogenous control is required especially when shifting from one task to another, as is the case in the task-switching paradigm. Recently, two different versions of the task-switching paradigm, the cueing and the alternating runs paradigm, have been investigated using fMRI. The aim of the present study was to explore neural correlates of endogenous control in task-switching by contrasting both versions. This was done by comparing two different external cue types (see Annual Report 2002). One of the cue types is the "transition cue", which provides information about repeating or switching the task but not about task identity. The second cue type is the "task cue", which is directly associated with the upcoming task set. We assume that the transition cue should require more endogenous control than the task cue, because, unlike the task cue, the transition cue requires the internal generation of the task set.

Fourteen subjects (six females) took part in this study. The random effects analysis of both cue types revealed significantly stronger activations for the transition cue in the left middle frontal gyrus along the left inferior frontal sulcus and the intraparietal sulcus bilaterally. We argue that this activation pattern reflects the coordination of updating and retrieval processes in order to implement the relevant task set. Increased activation was also found in the frontomedian wall (BA 8m), and is assumed to reflect the internal generation of the task set due to a less determined action context (Figure 9).

When comparing the present results with recent findings regarding the task cueing paradigm (see also Brass & von Cramon, 2002; 2003), it becomes evident that the transition cue reveals an activation shift in the anterior direction along the left lateral PFC and the frontomedian wall. Therefore, we obtained cross-regional interactions for two lateral prefrontal regions of interest (ROIs) including the mid-DLPFC and the inferior

2.6.8

Forstmann, B.U.¹, Brass, M.¹, Koch, I.² & von Cramon, D.Y.¹ frontal junction (IFJ). This was also done for two ROIs in the frontomedian wall enfolding BA 8m and a coordinate in the pre-SMA, which was appointed from the study of Brass and von Cramon (2002). The results revealed a functional gradient in the anterior-posterior dimension with the anterior regions showing a dominant role for internally guided compared to directly cued processes. We assume that this holds for both the coordination of information over a certain time interval, as well as for the internal generation of task sets in less determined action contexts.



Figure 9. Separately masked estimated beta values for each random effects analysis of cue type and nonevents (transition cue vs. non-event and task cue vs. non-event) with the random effects analysis of the main contrast (transition cue vs. task cue) with a Z-score higher than 3.1 (p<.0001 uncorrected). Only voxels being significantly activated and with a beta value higher than 0.2 are displayed. In addition, the difference of the mean estimated beta values for the two frontolateral (mid-DLPFC and IFJ) and two frontomedian (BA 8 and pre-SMA) ROIs are displayed.

2.6.9 Neural mechanisms of advance preparation in task switching

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In this event-related fMRI study we investigated brain processes associated with advance preparation in task switching. Previous results by one of us (Goschke, 2000) had shown that a central component of advance preparation consists of the retrieval of a verbal task-representation or "self-instruction". When participants verbalized the next task prior to the stimulus, switch costs were reliably reduced compared to when they were given no time to prepare. This reduction of the switch cost was completely eliminated, however, when task verbalization was prevented by an articulatory suppression task. Based on these results and own previous neuroimaging studies of verbal working memory

(Gruber, 2001; Gruber & von Cramon, 2003), we hypothesized that processes mediating advance preparation may be implemented by (at least some of) the same cortical regions as the verbal rehearsal mechanism. In the present study, 12 healthy right-handed volunteers underwent fMRI while performing a task-switching paradigm, in which geometric objects differing in shape and color had to be classified according to either color or shape. The critical independent variable was a manipulation of the cue-target-interval (CTI) in the range from 0 to 1500 ms. This manipulation made it possible to dissociate brain activity changes related to the processing of either the cue or the target. The statistical analyses confirmed our hypothesis that a network of left premotor and parietal as well as right cerebellar brain areas was activated during advance preparation for a task switch (Figure 10). This pattern of brain activations is consistent with our assumption that verbal task retrieval is an essential component of advance reconfiguration of task-sets. Further analyses will determine the functional connectivity between the activated brain regions in order to assess the dynamic interactions between brain systems involved in task-set reconfiguration.



Figure 10. Left premotor and parietal activations associated with the advance (re)configuration of task sets.

The CoRN: A neural correlate of error correction

Evidence in the literature for the proposed relationship of the error-related negativity (ERN) and immediate error correction is rather limited and inconsistent. We investigated corrective behavior and the ERN in two groups of healthy participants who performed a modified speeded flanker task. The correction-instructed (CI) group was asked to immediately correct all encountered errors. The correction-non-instructed (CN) group was unaware that corrective responses were recorded.

Participants of the CN group showed an immediate error correction rate of 17%. The intention to correct errors (CI) raised the correction rate to nearly 100% suggesting an additional intentional process. Participants in the CN group also showed immediate error correction, though to a lower degree. As illustrated in Figure 11, erroneous responses elicited an ERN. Only on corrected errors the ERN was followed by a second negative-going deflection peaking between 200 and 240 ms after the onset of an incorrect response. For the first time, we report an ERP component related to immediate error correction, the Correction-related Negativity (CoRN). This result supports the view that error correction is a dissociable sub-process of performance monitoring.

In support of this view, the data suggest different types of error correction depending on correction speed: Incidental fast error corrections and intentional slow error correction.

2.6.10

Fiehler, K., Ullsperger, M. & von Cramon, D.Y. The ERN and the CoRN latencies were modulated by the occurrence and the temporal characteristics of immediate error corrections (Figure 11). The ERN peaked significantly later for slowly corrected errors than for incidentally/rapidly corrected errors. This assumption was also supported by the results of the lateralized readiness potentials.



Figure 11. Response-locked grand averages for incidentally corrected (red, solid line) and uncorrected errors (pink, solid line) in the CN group and for slow (blue, dashed line) and fast (blue, solid line) error corrections in the CI group at FCz. Vertical lines mark mean response time of corrections, 1 =incidental error correction in the CN group, 2 = fast error correction in the CI group, 3 =slow error correction in the CI group; the first (erroneous) response occurred at *t*=0.

2.6.11 Is error correction reflected on the brain level?

Fiehler, K., Ullsperger, M. & von Cramon, D.Y. Error detection and error correction represent an important domain of performance monitoring. It has been proposed that the anterior cingulated cortex (ACC), especially the human homologue of monkey rostral cingulate motor area, called rostral cingulate zone (RCZ), plays a crucial role in error detection. The hemodynamic correlates of error correction, however, are less examined. We investigated corrective behavior in two groups of participants: One group who was asked to immediately correct all encountered errors (the correction-instructed [CI] group), and a second group who was unaware that corrective responses were recorded (the correction-non-instructed [CN] group). Participants performed a speeded modified flankers task.



Figure 12. Left: fMRI activation of error detection (incompatible correct vs. incompatible erroneous trials) on a coronal (y=1) slice of a 3D structural MRI; right: fMRI activation of error correction (incompatible corrected error trials vs. incompatible uncorrected error trials) on a coronal (y=1) slice of a 3D structural MRI.

Behavioral data provide evidence for an instruction-based behavior revealing a significantly higher correction rate for the CI group. As depicted on the left side of Figure 12, erroneous responses showed a higher activation in the RCZ supporting its important role in error processing. Additional error-related activation was observed in the pre-supplementary motor area (pre-SMA). One could speculate that this reflects post-response conflict monitoring.

In order to investigate error correction, we contrasted corrected errors occurring in the CI group with uncorrected errors occurring in the CN group. The group comparison revealed mainly two areas on the frontomedian wall related to immediate error correction: the RCZ and the superior pre-SMA (Figure 12, right). The data suggest that cortical areas involved in error detection also play a role in the implementation of immediate error correction.

Heart rate responses to performance monitoring

Error monitoring has often been described by means of event-related potentials and/or functional magnetic resonance imaging while measures reflecting activity of the autonomic nervous system such as heart rate (HR) or skin conductance were less considered. In our study we examined HR changes associated with response conflict and error processing comprising error detection and immediate error correction. In order to investigate corrective behavior, participants were randomly divided into two groups: The correction-instructed (CI) group, which was asked to immediately correct all encountered errors and the correction-non-instructed (CN) group, which was unaware that corrective responses were recorded. Participants performed a speeded modified



Fiehler, K., Ullsperger, M., Grigutsch, M. & von Cramon, D.Y.



Figure 13. Response-locked averages of HR changes in beats per minute (bpm) for incompatible correct trials (solid, black line) and uncorrected error trials (solid, gray line) in the CN group, and for incompatible correct trials (dashed, black line) and corrected error trials (dashed, gray line) in the CI group.



Figure 14. Stimulus-locked averages of HR changes in beats per minute (bpm) for compatible correct trials (solid, black line) and incompatible correct trials (dashed, black line).

flankers task. The intention to correct errors significantly increased the correction rate. In line with previous results, errors as well as correct responses elicited cardiac slowing being more pronounced for errors (Figure 13). This result suggests that error processing is accompanied by an autonomic response.

Both corrected and uncorrected errors evoked cardiac slowing, but there was a tendency towards an increase of deceleration in the response for uncorrected errors (see Figure 13). This result was interpreted in terms of motivational significance of the errors which seemed to be enhanced in the CN group: Non-instruction of error correction led to a more cautious response behavior reflected by less errors, more late responses as well as post-error slowing after committing an error. In contrast to previous findings, we found evidence that HR slowing is also sensitive to the degree of pre-response conflict: High response conflict occurring during incompatible correct trials elicited a greater HR deceleration than low response conflict occurring during compatible correct trials (Figure 14). We conclude that cardiovascular response is modulated by response conflict as well as error monitoring.

2.6.13 The posterior frontomedian cortex (BA 8m) and uncertainty in decision-making

Volz, K.G., Schubotz, R.I. & von Cramon, D.Y. In a previous fMRI study (Volz et al., in press), mesial Brodmann Area 8 (BA 8m) was identified as being involved in lower and higher degrees of decision conflict due to knowledge deficits. The present fMRI study sets out to investigate if activation within BA 8m is reduced only by increasing the frequency knowledge (real learning, RL), or also by increasing the frequency of positive feedback (pseudo learning, PL). In the RL condition, participants were provided with valid feedback and could thereby reduce their uncertainty of knowledge. In contrast, participants got no valid information from the feedback in the PL condition; however, a learning effect was simulated by gradually increasing positive feedback according to a learning model, which was derived from pilot data. Unspecific slow effects were controlled by subtracting a control condition (CC) from the conditions of interest. Direct contrasts between RL>CC and PL>CC revealed significant activation within BA 8m, the inferior frontal junction area (IFJ), Precuneus (Pcu), and intraparietal sulcus (IPS) (see Figure 15). A direct contrast between PL>RC revealed no significant difference within any brain region. Hence, the increasing



Figure 15. The left panel shows the main task effect (Z>3.09) for real learning vs. control condition; the right panel the main task effect for pseudo learning vs. control condition. Group-averaged activations are shown on sagittal (x=-5) and axial (z=32;50) slices of an individual brain normalized and aligned to the Talairach stereotactic space.

frequency of positive feedback appears to suffice to reduce activation within BA 8m. Accordingly, activation within BA 8m, which is suggested to be involved in uncertainty in decision-making, does not reflect insufficient knowledge, but the subjective trust in the level of knowledge.

Emotional and temporal aspects of situation model processing during text comprehension: An event-related fMRI study

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Language processing in context differs in fundamental ways from word and sentence comprehension. One subcomponent of complex language comprehension is the building of a so-called situation model, i.e., a mental model of the general gist of the text. In narrative texts, the situation model contains information on the what, where, who, when and why of the story. The present experiment investigated the on-line updating of the situation model using an inconsistency paradigm. Two information aspects were selected, temporal information (the "when"-aspect), and emotional information. Thirty-two stories were presented, half of which contained an inconsistency on the situation model level. Information type and consistency were fully crossed. Twenty participants were scanned while listening to the stories and performing an off-line consistency judgment. The results for an event-related analysis of the period from the target information until the end of the stories included an interaction between information type and consistency. For the emotional stories, the integration of the inconsistency into the unfolding situation model required the contribution of the fronto-median cortex (BA 8/9/10). In contrast, the integration of inconsistent information regarding the temporal aspect engaged a fronto-parietal network related to working memory processes. Taken together, these results show that situation model building is not a unitary process, but crucially depends on the information type presented.



Figure 16. Shown are activations from the contrast comparing inconsistent to consistent stories, analyzed during the short epochs (ca. 8 s) from presentation of the target information until the end of the stories. (A) The temporal stories elicited activation in bilateral inferior frontal cortex (BA 47/12). (B) The activation for the emotional inconsistencies lies in the fronto-median cortex, in a region previously implicated during inferencing and Theory-of-Mind processes (BA 8).

2.6.14

Ferstl, E.C.¹, Rinck, M.² & von Cramon, D.Y.¹

2.6.15 Making sense of nonsense: An fMRI study of task induced coherence processes

Siebörger, F.T., Ferstl, E.C. & von Cramon, D.Y. A central process for text comprehension is the establishment of coherence. The anterodorsal fronto-median cortex (adFMC, medial BA9/10) has been shown to be crucial for coherence building (Ferstl & von Cramon, 2001). Because of its involvement in other higher cognitive demands (Theory of Mind, emotional processing, etc.), we hypothesize that adFMC activation during comprehension of coherent sentence pairs reflects a domain independent, non-automatic process rather than stimulus properties. We conducted an event-related fMRI study, using a task aimed at inducing a 'search for coherence' even on *incoherent* sentence pairs and thus eliciting FMC activation. Fourteen participants were scanned while they listened to 30 coherent and 90 incoherent sentence pairs and judged the perceived strength of coherence on a 4-point scale (pragmatical relationship graded from 'directly evident' = 1 to 'unimaginable' = 4).

The behavioral data shows that the participants indeed used their creativity: 61% of the incoherent sentence pairs were rated as somewhat related and the response times for those trials were significantly prolonged. The functional data replicated the finding of adFMC activation during the processing of coherent texts (Figure 17A). As expected, this was not found when the differing decision times were taken into account: for a later stage of processing, during the 'search for coherence', the adFMC was equally strongly activated in all conditions. Furthermore, in this analysis the trials with weak or no coherence (response 2, 3, or 4) compared to trial with directly evident coherence (response 1) activated BA 8 more strongly (Figure 17B), an area which has been associated with decision making under uncertainty (Volz et al., 2003). In line with this interpretation the timelines (Figure 17C) indicate that the intermediate categories 2 and 3 drive this effect.



Figure 17. Averaged fronto-median activation map of the contrast response 1 vs. 2, 3, 4 ('coherence directly evident' vs. all other coherence ratings) mapped on a mean brain (x=-5) for (A) the *early event* (time-locked 1 second before offset of the 2nd sentence, Z-values thresholded at Z=3.8), (B) the *late event* (time-locked 1 second before the individual response, Z-values thresholded at Z=3.1), and (C) time courses for the 4th response responses in the activated mesial BA 8 area in the late event analysis.

All joking aside: A study on verbal humor and linguistic revision

Siebörger, F.T. & Ferstl, E.C.

Verbal humor is characteried by essentially three components: a *coherent* text, the cognitive resolution of a linguistic incongruity (*revision*) and an *affective* reaction. The process of coherence building via revision is a central element in modern theories of verbal humor. To show that this is not a sufficient constituent of jokes, we aimed at developing non-joke texts nevertheless requiring linguistic revision ('revision-non-jokes').

Examples:

Joke: Die Wirtin zum unglücklichen Stammgast: "Das ist ja schrecklich! Deine Frau ist mit deinem besten Freund durchgebrannt?" Er: "Ja, alles ist so sinnlos ohne ihn."

Revision-non-joke:

Katrin beim Frühstück zu ihrem Mitbewohner Mark: "Wie war eigentlich der französische Film gestern?" Er: "Enttäuschend, wir haben bei beiden Vorstellungen kaum Karten verkauft."

Additionally, we constructed straightforward as well as incoherent control texts, in order to disentangle all three elements of verbal humor (coherence, revision, affect) on the text level.

To evaluate the material, 32 healthy participants read 34 texts of each kind in a pseudorandomized order. The texts were presented on a computer screen, self-paced, sentence by sentence. The task was (a) to decide whether the text was delusive at first, and (b) to rate how funny it was on a 9 point scale. The results for the reading times and the revision-detection are shown in Figure 18A and 18B. For the wittiness-rating, the median was 3 for jokes and 0 for all other text conditions.

The results show that revision-non-jokes indeed require a linguistic revision comparable to those in jokes. However, in contrast to the jokes, neither the revision-non-jokes nor the straightforward or incoherent texts were perceived as funny. The hypothesis that linguistic revision is not a sufficient feature of verbal humor is, therefore, corroborated. Furthermore, the reading times confirm that the processing of jokes is not catchier in general. The material seems equally applicable for functional imaging and lesion studies.



Figure 18. For each text condition, the reading time for the 3rd sentence (A), and the correct responses for the revision-detection (B) is plotted.

Thirty years after its first successful demonstration, magnetic resonance imaging (MRI) has become an indispensable tool for clinical diagnosis as underlined by the long-awaited award of the 2003 Nobel Prize in Physiology or Medicine to its pioneers, Paul Lauterbur and Sir Peter Mansfield. It is almost equally indispensable in the neurosciences as it does not only reveal fine details of anatomy, but also permits imaging of tissue functioning. It is thus its flexibility that makes MRI such a powerful technique and leads to ongoing fruitful methodological research.

Quite naturally, a major focus of activity in the NMR group was on functional MRI (fMRI). Although the blood oxygen level dependent (BOLD) effect provides a solid workhorse for fMRI studies, details of its biophysical basis are still not completely understood. As an approach to separate contributions to the intravascular signal change quantitatively, flow dephasing and rephasing was applied to spin-echo (SE) fMRI (2.7.1). Recent claims in literature that changes in the extravascular spin density upon neuronal activation give rise to a non-BOLD type of functional contrast were ruled out by another series of SE experiments (2.7.2). By implementing radiofrequency (RF) spoiling into a three-dimensional (3D) echo planar imaging (EPI) sequence, the sensitivity to so-called physiological noise could be significantly reduced (2.7.3). This strategy improved the detection of resting-state BOLD signal fluctuations, which are believed to reflect functional connectivity.

Concepts of perfusion and diffusion imaging continued to be another core area of research. A theoretical study thoroughly investigated the efficiency of continuous adiabatic spin labeling (CASL) under physiological conditions (2.7.4). Experimentally, systematic variation of the delay between CASL and image acquisition yielded valuable information on arterial and tissue transit times (2.7.5). To achieve undistorted, high-resolution white-matter fiber tractography, navigator techniques for online motion correction were adapted for 3D diffusion tensor imaging (DTI) (2.7.6). While DTI visualizes anatomical connectivity, detection of cortical cell swelling related to task activation leads to diffusion-weighted fMRI (2.7.7).

Multiple-pulse sequences can be designed to observe long-range dipolar interactions between separate water molecules (2.7.8). While an experimental difficulty is that the detectable signals are subtle, there is hope that they provide a means to tailor fMRI to detecting susceptibility gradients on a mesoscopic scale adjusted by the experimenter. Two further projects were related to quantitative anatomical imaging and spectroscopy. Magnetization transfer imaging was optimized at 3 Tesla for future whole-brain analysis of the white-matter pathologies such as multiple sclerosis (2.7.9). Refinement of localized spectroscopy with segmented spatially selective pulses permitted excitation of anatomically shaped structures (2.7.10). On the hardware side, the previously developed

helmet coil for whole-brain coverage was certified in January, which cleared the way to its use in standard human experiments (2.7.11).

Besides pursuing research projects, a considerable amount of energy of the staff members was spent on setting up the Institute's new MAGNETOM Trio scanner. With a delay of three months, it was finally delivered to Leipzig on March 3, with the system being available to the Institute after three weeks of installation. After a few weeks of debugging, designing new protocols, and adapting post-processing software (2.7.12), anatomical patient studies as well as fMRI experiments started from May onwards. Disregarding occasional faults of single components, the hardware is essentially sound and the Institute's experimental capacity has considerably improved.

2.7.1 Separating the contributions to the intravascular signal change in spin-echo fMRI at 3 Tesla

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Diffusion-weighted (dw) fMRI is a valuable tool for quantifying the origin of the functional signal (i.e., larger vessels, capillaries, or extravascular space). To determine the contributions of these components, the approach of flow rephasing and dephasing was applied to fMRI. Diffusion weighting was introduced into spin-echo EPI by two consecutive bipolar gradient pulses. A second variant of this single-shot acquisition scheme with flow-compensation was obtained by reversing the first bipolar pulse. A region of interest with significant correlation (Z>2.6) on a non-dw measurement was used as a mask to select the time courses of the dw interleaves within the same trial. The fractional signal change was then calculated by averaging the time courses in



Figure 1. The relative signal change plotted versus the *b*-value for the flow-rephased and flow-dephased experiment.

dependency of the *b*-value as shown in Figure 1. Both curves show a large drop of the functional signal for small *b*-values. This can be assigned to spins showing a pseudo-random movement (e.g., turbulent and pulsatile flow). The decay of 0.5-0.6% for the flow-rephased signal can, therefore, be attributed to larger vessels where blood flow is fast. The constant difference of 0.3-0.4% between the two curves for higher *b*-values can be explained by a component with coherent flow. Because the difference remains constant over a wide range of *b*-values, this fraction may be assigned to smaller blood vessels with a smaller velocity. These data suggest that a *b*-value of 50 s/mm² without flow-compensation is sufficient to suppress nearly all of the intravascular contribution to the functional signal.

Is there a change in spin density associated with fMRI?

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Recently, a change in spin density upon neuronal activation was postulated to provide contrast in spin-echo (SE) fMRI at short echo-times. It is of paramount importance for the interpretation of fMRI to determine whether such a mechanism exists. To study the fMRI contrast as a function of echo-time, SE experiments with a varying echo time (TE) were measured in an interleaved fashion. In addition, a third pulse was applied subsequently to acquire a stimulated echo (STE) with the same effective TE (hence, with identical sensitivity to changes in spin density), but different weighting for perfusion and diffusion. A standard SE measurement (TE=80 ms) was appended to create a fixed mask of activated regions (p<.001) to compute comparable signal changes for the remaining experiments.



Figure 2. Signal changes as a function of TE.

2.7.2

Jochimsen, T.H.¹, Möller, H.E.¹ & Norris, D.G.² The course of fMRI contrast shown in Figure 2 was fitted to a straight line yielding

$\Delta S/S_0 [\%] = (26 \pm 2) \text{TE/s} + (0.02 \pm 0.05)$	(SE data)
$\Delta S/S_0$ [%] = (21±2) TE/s – (0.11±0.05)	(STE data)

A significant signal change at TE=0 is not observed consistent with the BOLD model. In addition, the increased sensitivity of the STE experiment to perfusion and diffusion decreases the fMRI contrast, confirming recent results that the intravascular compartment is the dominant source at short TE (section 2.7.1). Use of an independently measured mask with a high statistical significance provides robust values without inclusion of false-positives, which would produce an artificial baseline fMRI contrast. The interpretation that SE signal changes at short TE are mainly due to changes in spin density is contradicted by the decreased contrast in the STE experiment.

2.7.3 Quantification of the signal stability in resting-state fMRI

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Spatiotemporally structured noise, such as physiological noise, is a potential source of artifacts in functional magnetic resonance imaging (fMRI) and is the main limiting factor for the detection of small blood oxygen level dependent (BOLD) signal variations. In this project, fMRI is employed to detect spontaneous fluctuations of the BOLD signal in the resting human brain. The sensitivity to noise is investigated for a variety of imaging techniques. We demonstrate that incomplete relaxation of the transverse and the longitudinal magnetization between subsequent scans increases the level of temporally



Figure 3. Z-Maps representing interregional correlations of the primary sensorimotor cortex with other brain regions. For each voxel, the largest z-value of all seed voxels (marked in blue) is plotted. The yellow-to-red scale represents z-values from 3.1 to 6.

and spatially correlated signal fluctuations. In three-dimensional (3D) echo-planar imaging (EPI), the noise level is significantly increased by instabilities of the transverse steady-state magnetization as the repetition time, T_R , must be of the order of or less than T_2 . By implementing radio frequency (RF)-spoiling in the 3D EPI sequence, temporal signal fluctuations and erroneous interregional correlation in connectivity maps are diminished to a level comparable to 2D EPI (Figure 3).

Efficiency of flow-driven adiabatic spin inversion: A computer simulation



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Perfusion imaging using magnetically labeled water as an endogenous tracer is capable of measuring regional cerebral blood flow (Annual Report 2001, section 2.9.2; Annual Report 2002, section 2.8.5). Continuous arterial spin labeling (CASL) can be achieved by radiofrequency (RF) irradiation in the presence of a magnetic field gradient along the carotid artery, which results in an adiabatic inversion of the flowing spins. For quantification of perfusion, a reliable determination of the inversion efficiency of CASL is required. Among the most crucial problems are the influences of the blood flow dynamics and the RF field at the location of the carotid artery.

For further investigation, numerical simulations of the inversion process were performed under a variety of conditions, including both technical and physiological details. The profile of the RF field was found to influence the inversion efficiency only at small distances between the RF surface coil and carotid artery and can be neglected at greater distances (Figure 4). The inversion efficiency was further found to be relatively insensitive to the blood flow velocity within the physiological range (15 cm/s–70 cm/s) as shown in Figure 5. The influence of the cardiac cycle was found to be negligible as long as a sufficiently long labeling period is maintained, which is the case for CASL. Assuming typical conditions in dual-coil CASL, inversion efficiencies of about 85% can be obtained.



Figure 4. Dependence of the inversion efficiency on the distance from the RF coil.

2.7.4

Trampel, R.¹, Jochimsen, T. H.¹, Mildner, T.¹, Norris, D.G.² & Möller, H.E.¹



Figure 5. Dependence of the inversion efficiency on the blood flow velocity.

2.7.5 Dependence of continuous arterial spin labeling at the human carotid artery upon the post-label delay

Mildner, T., Möller, H.E., Driesel, W. & Trampel, R.

Continuous arterial spin labeling (CASL) for perfusion imaging in humans can be achieved by using a local surface coil to label blood in the common carotid artery (Annual Report 2001, section 2.9.2). Recently, CASL was used in a functional perfusion study to map cerebral blood flow changes in subjects performing a motor paradigm (Annual Report 2002, section 2.8.6).

For a further establishment of the method, knowledge of the transit times is essential with respect to both, sensitivity and quantification of perfusion. The ASL signal change was predicted to be independent of the transit time, if a sufficiently long post-label delay (PLD) is used. Two types of transit times can be considered, the arterial transit time, δ_a , and the tissue transit time, δ . Briefly, δ is the time the tracer needs to travel from the labeling region to the tissue of interest, whereas δ_a is the time after which the tracer has reached the vascular system within the voxel of interest. Measurements with and without the suppression of intravascular signal by using crusher gradients are required to extract both quantities.



Figure 6. ASL signal change obtained for one subject in the same session for PLD=700 ms (top) and PLD=1600 ms (bottom) by CASL at the position of the right carotid artery.

Figure 6 demonstrates the excellent quality of the maps of ASL signal change. The influence of the PLD is especially evident in smaller regions with higher signal changes. A longer PLD markedly reduces such "hot spots", whereas its influence is small in other regions.

The PLD dependence was measured with and without suppression of intravascular signal contributions and fitted to the Alsop-Detre model yielding $\delta_a = 1600 \text{ ms}$ and $\delta = 1930 \text{ ms}$ for the transit from carotid bifurcation to the level of the primary motor cortex. The overall sensitivity change averaged over the slice of interest was low for PLDs between 1000 and 1700 ms. For unambiguous quantification of perfusion, PLD values above 2000 ms should be used.

3D diffusion tensor imaging with 2D navigated and online motion corrected RARE

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Diffusion-tensor imaging (DTI) is a powerful method for mapping cerebral microstructure. The diffusion preparation makes the signal sensitive to Brownian motion of the water molecules. It is, however, also susceptible to bulk subject motion or pulsation, which leads to phase errors. To overcome such artefacts, we exploited a two dimensional (2D) Cartesian navigator with online motion correction (Annual Report 2002, section 2.8.8) combined with a 3D rapid acquisition with relaxation enhancement (RARE) sequence. Using ECG-triggering, the diffusion preparation started 400 ms after the Rwave to reduce pulsation as the navigator corrects only for rigid body motion. A twice refocused diffusion weighting scheme was optimized for eddy current effects. The 2D blipped EPI navigator was applied orthogonal to the diffusion direction to register all phase errors due to subject rotation and translation.

Sections from coronal slabs are shown for different diffusion directions in Figure 7. The anisotropic fibre structure of the corpus callosum is clearly visible. In Figure 8, eigenvectors corresponding to the maximal eigenvalue of the diffusion tensor indicate



Figure 7. Coronary sections for seven diffusion directions.



Figure 8. Axial section of the eigenvectors to the corresponding maximum eigenvalue of the diffusion tensor.

2.7.6

von Mengershausen, M.¹, Norris, D.G.² & Driesel, W.¹ fibre trajectories. Remaining artefacts may be related to movements during the long measurement time producing partial volume effects or residual eddy currents effects in the sequence. However, 3D DTI based on RARE seems to be a promising approach to high resolution undistorted tractography.

2.7.7 Transient changes of the apparent self-diffusion coefficient during task activation

Goerke, U. & Möller, H.E.

Previous reports suggest that the apparent self-diffusion coefficient (ADC) of extracellular water decreases during stimulation. High diffusion weighting is required for a sufficiently sensitive detection of the subtle changes of the ADC. To reduce signal attenuation related to cardiac pulsations, ECG-triggering was implemented in a recently developed stimulated-echo sequence (Annual Report 2002, section 2.8.9).

A visual paradigm was presented to six female and four male subjects. In the fMRI experiments consisting of three 90°-pulses, the diffusion-weighted primary (*pr*) and the stimulated (*st*) echoes were acquired with different diffusion weighting. Each slice was acquired 380 ms after the R wave. The exact time points of data acquisition and the onsets of stimulation and rest periods were recorded, along with the image data. The ADC was calculated from the ratio of the stimulated over the primary echo. Further data analysis was adapted for a variable repetition time (Figure 9). For all ten subjects, mean trial averages of the voxels in the visual cortex with Z<-2.33 (*p*<.01) were calculated (Figure 10). A spin-echo BOLD-sensitized data set of a single subject was statistically analyzed using the same procedure as for ADC data sets using the threshold Z>3.1.

Using ECG-triggered acquisition, the average standard deviation of temporal signal instabilities in the ADC time courses were significantly reduced. In nine out of ten subjects, significant decreases of the ADC (Z<-2.33, p<.01) were found in the Z-maps (Figure 9). This finding suggests that the detected signal changes take place in the extravascular compartment, indicating that changes in the ADC may probe neuronal activity more directly than the BOLD effect. Further experiments will be performed to investigate the physiological mechanism of the signal changes.







Figure 10. Bold and ADC trail averages. The orange box represents the stimulation period. The dashed line marks the maximum Bold signal change.

FMRI with intermolecular multiple-quantum coherences

Schäfer, A. & Möller, H.E.

In traditional magnetic resonance imaging (MRI), single quantum coherences (SQC) are observed. Multiple pulse methods make it possible to observe other coherences between states of a multi-spin system, which are made to evolve during some time interval and subsequently transformed into observable magnetization. In a typical liquidstate experiment, *inter* molecular multiple-quantum coherences (iMQC) are not observed. This is due to the fact that short-range dipolar interactions are averaged to zero in time by rapid molecular motion, whereas long-range intermolecular interactions average to zero in space as long as the sample is magnetically isotropic. However, magnetic field gradients can break this isotropy, and long-range intermolecular dipolar couplings can reappear in a mode determined by the experimenter. It has been suggested that the contrast in intermolecular double-quantum coherences (iDQC) imaging can be derived from variations in magnetic susceptibilities over a distance between 10 µm and a few millimeters, thus smaller than the normal voxel size. The signal of iDQC is scaled as $3 \cos^2 \theta - 1$, where θ is the angle between the interspin vector and the main magnetic field. The direction of the interspin vector is determined by the direction of the correlation gradients, which can be used to verify that the generated contrast truly originates from iMQC (Figure 11).

A motivation for using iMQCs in functional MRI (fMRI) is based on the fact that multi-spin coherences have a different sensitivity to susceptibility gradients than SQC. In a first fMRI study with visual stimulation task, a signal change of over 13% was observed (Figure 12).



Figure 11. The iDQC signal scales as $3 \cos^2 \theta - 1$ (from top left to bottom right: $\theta = 0^\circ$, 20° , 40° , 54.7° , 70° , 90°). The signal vanishes at the magic angle $\theta = 54.7^\circ$.



Figure 12. iDQC activation map superimposed on a conventional anatomical T_1 -weighted image.

2.7.9 Whole-brain magnetization-transfer contrast imaging at 3 Tesla

Wetzel, T. & Möller, H.E.

Magnetization transfer (MT) occurs if spins in two distinct environments exchange magnetization via cross relaxation or chemical exchange. In a two-pool tissue model, protons are assumed to exist in a highly mobile liquid water state (free pool) or on semisolid macromolecular sites of restricted motion, such as proteins or membranes (restricted pool). In attempts to isolate MT effects, acquisitions are often performed with and without saturation of the restricted pool, and MT ratio (MTR) images are computed. Such MTR maps are of special interest in neurodegenerative diseases like multiple sclerosis. While this is a standard application at 1.5 Tesla, results are not immediately comparable at 3 Tesla as relaxation times are different. Additionally, the specific absorption rate (SAR) may impose experimental limitations at higher fields due to the increased amount of RF energy required for effective saturation of the restricted pool.

We implemented and optimized an MTR imaging sequence, which covers the whole brain, but is still short enough for inclusion in routine patient examinations (Figure 13). Imaging is based on a two-dimensional gradient-echo (GE) sequence (flip angle 30° , repetition time 750 ms, echo time 10 ms, voxel size $1 \times 1 \times 3$ mm) with a total acquisition time of 4:02 min for 44 slices.



Figure 13. Reference GE image (left), MT-weighted image (middle), and computed MTR map (right).

2.7.10 Localized spectroscopy with segmented 2D spatially selective pulses

Körber, M.¹, Riemer, T.¹, Jochimsen, T.H.² & Möller, H.E.² ¹ Interdisciplinary Center for Clinical Research (IZKF), University of Leipzig ² Max Planck Institute of Cognitive Neuroscience

Spectroscopic information from an anatomical structure is typically obtained by placing a rectangular voxel in the region of interest or by performing a chemical shift imaging (CSI) experiment. To minimize partial-volume effects, the rectangular voxel needs to be smaller than the anatomical structure which wastes signal intensity, whereas CSI experiments often require corrections for undesired contributions. Two-dimensional (2D) radiofrequency (RF) pulses can be used to excite almost arbitrary shaped volumes, thus maximizing the SNR as compared to single-voxel spectroscopy. We have recently shown that 2D pulses can be used for spectroscopy of disk-shaped volumes (Annual Report 2002, section 2.8.11). Continuing along this direction, the localization quality was investigated for arbitrary shapes. Figure 14A shows a target region within the parietal white matter that was selected from an anatomy image. It was stored for subsequent use in an experiment designed to excite this pattern in a phantom. The use of short pulses (2 ms) results in a poor localization indicated by a severe spiral artifact throughout the phantom (Figure 14B). Using a segmented excitation scheme, the phase-sensitive addition of eight segments leads to a reasonable localization, while maintaining the desired bandwidth (Figure 14C). Implementation of the method within the ODIN framework (Annual Report 2002, section 2.8.3) instantanely allows the use of other NMR active nuclei such as ³¹P for studies of the energy metabolism.



Figure 14. Excitation of an arbitrarily shaped region using 2D-pulses: Target region marked in yellow on a T_1 -weighted image (A), images (RARE) of a gel phantom acquired with the target profile using only one segment (B), and the sum of eight segments (C).

A circularly polarized helmet coil for MRI and MRS

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In all *in vivo* magnetic resonance (MR) applications, a careful design of the radiofrequency (RF) coil is fundamental for optimizing the signal-to-noise ratio. Refinement of previous designs of a circularly polarized helmet coil (Annual Report 2000, section 2.9.4) led to a structure with the highest possible symmetry and structure elements as close as possible to the head (Annual Report 2002, section 2.8.1).

The coil is based on an assembly of two coplanar dual-loop coils of the split-circle design, which are arranged in a crossed fashion. Both coils circumscribe the human head. To optimize the design, numerical calculations of the distribution of the RF field \mathbf{B}_1 were performed and analyzed with respect to the efficiency and the occurrence of unwanted hot spots. Experimental verification included measurements with a pick-up coil as well as *in situ* experiments in a gel phantom at 3 Tesla. Best results were obtained with 5 cm wide copper strips carrying the RF currents and an overall helmet length of 20 cm (Figure 15). This geometry provides sufficient space for commercial audiovisual stimulation devices for fMRI experiments. The corresponding vector field in axial slices demonstrated a high degree of homogeneity and circular polarization in the region of

2.7.11

Driesel, W.¹, Merkle, H.², Hetzer, S.¹, Riemer, T.³, Zysset, S.¹ & Möller, H.E.¹



interest. Initial applications in healthy volunteers included anatomical MRI, singlevoxel spectroscopy (Figure 16) as well as functional imaging.

Figure 15. Contours of the RF field distribution in the *yz*-plane computed for different widths (2 cm, 5 cm, and 8 cm from left to right) of the copper foil on the spokes and for different lengths (24 cm, 20 cm, and 16 cm from top to bottom) of the helmet coil. The color code represents the \mathbf{B}_1 amplitude generated by a unit current in the coil. The white ellipse indicates the assumed position of the head.



Figure 16. Proton PRESS spectrum (TR 5 s, TE 25 ms, 150 acquisitions) recorded from a 3.4-mL voxel within the parieto-occipital white matter with contributions of *N*-acetylaspartate (NAA), N-acetylaspartylglutamate (NAAG), total creatine (Cr), total cholines (Cho), glutamate (Glu), glutamine (Gln), and *myo*-inositol (m-In).

DICOMj—A Java-based DICOM image viewer for Linux

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The lack of Linux applications to read and view image data based on the most recent DICOM standard [http://medical.nema.org/dicom] led to the development of a new, fully Java-based DICOM viewer (DICOMj). The import of magnetic resonance (MR) image series as produced by the Institute's MAGNETOM Trio was one of the main requirements. Furthermore, basic view functionalities like zooming, window level/width adjustment, and the display of basic image and series parameters were mandatory.

Our "application framework" developed in the past to easily create applications for MR data processing, visualization, and analysis was used as starting point for DICOMj. This framework is fully Java-based and consequently ensures an application's instant availability on a variety of operating systems, including Linux. The framework's modular architecture guarantees the simple extensibility of the resulting applications. DICOMj was developed in less then two months on top of this framework and meets all the above requirements. It provides the operator with a comfortable user interface for routine work.

Circel T1: 400.0 T2: 110.0 T1: 0.0

Figure 17. DICOMj at work.

2.7.12

Schlumm, T.¹ & Riemer, T.²

The working group 'Mathematical Methods in fMRI' focuses on the development of new methods for the evaluation of magnetic resonance data. As in recent years, a major aspect of our work was the improvement of our software package 'Lipsia' (Leipzig Image Processing and Statistical Analysis). Lipsia is the in-house software for the analysis of functional magnetic resonance data. During the past year, we have adapted Lipsia to our new 3 Tesla Siemens scanner. Our software is now fully compatible with the Siemens/DICOM environment. In addition, new algorithmic developments were made especially with respect to dealing with the multiple comparison problem. New visualization capabilities were also added (2.8.1).

Recently, Bayesian methods have received quite a lot of attention as a new approach to the analysis of fMRI data. Bayesian approaches offer several advantages over the "classical" statistical methods that are based on null hypothesis testing (NHST). With NHST, we can only hope to disprove an uninteresting null hypothesis such as "the effect is non-existent", and conclude that the converse is true. With Bayesian methods we can directly investigate the hypothesis itself, not its uninteresting opposite. At first glance, this may seem to be a sophisticated but purely academic detail. However, it turns out to be of great practical consequence. For example, it allows us to directly derive conclusions like "the probability that the time to peak differs by less than 0.5 seconds between two groups of subjects is 99%". Such statements are inherently impossible to make in the context of NHST.

However, the advantages of Bayesian methods come at a price, namely a very high computational load which in many cases becomes prohibitive. Therefore, we have developed a Bayesian method that is restricted to higher level fMRI analysis (2.8.2). This method still retains many advantages of the Bayesian approach, but its computational load is very low. It has thus become a viable technique.

Other methodological work aimed at investigating the temporal behavior of the BOLD response. In previous work, we found a very high variability in the phase shift. To better understand this phenomenon, we developed a wavelet-based method for computing phase shifts. Wavelets are better suited for this purpose than previously used methods, because they do not presuppose stationarity of the time series (2.8.3 and 2.8.4).

In the context of high-resolution T1-weighted MRI data, we developed a method for deriving a "standard" gyral brain model (2.8.5). Such a model is important for intersubject registration. Currently, in inter-subject registration a single brain is selected at random from a data pool, and subsequently used as a model onto which all other brains are geometrically aligned. This procedure may, of course, introduce a bias into subsequent processing steps. Our new synthetically derived model alleviates this problem. Another focus of our work was the development of software for the analysis of diffusion tensor imaging data (DTI) (2.8.6). DTI is an imaging technique that allows to investigate white matter fiber bundles that are largely invisible in T1- or T2-weighted MRI data. DTI will probably play a much larger role in the years to come, and we have now made our first steps into this exciting new field.

2.8.1 LIPSIA – Leipzig Image Processing and Statistical Inference Algorithms

Lohmann, G., Müller, K., Neumann, J., Anwander, A., Hagert, A., Zysset, S., Bohn, S. & von Cramon, D.Y. Lipsia is a software package for the analysis of functional magnetic resonance imaging (fMRI) data. The package comprises various tools for preprocessing, spatial transformation, statistical evaluation as well as segmentation and visualization. During the last year, the software was extended for data acquired at our new Siemens Trio MR scanner. All Lipsia programs were successfully tested for the new data format. Lipsia was augmented by a new group analysis based on Bayesian statistics. This analysis allows the calculation of activation probabilities from parameter estimates of the General Linear Model. The statistical tools were also supplemented by the False Discovery Rate (Benjamini and Hochberg, 1995). Lipsia further provides new tools for the correlation analysis of fMRI data.



Figure 1. Visualization of activated brain regions in LIPSIA. Particular emphasis was placed on further development of the visualization of cortical folding patterns and fiber tracks. Graph data can be geometrically linked to the coronal, sagittal and axial slices. A single mouse click shows the corresponding regions in all windows.

Bayesian second-level analysis of functional magnetic resonance images

The most widely used methods for the statistical analysis of functional magnetic resonance images (fMRI) are based on a linear model of the hemodynamic response function and the detection of activated voxels by means of null hypothesis significance tests (NHST). Such tests have a number of drawbacks, such as the difficult and counterintuitive interpretation of the test results and the need to adjust them for multiple comparisons. Moreover, such methods can only disprove, but not prove a hypothesis, which makes answering complex scientific questions difficult. We have developed a new method for the second-level analysis of fMRI data, i.e., for the analysis of groups of subjects. This method is based on Bayesian statistics and overcomes the problems of NHST-based approaches.

Inputs to the method are parameter estimates for experimental contrasts in single subjects. These estimates are combined by means of Bayes' Theorem, resulting in posterior probability distributions from which probabilities of activation in the entire group of subjects can be calculated. By providing activation probabilities the new method facilitates inferences, such as the comparison of groups of subjects, which are hard or impossible to formulate in terms of classical NHST. Moreover, Bayesian analysis does not require an adjustment for multiple comparisons and is very robust against outliers, which in the classical analysis have a large influence on the statistical significance of the results. It is, therefore, particularly effective in the detection of cortical activation caused by small experimental contrasts.



Figure 2. A comparison of classical and Bayesian second-level analysis of fMRI data for the Stroop interference task. A classical analysis shows the statistical significance of activations (left), the Bayesian analysis provides probabilities of activation (right).

2.8.2

Neumann, J. & Lohmann, G.

2.8.3 Investigating the wavelet coherence phase of the BOLD signal

Müller, K., Lohmann, G., Neumann, J., Grigutsch, M., Mildner, T. & von Cramon, D.Y. The temporal dynamics of the blood oxygenation-level dependent (BOLD) signal is still not fully understood. Current methods of averaging the BOLD signal in the time or spectral domain are restricted to stationary processes, i.e., processes that show a similar behavior over time. The wavelet coherence phase is a measure that overcomes this limitation. It provides a description of the temporal behavior of the BOLD signal even for the non-stationary case. In particular, temporal changes of the phase can be investigated. This makes the wavelet coherence phase more suitable for the investigation of BOLD dynamics than an average measure obtained by correlation or spectral methods.



Figure 3. Time-frequency scalograms of the BOLD signal of an individual subject evoked by a visual hemifield stimulation using stimulus lengths of 15, 6, and 2 seconds. The first and the second row show scalograms for activated and non-activated brain regions. For activated voxels, most of the energy is located in the frequency scales that are associated with the full cycle length of a trial. Non-activated brain regions show a more scattered distribution of the wavelet spectrum. The third and the fourth row show scalograms of the wavelet coherence phase of the BOLD signal of the activated and non-activated region w.r.t. a selected reference region.
The variability of the BOLD wavelet coherence phase

In order to investigate the variability of the wavelet coherence phase of the BOLD signal, a correlation analysis was performed between the circular variance of the phase shift and the associated activation strength. Because of the periodic stimulation, the wavelet coherence phase showed a stable behavior in regions that strongly responded to the paradigm. Other regions showed a temporal variability of the phase shift. The lower the strength of activation, the higher the variability of the phase. In main activated regions, the mean wavelet coherence phase supports the results obtained by spectral analyses.

2.8.4

Müller, K., Lohmann, G., Neumann, J., Grigutsch, M., Mildner, T. & von Cramon, D.Y.



Figure 4. Individual maps of the mean wavelet coherence phase (first row) and maps of the spectral density phase shift (second row) of the BOLD signal evoked by a visual hemifield stimulation using stimulus lengths of 15, 6, and 2 seconds. Phase shifts were computed for brain regions that show a minimum sample coherence of 0.8 (visual cortical areas). Regions with an early response (color coded in yellow) can be separated from regions with a late response (color coded in red). Correlation between the mean wavelet coherence phase and the spectral density phase shift is above 0.9 independent of the duration of visual stimulation. For brain regions with a weakly stationary behavior, the spectral density yields nearly the same phase shifts as the mean wavelet coherence phase.

2.8.5 Constructing a synthetic brain template for inter-subject registration

Lohmann, G.

One of the most difficult problems in the analysis of magnetic resonance data of human brains is the problem of inter-subject registration. Inter-subject registration aims at geometrically aligning brain data of different subjects. Generally, one standard brain is chosen that serves as a template onto which all other brains are registered. The choice of such a model brain is mostly arbitrary and may severely bias subsequent processing steps. To alleviate this problem, we have developed a method of constructing a synthetic model brain that is derived from brain data of a large group of subjects and that is geometrically representative of this group. This synthetic template can then serve as a model for inter-subject registration.

Our input data consisted of 96 T1-weighted MRI data of healthy subjects acquired on the Institute's 3-Tesla magnetic resonance scanner (Bruker Medspec 300) using a MDEFT pulse sequence. The spatial resolution was 1x1x1 mm. A sequence of image processing steps revealed a primary gyral structure that could be identified semi-automatically in all data sets. Secondary or tertiary cortical folds were ignored for this project. These primary gyri were then assembled into a common geometric reference frame, and a generic model was extracted using a nonlinear principal component analysis and principal curves. This generic model resides at the geometric center of all 96 original data sets.



Figure 5. The generic brain model derived from 96 individual brain data sets. Major gyri appear as colored polygons that serve as landmarks in subsequent inter-subject registrations. Semi-automatical tools were developed for identifying the corresponding gyri in each individual data set.

2.8.6 Investigation of 3D anatomical connectivity from diffusion tensor imaging (DTI)

Anwander, A., Lohmann, G., von Mengershausen, M. & Möller, H.E. Diffusion tensor imaging reveals information on fiber tracts that connect cortical areas. The new Siemens Trio MR scanner allows fast whole head DTI acquisitions. To analyze the DTI data together with functional maps, we integrated the visualization of DTI data in the standard visualization tool. To investigate the anatomical connectivity and fiber orientation in human brain white matter, we extracted the trajectories of individual fiber tracts from a DTI tensor map. This tracking algorithm generates a trajectory by following the main fiber direction in the DT image starting from a seed point or a seed region. For the assessment of the statistical degree of anatomical connectivity in regions with merging/crossing or splitting fiber bundles, a Monte-Carlo type 3D random walk algorithm was implemented (Koch et al., 2002). The Figures 6 and 7 show exemplary visualizations of the diffusion tensor information.



Figure 6. Distinction of thalamic regions based on characteristic fiber orientation from diffusion tensor images. The left figure shows a region of interest in a sagittal slice of a T1 weighted MR image. The right figure shows the principal fiber orientations in the color-coding according to the red-green-blue sphere shown at the top with red indicating mediolateral, green anteroposterior and blue superoinferior direction. The black lines indicate the in-plane components of the fiber orientation. Fiber directions in voxels with low anisotropy are suppressed.



Figure 7. Investigation of the 3D statistical connectivity of the white matter fibers from the particle-jump algorithm. The color map indicates the degree of connectivity with a seed point in the visual cortex (light green area). Bright colors indicate a high connectivity. In this example, the color map is overlaid on the b0 component of the DTI scan.

This year's report again can be separated into methodological and psycho-cognitive contributions. The most important result is very likely the dramatic acceleration in calculating the so-called lead field bases and the influence matrix which both are needed to solve the EEG and/or MEG inverse problem (2.9.1). This new technique turns out to be very effective when estimating current density solutions for which the number of sources is much higher than the number of sensors. Additional techniques of optimization are described in (2.9.2). Accuracy of the inverse toolbox software was tested by analyzing real measurements from a rabbit's brain with realistically shaped volume conductors and comparing the source localization results with EcoG data (2.9.3). Another paper deals with final statistical analysis of current density solutions. This approach suggests region of interest definitions based on principal component analysis of these solutions (2.9.4).

An EEG study relates stronger γ -activity with access to our 'world-knowledge'-base (2.9.5). Investigating why γ -activity often varies in sensitivity when comparing similar cognitive paradigms, it could be demonstrated that the influence of stimulus salience is stronger for γ -activity than for ERP's (2.9.6). By analyzing γ -activity it could also be demonstrated that early visual processing is very significantly accelerated by a corresponding and consistent auditory channel, whereas no advantage was found for the opposite (2.9.7). MEG recordings during presentation of meaningful and meaningless hand signs were analyzed and the results nicely reveal a temporal well-sorted cooperation of neuronal subsystems (2.9.8). An EEG study investigates the extraction of meaning of a lexical element during speech processing under ideal and disturbed conditions (2.9.9). Another study focusing on auditory processing revealed that complex patterns are simultaneously processed both, in an holistic and an element-wise way (2.9.10). Finally, a combined EEG and MEG study conducted with musicians and non-experts demonstrated that musical phrase structures also elicit a positivity at the phrase boundary as observed earlier with language processing (2.9.11) (see also section 2.3).

2.9.1

Wolters, C.H.^{1, 2}, Grasedyck, L.² & Hackbusch, W.²

Efficient computation of lead field bases and influence matrix for the FEM based EEG and MEG inverse problem

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The inverse problem in electro- and magneto-encephalography (EEG/MEG) aims at reconstructing the underlying current distribution in the human brain using potential differences and/or magnetic fluxes that are measured non-invasively directly, or at a close distance, from the head surface. The simulation of EEG and MEG fields for a given dipolar source in the brain using a volume-conduction model of the head is called the forward problem. The Finite Element (FE) method, used for the forward problem, is able to realistically model tissue conductivity in homogeneities and anisotropies, which is crucial for an accurate reconstruction of the current distribution (Annual Report 2002, sections 2.10.12/13/14). So far, the computational complexity is quite large when using the necessary high resolution FE models. It is already known that the concept of the so-called lead field basis together with Helmholtz reciprocity can strongly reduce this complexity with regard to the EEG modality. We derived algorithms, which extend these concepts to both the EEG and MEG. In the state-of-the-art approach to the inverse problem, "number of sources", i.e., thousands of large sparse FE linear equation systems have to be solved. Our new approach only necessitates the solution of "number of sensors" of such FE equation systems for the computation of the EEG and MEG lead field bases (rectangular matrices with "number sensors" rows and "number FE nodes" columns) in a setup phase (only once per head model). After this setup, each EEG and MEG forward solution within the inverse problem then only needs the multiplication of the lead field bases by the source vector which can be carried out very fast. The speedup factor is more than 100 for a realistic choice of the number of sensors and sources. Our approaches can be applied to inverse reconstruction algorithms in both continuous and discrete source parameter space for EEG and MEG and for the blurred and the mathematical dipole model. For the latter source model, we furthermore have to make use of the H-matrix concept for an efficient storage of the singularity potential matrix (see Figure 1). In combination with parallel AMG-CG solvers with Multi-RHS treatment (see section 2.9.2), the presented approach leads to a highly efficient solution of FE-based source reconstruction problems.



Figure 1. Hierarchical H-matrix for storing the block of singularity potential vectors.

Multiple right-hand side treatment in parallel algebraic multigrid solver for fast finite element method based EEG and MEG source reconstruction

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If the Finite Element (FE) method is chosen for volume conductor modeling within the EEG/MEG inverse problem, the setup phase for the construction of the lead field bases (see section 2.9.1) requires the repeated solution of large sparse systems of linear equations. Therefore, preconditioning techniques for the iterative solution process are important to speed the computation. Previously (see Annual Report 2001, section 2.4.3), we presented a very efficient solution strategy, the parallel Algebraic MultiGrid preconditioned Conjugate Gradient (AMG-CG) approach. For an anisotropic tetrahedra FE head model with 892115 elements and 147287 nodes (Annual Report 2002, section 2.10.11), a speedup of 95 (SGI Origin2000) was achieved when compared with a standard solver in FE based source reconstruction, 9.5 through multigrid preconditioning and 10 through parallelization on 12 processors. We will now discuss a new strategy for a further speedup, the treatment of multiple Right-Hand Sides (RHS). The most computationally expensive operations in the AMG-CG are the matrix-vector multiplications within the CG and within the AMG-components smoother, defect calculation, interpolation and prolongation. If the vector for one RHS is exchanged against a whole block of vectors for multiple RHS and if this block is not stored as a matrix, but as a block-vector (first the first entries of the RHS's, then the second entries etc., resulting in a long vector), then each matrix entry only has to be accessed once and can be multiplied to all corresponding values in the block-vector. This results in much higher cache hit rates, which speeds up the computations. The speedup-results for multiple RHS on an AMD Athlon Linux-PC cluster with 900 MHz processors are illustrated in Figure 2. For the simultaneous treatment of 3 and 5 RHS, the inner loops were manually unrolled, leading to a further reduction of the solver time.



Figure 2. Anisotropic tetrahedra FE model, 147287 nodes: Speedup through treatment of multiple RHS.

2.9.2

Wolters, C.H.^{1, 2}, Anwander, A.¹, Haase, G.³ & Reitzinger, S.⁴

2.9.3

Anwander, A.¹, Flemming, L.², Güllmar, D.², Haueisen, J.², Knösche, T.R.¹ & Wolters, C.H.^{1,3}

Comparison of the boundary element method and the finite element method in ECoG/MEG source localization in an animal model

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Source localization in the human brain based on EEG and MEG data is becoming more and more important. Thus, information about source localization accuracy is indispensable. Source localization is based on volume conductor models, which can be realized using e.g., the boundary or finite element method (BEM/FEM). In our study we compare the source localization accuracy obtained with BEM and FEM models using the inverse toolbox of the SimBio project.

We simultaneously measured the electrocorticogram (ECoG) and the magnetoencephalogram (MEG) after peripheral nerve stimulation in the rabbit. FEM and the BEM models were generated from segmented MR images of the rabbit head. FEM computation was accelerated with an algebraic multigrid method as FEM solver within the NeuroFEM software. This speed-up enabled inverse source localization using a generic inverse problem toolbox (ANT Software). Both focal (single moving and rotating dipole) and distributed source models (minimum L2 norm) were employed. Figure 3 shows the volume conductor models with the sensor configuration.



Figure 3. BEM model (left) and FEM model (right) of the cortex of a rabbit with electrodes and gradiometer coils.

For the focal source models we found a very good agreement between the results computed with the FEM and BEM model. The source localization differences were below 1 mm for all source models. For the distributed source models we found the maximums to be identically localized. Using an isotopic FEM model we found no significant differences in source localization as compared to using a BEM model. Future work will include conductivity tensor imaging based anisotropy into the FEM model.

PCA-based ROI analysis – A new approach for spatio-temporal multiple source 2. estimation

For objective and routinous analysis of MEG data we consider that brain surface current source density (CSD) should be useful, because it can provide stable solution based on few assumptions. Previously, we have developed a procedure which allows statistical group analyses in CSD datasets (Nakamura et al., Annual Report 2002). However, it is difficult to separate closely-located multiple sources with this method because CSD shows a blurred activity distribution. In order to improve this point, we have further developed a new analytic procedure which allows reliable spatio-temporal multiple source estimation. The procedure, named PCA-based ROI analysis, is as follows: 1) We calculated CSD individually, and then solutions were spatially normalized onto Talairach's standard brain space by linear transformation. 2) A principal component analysis (Maess et al., 2002) (PCA) was applied to the CSD data in order to extract spatio-temporally separable independent factors in the time-series. At first, a rectangular matrix was constructed that had a column for each CSD node and a row for each time instant of all conditions by all subjects. Then the covariance matrix of the CSD matrix was submitted to a PCA. After extraction of spatial factors, these factors were rotated using varimax rotation. 3) Using spatial information from the PCA-factors, a region of interest (ROI) analysis was applied to the CSD data to obtain time courses of specific regional electrical activity. In each ROI, time courses for all conditions in CSD were calculated individually. Following on from this, significant activation and condition effects were statistically tested.

Figure 4 (next page) shows an example of the application of PCA-based ROI analysis. The result demonstrates that this method can extract spatio-temporally independent brain regional electrical activity from the CSD data with physiologically plausible distributions, and provides very useful information for understanding highly complicated brain processes during specific cognitive events.

Memory access explains human gamma responses

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Human brain activity in the gamma frequency range was shown to be a correlate of numerous cognitive functions. However, to date there is no coherent theory predicting under which experimental conditions gamma activity would arise. One mechanism underlying all of the above cognitive functions is access to memory and may thus explain the phenomenon. We tested the hypothesis that gamma activity is evoked whenever stimuli match memory representations. EEG was recorded from 16 subjects performing a choice reaction task. Visual stimuli were either known real-world objects with a memory representation or novel configurations never seen before (cf. Figure 5). All stimuli evoked an early gamma response, which was maximal over occipital electrodes. This evoked

2.9.4

Nakamura, A., Maess, B., Knösche, T.R. & Friederici, A.D.

2.9.5

Herrmann, C.S.^{1, 2}, Lenz, D.², Junge, S.², Busch, N.A.^{1, 2} & Maess, B.¹



Figure 4. A result of PCA-based ROI analysis, which was applied for a study for hand sign recognition (see section 2.9.8). Spatial distribution of each factor extracted by PCA (column PCA), ROI patterns created from PCA (ROI) and time courses of averaged CSD in each ROI (time course). Time courses of the 3 conditions are plotted with red (HM+), blue (HM-), and green (HC). Time courses, which showed statistical significant condition differences (p<.05, ANOVA after Bonferoni correction), are indicated by asterisks. Time windows during which statistically significant condition differences occurred (p<.05) are indicated in red (HM+ > HM-), yellow (HM+ > HC), and green (HC > HM+) bars.

gamma activity was significantly larger for items which matched memory templates (cf. Figure 6). No significant differences were found for the comparison of round versus edgy figures. Therefore, we argue that gamma activity results from the feedback between memory and perception systems. This assumption for the first time integrates the data of many experiments and offers a unifying theory.



Figure 5. Examples of the stimuli used in the experiment. Two objects with a representation in long-term memory (LTM, red) and the corresponding non-objects, which are composed of the same parts, but have no representation in LTM (blue). Subjects were instructed to differentiate between round (top row) and edgy (bottom row) figures in order to keep the results free of confounds through LTM representation.



Figure 6. The early peak of gamma activity, which was evoked by the stimuli, shows a clear difference between known objects with LTM representation (red) and unknown non-objects (blue).

Size matters: Finding the optimal stimulus configuration for investigations of the visual evoked gamma-band-response

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- ⁴ Cellular Neurobiology Group, Institute of Medicine, Research Center Jülich

In recent years, there has been a growing interest in complementing the classical analysis of EEG and event-related potentials (ERPs) with various approaches of analysis in the frequency domain. In particular, the called gamma-band ranging from 30 Hz to 80 Hz has been found to correlate with various cognitive processes. However, numerous

2.9.6

Busch, N.A.^{1, 2}, Debener, S.^{3, 4}, Kranczioch, C.^{3, 4}, Engel, A.K.^{3, 4} & Herrmann, C.S.^{1, 2}

attempts to investigate gamma-band oscillations in human EEG have failed to find a gamma-band-response (GBR) at all. Hence, some authors cast doubt on the functional significance of the GBR in human EEG. It is possible, though, that a strong GBR can only be elicited by a stimulus with suitable physical properties. Thus, we investigated the degree to which the visual evoked GBR is modulated by stimulus properties. To this end, we presented stimuli of variing size $(1,5^\circ, 4^\circ \text{ and } 8^\circ \text{ visual angle})$, eccentricity (central, 4,3° or 8,6° to the left), and duration (50 ms, 150 ms or 250 ms) in a simple choice reaction task. EEG was recorded from 23 subjects who had to discriminate circles and squares, irrespective of the stimulus properties of interest. The results showed a strong modulation of the GBR by stimulus properties (Figure 7). GBR amplitudes were larger for larger and central stimuli. For short stimulus durations, the onset and offset peaks of the GBR superimposed resulting in a larger early peak. We found these exogenous modulations of the GBR to be even more pronounced than those of early ERP (P1 and N1). The implications of our results are twofold. First, cognitive effects on the GBR can only be determined, if the magnitude of the GBR is sufficient. Thus, use of a salient stimulus (central presentation, size larger than 4° visual angle) is preferable. Second, if different experimental conditions involve the use of stimuli with different physical properties, one must be careful not to confound bottom-up with topdown effects.



Figure 7. Evoked GBR at electrode E58 (corresponding to O1) in the size-, eccentricity- and duration block. Large and central stimuli evoked larger GBR amplitudes. For short stimuli durations, the onset and offset peaks of the GBR superimpose.

2.9.7 Bimodal audio-visual processing enhances event-related gamma responses

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Stimuli usually capture our attention more easily when they are presented in multiple sensory modalities simultaneously, i.e., when auditory and visual stimuli are perceived at the same time. The goal of the present experiment was to investigate how event-related gamma-band responses (GBRs, 30-80 Hz) in the EEG reflect such audio-visual processing. A randomized stream of unisensory auditory, unisensory visual, and multisensory audio-visual stimuli was centrally presented while subjects were instructed

to detect occasional deviant visual or auditory target stimuli in a visual or an auditory attention block, respectively. Multisensory audio-visual stimuli were presented with stimulus asynchronies of auditory and visual inputs ranging between ±125 ms. In order to prevent superposition of event-related oscillatory responses, GBRs of five different 50 ms subranges of the ± 125 ms SOA range were calculated and compared with GBRs of unisensory control stimuli (e.g., auditory precedes visual by 125 to 75 ms, by 75 to 25 ms, etc.). We found enhanced evoked gamma responses for bimodal as compared to unimodal stimulation. In the attended visual block, we found enhanced posterior eventrelated GBRs to visual stimuli when unattended auditory stimuli either preceded visual stimuli by 50±25 ms or when audio-visual stimuli were presented simultaneously (Figure 8, top left). For unattended auditory stimuli in the same block, we found enhanced eventrelated GBRs over anterior scalp areas particularly for simultaneously presented audiovisual stimuli, indicating a higher time sensitivity of the auditory system in audio-visual processing (Figure 8, top right). Next, we analyzed event-related GBRs in the attended auditory block. For auditory stimuli, we found no differences between the 5 SOA time windows and the unisensory control stimuli, suggesting that unattended visual stimuli do not affect early processing of attended auditory stimuli (Figure 8, bottom right). However, frontal GBRs for unattended visual stimuli were enhanced when audio-visual stimuli were presented simultaneously (Figure 8, bottom left). The frontal topography of this effect indicates a crucial involvement of the auditory system, suggesting a close relationship between oscillatory activations in auditory and visual cortex areas. To summarize, our study showed that event-related GBRs reflect early audio-visual processing, which is highly time sensitive and dominated by the auditory system.



Figure 8. The figure shows event-related gamma responses in the attend visual and attend auditory condition for five different SOA time windows (ranging between ± 125 ms) and unisensory control stimuli. The study demonstrated that event-related gamma responses reflect very early audio-visual processing.

2.9.8 Cooperation of different neuronal systems during hand sign recognition

Nakamura, A.¹, Maess, B.¹, Knösche, T.R.¹, Gunter, T.C.¹, Bach, P.² & Friederici, A.D.¹ ¹ Max Planck Institute of Cognitive Neuroscience ² Max Planck Institute for Psychological Research, Munich

Hand signs with symbolic meaning can often be utilized more successfully than words to communicate an intention, however, the underlying brain mechanisms are undefined. We measured visual event-related MEG responses to meaningful (HM+) and meaningless (HM-) hand signs while participants assessed the meaningfulness of hand postures. We also measured MEG responses to hands (HC) (using the same images as HM+) and faces (FC) during their categorization. We analyzed the detailed temporal structure of multiple electrical activity using PCA-based ROI analysis in 13 subjects, and detected well-orchestrated multiple regional electrical activity (see section 2.9.4). The present study enabled us to depict global aspects of information processing in the spatio-temporal domain during hand sign recognition. Figure 9 shows our hand sign recognition model, consisting of processes in the primary visual, mirror neuron, social recognition and object recognition systems. After the primary visual processes peaking around 120 ms, different aspects of information are processed in parallel in anatomically distinct brain areas (about 170 to 200 ms). Thereafter, distinct brain areas are activated simultaneously



Figure 9. Schematic presentation of possible brain mechanisms to recognize hand signs based on the results of PCA-based ROI analysis (see 2.9.4). Brain pictures with ROIs are grouped into four neuronal systems; the primary visual (color coded in yellow), mirror neuron (green), social recognition (orange), and object recognition (blue) systems. They are arranged horizontally according to the peak latencies in ROI activation. Brain regions, which showed similar condition effects and time courses in the HM+ condition, are surrounded by black dotted lines.

in the HM+ condition (230 ms), suggesting cooperation across different neuronal systems during the assessment of the meaning of hand signs. At around 340 ms, the somatomotor cortices are maximally active, probably reflecting mapping processes onto the internal representations. Finally, different brain regions are again activated in concert (370-380 ms). The right inferior prefrontal region was continuously activated after the latency about 150 ms, suggesting top-down and/or supervisory processes.

We also found marked right hemispheric predominance, suggesting that hand expression is processed in a manner similar to that in which social signs, such as facial expressions, are processed.

Processing of normal and acoustically disturbed words within sentences as measured by ERPs

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Speech is often heard in noisy environments. Even when some of the speech sounds are not acoustically present, we may not perceive any disturbance in continuous speech. In such cases, semantic context influences the perceptual synthesis of missing speech sounds.

The present study aimed to study brain activation related to "phonemic restoration", a phenomenon that has been studied behaviorally by R. Warren and colleagues (1970a; 1970b; 1971; 1974; 1984). We manipulated auditorily presented sentences in which the final word was either highly or little expected given the preceding sentence context. The N400 was used as an index of semantic processing of the final words, which were presented either with or without a cough replacing its initial part. Thus, altogether four types of sentences were used.

In an additional behavioral experiment, mean reaction time was slower for repeating low probability words than high probability words and further, slower for cough replaced words than normal words. Event-related potentials of 27 volunteers were recorded with a 64-electrode cap. The results showed negative response for the low cloze probability compared to high cloze probability final words (the N400-effect). Further, a prominent N1-P2 was elicited by the words beginning with cough replacement reflecting brains' automatic reaction to coughs. It was followed by a negative deflection with double peaks at 330 and 410 ms, which may be considered as N400, although it was more positive than in normal words. Usually, novel stimuli, which catch the attention in a sequence of sounds, elicit a prominent P3a-response after N1. However, for the cough-inserted final words there was no P3a, but a negative deflection followed the N1-P2-complex. Normal P3a was elicited by the sentence beginning words. Thus, the P3a for the coughs may be attenuated by an overlapping N400 response. This would mean that despite of automatic detection of coughs, as indicated by N1-response, the semantic processing of the words with cough-replacement takes place in the time window of

2.9.9

Sivonen, P.^{1, 2}, Maess, B.¹, Lattner, S.¹ & Friederici, A.D.¹ N400. Thus, the results indicate that bottom up processes as well as processes of semantic integration take place in perception of speech when it is disturbed by environmental sounds, such as coughing.

2.9.10 Magnetic mismatch negativity: Subcomponents of complex pattern reveal self adaptive temporal analysis

Schauer, M. & Maess, B.

Processing of auditory input by human brain has to be done sequentially as information is presented in a temporal stream and not at once. The analysis is highly automated which is demonstrated by the well-established mismatch negativity (MMN) paradigm. It is usually performed with persons not attending to the auditory stimulation. Such paradigms are based on a repetitive presentation on the same stimulus followed by the change to a different one. The change is represented in ERP-recordings by a frontal negativity at around 150 to 200 ms. Complex stimuli may have a much longer duration than the MMN latency, e.g., the stimuli of 550 ms duration applied here. Presenting these in a sequence allows the definition of a point of deviation for each stimulus transition. By systematic variation of the deviance points, we investigated when the brain detects the pattern violation. Our hypothesis was that we will either find a mismatch effect whose latency follows the occurrence of the deviance points, or a mismatch effect whose latency is constant and related to the stimulus completion. In the latter case, a rather holistic stimulus analysis could be assumed. The first case, however, would support arguments for an element wise analysis of the complex stimulus.

As stimuli, four different characters of the international Morse code were used (X, C, P and Ä). Stimuli were presented in a roving standard paradigm. Subjects were watching a silent movie and were instructed to ignore the auditory input. Magnetoencephalographic data of 20 healthy subjects were recorded. The analysis of strength and orientation in a distributed dipole model yields that deviance is detected mostly at that latency at which the stimulus differs from the preceding series. From that may be deduced that the latency difference between responses of stimuli with late and early deviance points reflects the deviance point distance itself. However, this is true only for the right hemisphere. Most subjects of the sample preferred the right hemisphere. Additionally, all deviant stimuli



Figure 10. Confidence intervals of the factor level contrasts in the latency ANOVA with factors deviance point (vertical) and hemisphere (horizontal). The color red and blue mark the short and long time scale analysis, respectively. The latencies of right detected mismatch negativities follow the stimulus deviance in short time scale analysis in contrast to that of long time scale analysis.

evoke a component at about 250 ms after the stimulus completion that is independent on the deviance point. Its field topography is similar to that of a mismatch activity. The finding confirms that element wise and holistic group analysis was performed simultaneously. The onsets inside the stream initiate probably processes in different time scales to analyze the auditory input. The simultaneous deviance detections correspond to a short and long time scale analysis of the input stream.

The perception of phrase structure in music

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Sequential information in music as well as language does not form uniform streams, but can be subdivided into phrases of several levels. Prosodic phrase boundary markers (e.g., pauses) support a speedy and accurate processing. For auditory speech, a recent study gives direct electrophysiological evidence for the immediate use of prosodic markers for the resolution of syntactic ambiguities (Steinhauer et al., 1999).

Each phrase boundary was indicated by a positive shift with a centro-parietal distribution, called Closure Positive Shift (CPS). The question arises whether a similar component can be found indicating the detection of phrase boundaries in music, and what would be the underlying neural network. We present evidence that there is indeed such a component. Musicians listened to unknown piano sequences consisting of two phrases. For the baseline condition, the pieces were altered by removing the phrase boundary. ERP was measured at 32 electrodes and revealed a significant positive component in response to the phrase boundary with a peak latency of 550 ms after phrase boundary offset, an amplitude of about 2 µV, and a centro-parietal distribution. Moreover, parallel measurements with a whole head MEG system were used to gain additional insight into the underlying generator configurations. The source localization using the multiple signal classification (MUSIC) method (Lewis et al., 1992) applied to both the ERP and the MEG data revealed a network consisting of structures of the limbic system, including anterior and posterior cingulate as well as posterior hippocampus. These areas are known to play a role in the direction of attention (anterior cingulate) and the formation of memory traces (posterior cingulate, hippocampus). The present findings indicate that the CPS might reflect a universal segmentation process, which applies to musical perception as well. In order to eventually confirm this hypothesis, it will be necessary to have a closer look onto the language CPS as well, in particular in terms of its underlying generators.



Figure 11. ERP traces for phrased (original) and non-phrased (modified) melodies. Trigger point is the offset of the phrase boundary (pause)

2.9.11

Knösche, T.R.¹, Neuhaus, C.², Haueisen, J.², Maess, B.¹, Alter, K.¹, Friederici, A.D.¹ & Witte, O.W.²



Figure 12. Brain regions that are possible candidates for contribution to the measured MEG data, revealed by the MUSIC method.



Figure 13. Brain regions that are possible candidates for contribution to the measured ERP data, revealed by the MUSIC method.

Teaching

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• Member of the Editorial Board of "Cortex"

Journal Referee

- Brain
- Cerebrovascular Diseases
- Cortex
- Journal of Neurology
- The Journal of Neuroscience
- NeuroImage
- Neuropsychologia
- Neuropsychology
- Neuroscience Letters
- Science

Referee for Scientific Institutions

- Canada Research Chairs Program College of Reviewers
- Bundesministerium für Bildung und Forschung (BMBF)/Federal Ministry of Education and Research (BMBF)
- Deutsche Forschungsgemeinschaft (DFG)/German Research Foundation
- INSERM Expert Base
- Netherlands Organization for Scientific Research

3.3 Visitors 2003

Elena Natale, Ph.D., Department of Neurological Sciences and Vision, Section of Human Physiology, University of Verona, Verona, Italy 8-11 January 2003

Michael Hoen, Associate Professor, and Peter F. Dominey, Ph.D., Sequential Cognition and Language Group, Institute for Cognitive Sciences, Bron, France 21-23 January 2003

Helen De Hoop, Dr., Department of Linguistics, University of Nijmegen, Nijmegen, The Netherlands 22-24 January 2003

Natalie Philips, Associate Professor, Department of Psychology/CRDH, Concordia University, Montreal, Quebec, Canada 24 January - 11 April 2003

Orit Rubin, Dr., Department of Behavioral Sciences, Ben-Gurion University of The Negev, Beer-Sheva, Israel 1-7 February 2003 18 June - 1 July 2003 *David G. Norris, Professor*, F.C. Donders Center for Cognitive Neuroimaging, Nijmegen, The Netherlands 3-4 February 2003 28-29 October 2003

Ralf Rummer, PD Dr., Department of Psychology, Saarland University, Saarbrücken, Germany 4-6 February 2003

Chris Darwin, Professor, Experimental Psychology, University of Sussex, Brighton, United Kingdom 16-20 February 2003

Heather van der Lely, Dr., and *Elisabeth Fonteneau, Research Assistant,* Center for Developmental Language Disorders and Cognitive Neuroscience, Department of Human Communication Science, University College London, London, United Kingdom 17-18 March 2003

Bamidele Awojoyogbe, Ph.D., Abdus-Salam International Center for Theoretical Physics, Trieste, Italy 3-5 April 2003

Christophe Pallier, Ph.D., Cognitive Neuroimaging Research Unit, INSERM U562, Orsay, France 8-18 April 2003

Elizabeth Hoffman, Ph.D., Center for the Study of Learning, Georgetown University Medical Center, Washington, DC, USA 26 April - 1 May 2003

Peter Dechent, Dr., Biomedical NMR Research GmbH, Max Planck Institute for Biophysical Chemistry, Göttingen, Germany 30 April - 1 May 2003

Brian McElree, Associate Professor, Cognition and Perception Program, Department of Psychology, New York University, New York, NY, USA 4-7 May 2003

Laurie A. Stowe, Associate Professor, Department of Linguistics, Faculty of Arts RuG, Groningen, The Netherlands 4 May - 14 June 2003

Iring Koch, Dr., Cognition and Action, Max Planck Institute for Psychological Research, Munich, Germany 12-15 May 2003 *Guntram Berti, Dr.,* Department of Mathematics, Technical University of Cottbus, Cottbus, Germany 2-3 June 2003

Jochen Finkberg, Dr., C&C Research Laboratories, NEC Europe Ltd., Sankt Augustin, Germany 2-3 June 2003

Jens Georg Schmidt, Dr., C&C Research Laboratories, NEC Europe Ltd., Sankt Augustin, Germany 2-3 June 2003

Marc Schröder, Dr., Language Technology Laboratory, German Research Center for Artificial Intelligence GmbH (DFKI), Saabrücken, Germany 3-5 June 2003

Mari Tervaniemi, Ph.D., Cognitive Brain Research Unit, Department of Psychology, University of Helsinki, Helsinki, Finland 18-30 June 2003 16-20 September 2003

Brechtje Post, Dr., Phonetics Laboratory, University of Oxford, Oxford, United Kingdom 29 June - 13 July 2003

Maarten van Casteren, Cognition and Brain Sciences Unit, MRC Medical Research Council, Cambridge, United Kingdom 29 June - 13 July 2003

Kalina Christoff, Ph.D., Cognition and Brain Sciences Unit, MRC Medical Research Council, Cambridge, United Kingdom 3-6 July 2003

Jochen Kaiser, PD Dr., Institute of Medical Psychology and Behavioral Neurobiology, University of Tübingen, Tübingen, Germany 3-5 July 2003

Klaus Oberauer, Dr., Cognitive Psychology Unit, Department of Psychology, University of Potsdam, Potsdam, Germany 3-5 July 2003

Matthew Rushworth, Dr., Department of Experimental Psychology, University of Oxford, Oxford, United Kingdom 3-5 July 2003 *Edmund Wascher, PD Dr.,* Max Planck Institute for Psychological Research, Munich, Germany 3-5 July 2003

István Winkler, Ph.D., Department of General Psychology, Institute for Psychology, Hungarian Academy of Sciences, Budapest, Hungary 3-5 July 2003

Clay Holroyd, Ph.D., Cognitive Psychophysiology Laboratory, Department of Psychology, Princeton University, Princeton, NJ, USA 6-10 July 2003

Stefanie Jannedy, Ph.D., Department of Linguistics, Ohio State University, Columbus, OH, USA 10-11 July 2003

Russell Poldrack, Ph.D., Department of Psychology, University of California, Los Angeles, CA, USA 11-26 July 2003

Daniela Perani, Professor, Institute of Neuroscience and Bioimaging - CNR, Milano, Italy 12-27 July 2003

Mikael Johannson, Dr., Experimental Neuropsychology Unit, Saarland University, Saarbrücken, Germany 15-16 July 2003 14-15 October 2003

Sophie Scott, Dr., Departments of Psychology and Phonetics, University College London, London, United Kingdom 19-25 July 2003

Andrew E. Kertesz, Professor, Robert R. McCormick School of Engineering and Applied Sciences, Northwestern University, Evanston, IL, USA 20-21 July 2003

Yueija Luo, Professor, Key Laboratory of Mental Health, Institute of Psychology, The Chinese Academy of Sciences, Beijing, China 21 July - 4 August 2003

Jubin Abutalebi, MD, Neurology Department, University of Brescia Medical School, Brescia, Italy 22-25 July 2003 *Josef P. Rauschecker, Professor,* Department of Physiology and Biophysics, Georgetown Institute for Cognitive and Computational Sciences, Georgetown University School of Medicine, Georgetown University, Washington, DC, USA 22-24 July 2003

Diana Van Lancker Sidtis, Professor, and *John J. Sidtis, Research Professor,* Nathan Kline Institute for Psychiatric Research, Orangeburg, NY, and New York University, New York, NY, USA 22-23 July 2003

Amy Schafer, Assistant Professor, Department of Linguistics, University of Hawaii, Honolulu, HI, USA 26 July - 3 August 2003

Herbert Schriefers, Professor, Nijmegen Institute for Cognition and Information (NICI), University of Nijmegen, Nijmegen, The Netherlands 4-9 August 2003 28-31 August 2003

Sergio Baauw, Dr., Utrecht Institute of Linguistics OTS, Utrecht University, Utrecht, The Netherlands 29-30 August 2003

Markus Bader, Professor, Department of Linguistics, University of Konstanz, Konstanz, Germany 29-30 August 2003

John Hoeks, Dr., Department of Linguistics, University of Groningen, Groningen, The Netherlands 29-30 August

Elsi Kaiser, Ph.D., Department of Linguistics, University of Pennsylvania, Philadelphia, PA, USA 29-30 August 2003

Monique J.A. Lamers, Dr., Department of Neuropsychology, Otto von Guericke University of Magdeburg, Magdeburg, Germany 29-30 August 2003

Katy Carlson, Ph.D., Department of Linguistics, Northwestern University, Evanston, IL, USA 29-30 August

Charles Clifton, Jr., Professor, Psychology Department, University of Massachusetts, Amherst, MA, USA 29-30 August 2003 *Caroline Féry, Professor,* Institute for Linguistics, University of Potsdam, Potsdam, Germany 29-30 August 2003

Janet D. Fodor, Professor, The Graduate Center, The City University of New York, New York, USA 29-30 August 2003

Sandra Pappert (Muckel), Dr., Department of Linguistics, University of Leipzig 29-30 August 2003

Nicole Richter, Ph.D. Student, University of Leipzig, Leipzig, Germany 29-30 August 2003

Christoph Scheepers, Dr., Department of Psychology, University of Dundee, Dundee, United Kingdom 29-30 August 2003

Matthias Schlesewksy, Dr., Junior Research Group Neurolinguistics, Phillips University Marburg, Marburg, Germany 29-30 August 2003

Wietske Vonk, Professor, Max Planck Institute for Psycholinguistic, Nijmegen, and CLS, Department of Linguistics, University of Nijmegen, Nijmegen, The Netherlands 29-30 August 2003

Sandra Vos, F.C. Donders Center for Cognitive Neuroimaging and Nijmegen Institute for Cognition and Information (NICI), University of Nijmegen, Nijmegen, The Netherlands 29-30 August 2003

Thomas Weskott, Dr., Department of Psychology, University of Potsdam, Potsdam, Germany 29-30 August 2003

Frank Wijnen, Dr., Utrecht Institute of Linguistics OTS, University of Utrecht, Utrecht, The Netherlands 29-30 August 2003

Nikolai Novitski, Ph.D. Student, Department of Psychology, University of Helsinki, Finland 1-30 September 2003

Michael A. Arbib, Professor, Computer Science Department, Neuroscience Program, and USC Brain Project, University of Southern California, Los Angeles, CA, USA 23-27 September 2003

Harold Bekkering, Professor, Nijmegen Institute for Cognition and Information (NICI), University of Nijmegen, Nijmegen, The Netherlands 23-27 September 2003

David Caplan, Professor, Neurolinguistics Laboratory, Department of Neurology, Harvard Medical School, Massachusetts General Hospital, Boston, MA, USA 23-27 September 2003

David P. Corina, Associate Professor, Department of Psychology, University of Washington, Seattle, WA, USA 23-27 September 2003

Luciano Fadiga, Professor, Section of Human Physiology, Department of Biomedical Sciences and Advanced Therapy, University of Ferrara, Ferrara, Italy 23-27 September 2003

Merrill F. Garrett, Professor, Faculty of Social and Behavioral Sciences, University of Arizona, Tucson, AZ, USA 23-27 September 2003

Scott T. Grafton, Professor, Department of Psychological and Brain Science, Dartmouth Functional Brain Imaging Center, Hanover, NH, USA 23-27 September 2003

Marco Iacoboni, Associate Professor, Neuropsychiatric Institute, Ahmanson Lovelace Brain Mapping Center, University of California, Los Angeles, CA, USA 23-27 September 2003

Petr Janata, Research Assistant Professor, Department of Psychological and Brain Sciences and Center for Cognitive Neuroscience, Dartmouth College, Hanover, NH, USA

23 September - 8 October 2003

Michael T. Ullman, Associate Professor, Departments of Neuroscience, Linguistics, Neurology, and Psychology, Georgetown University, Washington, DC, USA 23-27 September 2003

Katrin Amunts, PD Dr., Brain Mapping Group, Institute of Medicine, Research Center Jülich GmbH, Jülich, Germany 24-26 September 2003

Yosef Grodzinsky, Professor, Department of Psychology, Tel Aviv University, Tel Aviv, Israel 24-26 September 2003 *János Horváth, Dr.*, Department of General Psychology, Institute for Psychology, Hungarian Academy of Sciences, Budapest, Hungary 29 September - 3 October 2003

Marc Pell, Assistant Professor, School of Communication Sciences & Disorders, Faculty of Medicine, McGill University, Montreal, Quebec, Canada 12-18 October 2003

Gareth Barnes, Ph.D., The Wellcome Trust Laboratory for MEG Studies, Neurosciences Research Institute, Aston University, Birmingham, United Kingdom 19-21 November 2003

Dorothee J. Chwilla, Dr., Nijmegen Institute for Cognition and Information (NICI), University of Nijmegen, Nijmegen, The Netherlands 3-11 December 2003

Christophe Phillips, Ph.D., Cyclotron Research Center, University of Liege, Liege, Belgium 3-5 December 2003

Allen Song, Assistant Professor, Brain Imaging and Analysis Center, Medical Center, Duke University, Durham, NC, USA 3-5 December 2003

Kaoru Horie, Professor, Prashant Pardeshi, Ph.D., and Hiroshi Yamashita, Professor, Tohoku University, Sendai, Japan 4 December 2003

Asher Koriat, Professor, Department of Psychology, University of Haifa, Haifa, Israel 8-9 December 2003

Guest lectures 2003

Elena Natale, Ph.D., Department of Neurological Sciences and Vision, Section of Human Physiology, University of Verona, Verona, Italy Electrophysiological correlates of spatial attention distribution in the visual field of neglect patients 10 January 2003

Michel Hoen, Associate Professor, and Peter F. Dominey, Ph.D., Sequential Cognition and Language Group, Institute for Cognitive Sciences, Bron, France Dynamics of function and content processing in linguistic and abstract sequences 22 January 2003 3.4

Peter Indefrey, Dr., Max Planck Institute for Psycholinguistics and F.C. Donders Center for Cognitive Neuroimaging, Nijmegen, The Netherlands In search of the two routes: Neuroimaging studies on reading 7 February 2003

Chris Darwin, Professor, Experimental Psychology, University of Sussex, Brighton, United Kingdom How is harmonicity used in grouping speech sounds? 18 February 2003

Katrin Amunts, PD Dr., Brain Mapping Group, Institute of Medicine, Research Center Jülich, Jülich, Germany Landkarten des menschlichen Gehirns und Sprache 19 February 2003

Wilfried Kunde, Dr., Institute of Psychology, Martin Luther University Halle-Wittenberg Ideo-Motorik: Wenn Kognition und Körper zusammen kommen 26 February 2003

Lawrence M. Parsons, Assistant Professor, Cognitive Neuroscience Program, Social, Behavioral, and Economic Sciences, National Science Foundation, Arlington, MA, USA Neuroimaging and neurological findings on the brain basis of musical cognition, performance, and invention 12 March 2003

Natalie Philips, Associate Professor, Department of Psychology/CRDH, Concordia University, Montreal, Quebec, Canada

Keeping the message alive: Working memory, executive control, and language processing in the aging brain 19 March 2003

Christophe Pallier, Ph.D., Cognitive Neuroimaging Research Unit, INSERM U562, Orsay, France Brain imaging of language plasticity in adopted adults: Can a second language replace the first? 16 April 2003

Peter Dechent, Dr., Biomedical NMR Research GmbH, Max Planck Institute for Biophysical Chemistry, Göttingen, Germany Functional magnetic resonance imaging of the human brain – Benefits from high spatial resolution 30 April 2003

Brian McElree, Associate Professor, Cognition and Perception Program, Department of Psychology, New York University, New York, NY, USA Enriched compositional processes in language comprehension 5 May 2003 Tricia Striano,

Ph.D., Max Planck Institute of Evolutionary Anthropology, Leipzig, Germany Developing and understanding others in infancy: Is behaviour enough? 14 May 2003

Laurie A. Stowe, Associate Professor, Department of Linguistics, Faculty of Arts RuG, Groningen, The Netherlands Studies of sentence comprehension 28 May 2003

Marc Schröder, Dr., Language Technology Laboratory, German Research Center for Artificial Intelligence GmbH (DFKI), Saarbrücken, Germany Experimental study of affect bursts 4 June 2003

Perrine Ruby, Ph.D., Cyclotron Research Center, INSERM, University of Liege, Liege, Belgium Cerebral mechanism involved in the distinction between first- and third-person perspective 2 July 2003

Michael A. Arbib, Professor, Computer Science Department, Neuroscience Program, and USC Brain Project, University of Southern California, Los Angeles, CA, USA Language evolution: Neural homologies and neuroinformatics 9 July 2003

Clay Holroyd, Ph.D., Cognitive Electrophysiology Laboratory, Department of Psychology, Princeton University, Princeton, NJ, USA Reinforcement learning and anterior cingulate cortex 9 July 2003

Russell Poldrack, Ph.D., Department of Psychology, University of California, Los Angeles, CA, USA The organization of left inferior prefrontal cortex for semantic and phonological processing 15 July 2003

Diana Van Lancker Sidtis, Professor, and *John J. Sidtis, Research Professor,* Nathan Kline Institute for Psychiatric Research, Orangeburg, NY, and New York University, New York, NY, USA

Historical and methodological perspectives on prosody: Towards a neurobehavioral model

22 July 2003

Josef P. Rauschecker, Professor, Department of Physiology and Biophysics, Georgetown Institute for Cognitive and Computational Sciences, Georgetown University School of Medicine, Georgetown University, Washington, DC, USA Parallel processing streams in primate auditory cortex 23 July 2003

Amy Schafer, Assistant Professor, Department of Linguistics, University of Hawaii at Manoa, Honolulu, Hawaii Prosodic reflections of syntactic and focal structure in sentence production 30 July 2003

Claus Zimmer, Professor, Department of Diagnostic Radiology, University Hospital, Leipzig, Germany, and Carsten Warmuth, Dr., Institute of Radiology, Charité Berlin, Berlin, Germany

MR-Spin Labeling zur Analyse des Blutflusses bei Erkrankungen des Gehirns 26 August 2003

Petr Janata, Research Assistant Professor, Department of Psychological and Brain Sciences, Center for Cognitive Neuroscience, Dartmouth College, Hanover, NH, USA Cortical representations of musical contexts 1 October 2003

Gareth Barnes, Ph.D., The Wellcome Trust Laboratory for MEG Studies, Neurosciences Research Institute, Aston University, Birmingham, United Kingdom Cognitive neuroimaging with MEG: Cortical oscillations and interactions 21 November 2003

Christophe Phillips, Ph.D., Cyclotron Research Center, University of Liege, Liege, Belgium

Parametric empirical Bayes solution of the source reconstruction problem in EEG 3 December 2003

Allen Song, Assistant Professor, Brain Imaging and Analysis Center, Medical Center, Duke University, Durham, NC, USA

Improving fMRI acquisition methods for uniform coverage and accurate localization 4 December 2003

Asher Koriat, Professor, Department of Psychology, University of Haifa, Haifa, Israel The intricate relationships between monitoring and control processes in metamemory 9 December 2003

Dorothee J. Chwilla, Dr., Nijmegen Institute for Cognition and Information (NICI), University of Nijmegen, Nijmegen, The Netherlands

ERP and RT evidence for inhibition between alternative meanings of ambiguous words 10 December 2003
Eckart Altenmüller, Professor, Institute of Music Phonology and Performing Arts Medicine, University for Music and Drama, Hannover, Germany Apollos' Gift and Curse: Adaptive and maladaptive plasticity in sensory-motor systems of musicians 11 December 2003

3.5

Congresses, workshops and colloquia

Congresses

Workshop "Syntax and Beyond"
International workshop on syntactic processing and its relation to the processing of discourse, information structure, semantics, and prosody
Alter, K., Augurzky, P., Heim, S., Hruska, C., Ischebeck, A., Lingel, S. & Schriefers, H. (NICI Department of Psychology, University of Nijmegen, The Netherlands) &
Stolterfoht, B., Toepel U. &
Weskott, T. (University of Leipzig, Center for Advanced Studies) &
Vonk, W. (Max Planck Institute for Psycholinguistics, Nijmegen + CLS Department of Linguistics, University of Nijmegen, The Netherlands)
Max Planck Institute of Cognitive Neuroscience, Leipzig, Germany, August 2003.

3. Jahrestagung der Gesellschaft f
ür Aphasieforschung und –behandlung
Ferstl, E.C.
Max Planck Institute of Cognitive Neuroscience, Leipzig, Germany, November 2003.

Workshop "Perception, Action, Syntax and the Brain: Broca's area and ventral premotor cortex in sensorimotor mapping and language" Fiebach, C.J. & Schubotz, R.I. Max Planck Institute of Cognitive Neuroscience, Leipzig, Germany, September 2003.

Workshops and colloquia

Workshop "Textverstehen und Textproduktion bei Aphasie: Diagnostik und Therapie" Ferstl, E.C. &

Regenbrecht, F. (Day Clinic of Cognitive Neurology, University of Leipzig, Leipzig, Germany)

6. Würzburger Aphasie-Tage, Würzburg, Germany, February 2003.

Workshop "Einführung in die Neurolinguistik: Aphasische und nicht-aphasische Sprachstörungen"
Ferstl, E.C., Kotz, S.A. &
Guthke, T. & Regenbrecht, F. (Day Clinic of Cognitive Neurology, University of Leipzig, Leipzig, Germany)
Training Academy of the Gesellschaft für Neuropsychologie (GNP)/Society for Neuropsychology, Leipzig, Germany, November 2003.

Symposium "Working memory and attention (I): Functional neuroanatomy" Pollmann, S.

Workshop on Working Memory, DFG Research Group "Arbeitsgedächtnis/Working Memory", Leipzig, Germany, July 2003.

Symposium "Competitive processes in perception and action" Pollmann, S.

Gemeinsame Tagung der Gesellschaft für Neuropsychologie und der International Neuropsychological Society, Berlin, Germany, July 2003.

Symposium "Human anterior prefrontal contributions to cognitive control" Pollmann, S.

35th Annual General Meeting of the European Brain and Behavior Society, Barcelona, Spain, September 2003.

Degrees	
Professorship	
Dr. Jörg Jescheniak	Appointment to Professor of Cognitive Psychology (C3), Department of Psychology, University of Leipzig
Doctoral Degrees	
Claudia K. Friedrich	Doktor der Naturwissenschaften, Dr. rer. nat. University of Leipzig
Ansgar Hantsch	Doktor der Philosophie, Dr. phil. University of Potsdam
Stefan Heim	Doktor der Naturwissenschaften, Dr. rer. nat. University of Leipzig
Hagen B. Huttner	Doktor der Medizin, Dr. med. University of Leipzig
Axel Kühn	Doktor der Medizin, Dr. med. University of Leipzig
Jöran Lepsien	Doktor der Naturwissenschaften, Dr. rer. nat. University of Leipzig
Ulrike Lex	Doktor der Medizin, Dr. med. University of Leipzig
Sophie Manthey	Doktor der Naturwissenschaften, Dr. rer. nat. University of Leipzig
Elisabeth Mottweiler	Doktor der Medizin, Dr. med. University of Leipzig
Thomas Arnold	Doktor der Naturwissenschaften, Dr. rer. nat. University of Konstanz

4.1

Angelika Wolf	Doktor der Philosophie, Dr. phil. University of Potsdam
Gert Wollny	Doktor der Naturwissenschaften, Dr. rer. nat. University of Leipzig
Carsten H. Wolters	Doktor der Naturwissenschaften, Dr. rer. nat. University of Leipzig

4.2 Awards

Bornkessel, I.	Dieter Rampacher Prize 2002, Max Planck Society
Fiebach, C.J.	Post-doctoral Scholarship of the Deutsch-Akademischer Austauschsdienst (DAAD)/German Academic Exchange Service
Rüschemeyer, SA.	Scholarship for the "European Diploma in Cognitive and Brain Sciences" at the Hanse Institute for Advanced Study, Delmenhorst, Germany, and the Universidad de La Laguna, Tenerife, Spain
Görke, U. & Möller, H.E.	Poster Award, 2nd Leipzig Research Festival for Life Sciences, Leipzig, Germany, October 2003
Preul, C., Tittgemeyer, M., Lindner, D., Trantakis, C. & Meixensberger, J.	Poster Award, 76th Congress Deutsche Gesellschaft für Neurologie mit Fortbildungsakademie (DGN), Hamburg Germany, September 2003
Ullsperger, M. & von Cramon, D.Y.	Poster Award, 76th Congress Deutsche Gesellschaft für Neurologie mit Fortbildungsakademie (DGN), Hamburg, Germany, September 2003.

5

PUBLISHED BOOKS AND BOOK CHAPTERS 5.1

Alter, K. (2003).

Prosodie.

In G. Rickheit, T. Herrmann & W. Deutsch (Eds.), *Psycholinguistik - Ein internationales Handbuch. Psycholinguistics – An International Handbook* (pp. 339-346), Berlin: Walter de Gruyter.

Alter, K. (2003).

Sentence segmentation: On the influence of prosodic boundaries and accents.

In A. Lacheret & J. Francois (Eds.), *Fonctions et moyens d'expression de la focalisation. Memoires du XIIIe colloque de la Société de Linguistique de Paris* (pp. 115-136), Paris: Bibliothéque de l'Information grammaticale.

Alter, K., Meyer, M., Steinhauer, K., Friederici, A.D. & von Cramon, D.Y. (2003) [2002]. Brain responses related to prosodic information in natural speech: An event-related fMRI study. In R. Rapp (Ed.), Sprachwissenschaft auf dem Weg in das dritte Jahrtausend.

Linguistics on the way into the third millenium (pp. 21-26), Frankfurt: Peter Lang.

Arnold, T. (2003).

Computergestützte Befundung klinischer Elektroenzephalogramme.

In Max Planck Institute of Cognitive Neuroscience (Ed.), *MPI Series in Cognitive Neuroscience, vol. 38*, Leipzig.

Cramon, D.Y. von & Schubotz, R.I. (2003).

Funktionen des prämotorischen Cortex des Menschen. In C. Weiller, U. Sliwka, H.C. Diener, C.W. Wallesch & E. Busch (Eds.), *Aktuelle Neurologie. Sonderband. Deutsche Gesellschaft für Neurologie. Neurologie 2003* (pp. 281-284), Stuttgart: Thieme.

Ferstl, E.C. (Ed.) (2003).

Beiträge zur 3. Jahrestagung der Gesellschaft für Aphasieforschung und –behandlung. Leipzig: Max-Planck-Institut für neuropsychologische Forschung.

Fiebach, C.J., Schlesewsky, M., Bornkessel, I. & Friederici, A.D. (in press).
Distinct neural correlates of legal and illegal word order variations in German: How can fMRI inform cognitive models of sentence processing?
In M. Carreiras & C. Clifton (Eds.), *The On-line Study of Sentence Comprehension*, Hove: Psychology Press.

Friederici, A.D., Schlesewsky, M. & Fiebach, C.J. (2003).

Wh-movement vs. scrambling: The brain makes a difference.

In S. Karimi (Ed.), Word Order and Scrambling (pp. 325-367), Boston: Blackwell.

Friederici, A.D. (in press).

The neural basis of syntactic processes.

In M.S. Gazzaniga (Ed.), The Cognitive Neurosciences, 3rd Edition, Cambridge: MIT Press.

Friederici, A.D. & Rüschemeyer, S.-A. (in press).

Language acquisition: Biological versus cultural implications for brain structure. In P.B. Baltes, P. Reuter-Lorenz & F. Rösler (Eds.), *Lifespan Development and the Brain: The Perspective of Biocultural Co-Constructivism*, Cambridge: Cambridge University Press.

Friedrich, C.K. (2003).

Prosody and spoken word recognition: Behavioral and ERP correlates.

In Max Planck Institute of Cognitive Neuroscience (Ed.), *MPI Series in Cognitive Neuroscience, vol. 36*, Leipzig.

Hantsch, A. (2003).

Fisch oder Karpfen? Lexikale Aktivierung von Benennungsalternativen bei der Objektbenennung. In Max Planck Institute of Cognitive Neuroscience (Ed.), *MPI Series in Cognitive Neuroscience, vol. 40*, Leipzig.

Heim, S. (2003).

Towards a common neural network model of language production and comprehension: fMRI evidence for the processing of phonological and syntactic information in single words.

In Max Planck Institute of Cognitive Neuroscience (Ed.), *MPI Series in Cognitive Neuroscience, vol. 35*, Leipzig.

Herrmann, C.S. (2003).

Aufmerksamkeit, Gedächtnis, Wahrnehmung: Empirisch-neurowissenschaftliche Beiträge zur Bewusstseinsforschung.

In J.C. Schmidt & L. Schuster (Eds.), *Der entthronte Mensch? Anfragen der Neurowissenschaften an unser Menschenbild* (pp. 115-137), Paderborn: Mentis.

Herrmann, C.S. (2003).

Gamma activity in the human EEG.

In J. Polich (Ed.), *Detection of Change: Event-Related Potentials and fMRI Findings* (pp. 167-183), Boston/ Dordrecht: Kluwer.

Herrmann, C.S. & Fiebach, C.J. (Eds.) (in press). **Sprache und Gehirn.** Frankfurt: Fischer Verlag.

Herrmann, C.S., Grigutsch, M. & Busch, N.A. (in press).
 EEG oscillations and wavelet analysis.
 In T. Handy (Ed.), Event-Related Potentials: A Methods Handbook, Cambridge: MIT Press.

Hruska, C. & Alter, K. (in press).

How prosody can influence sentence perception. In A. Steube (Ed.), *Information Structure*, Berlin/New York: Walter de Gruyter.

Kotz, S.A. & Frisch, S. (in press).

Neurobiologie der Semantik in Wort und Satz: Elektrophysiologische Evidenz und Läsionsstudien. In T. Goschke & M. Eimer (Eds.), *Enzyklopädie der Psychologie. Kognitive Neurowissenschaft*, Göttingen: Hogrefe.

Lex, U. (2003).

Sprachlateralisierung bei Rechts- und Linkshändern mit funktioneller Magnetresonanztomographie. In Max Planck Institute of Cognitive Neuroscience (Ed.), *MPI Series in Cognitive Neuroscience, vol. 37*, Leipzig.

Manthey, S. (2003).

Hirn und Handlung: Untersuchung der Handlungsrepräsentation im ventralen prämotorischen Cortex mit Hilfe der funktionellen Magnet-Resonanz-Tomographie.

In Max Planck Institute of Cognitive Neuroscience (Ed.), *MPI Series in Cognitive Neuroscience, vol. 34*, Leipzig.

Meyer, M. (2003).

Bildgebende Verfahren.

In G. Rickheit, T. Herrmann & W. Deutsch (Eds.), *Psycholinguistik - Ein internationales Handbuch. Psycholinguistics – An International Handbook* (pp. 181-189), Berlin: Walter de Gruyter.

Nubel, K., Kruck, S., Höhle, B., Suhl, U., Weissenborn, J. & Gross, M. (2003).

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5.5 PAPERS PRESENTED AT CONFERENCES

Alter, K.

The influence of pitch on sentence processing: Evidence from ERPs and fMRI experiments. 6th Tübingen Perception Conference, Tübingen, Germany, March 2003.

Alter, K.

The right hemisphere: Pitch processing in fMRI experiments. International Conference on Psycholinguistics, Barcelona, Spain, March 2003.

Alter, K.

Sentence segmentation: Pragmatic influences on the processing of prosodic boundaries and accents. HFSP Workshop on Music and Language Processing, Sydney, Australia, April 2003.

Alter, K. & Knösche, T.R.

An electrophysiological marker for phrase boundaries in speech and music.

30th Australasian Experimental Psychology Conference, Sydney, Australia, April 2003.

Alter K.

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Annual Meeting of the Nürnberger Medizinische Gesellschaft, Erlangen, Germany, October 2003.

Alter K.

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Annual Meeting of the Max-Planck Society, Berlin, Germany, November 2003.

Augurzky, P. & Alter, K.

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"Syntax and Beyond": International Workshop on "Syntactic Processing and its Relation to the Processing of Discourse, Information Structure, Semantics, and Prosody", Leipzig, Germany, August 2003.

Bornkessel, I.

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21st European Workshop on Cognitive Neuropsychology, Bressanone, Italy, January 2003.

Brass, M. & von Cramon, D.Y.

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Workshop "Aspects of Working Memory" of the DFG Research Group "Arbeitsgedächtnis", Leipzig, Germany, July 2003.

Cramon, D.Y. von

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119. Wanderversammlung, Baden-Baden, Germany, June 2003.

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76. Kongress der Deutschen Gesellschaft für Neurologie mit Fortbildungsakademie (DGN), Hamburg, Germany, September 2003.

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76th Congress of the Deutsche Gesellschaft für Neurologie mit Fortbildungsakademie (DGN), Hamburg, Germany, September 2003.

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Ferstl, E.C. (2003).

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Ferstl, E.C.

Neuropsychologie des Textverstehens: Ergebnisse aus klinischer und bildgebender Forschung. Autumn Meeting of the Deutsche Gesellschaft für Sprachheilpädagogik (DGS), Landesgruppe

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Fiehler, K. & Ullsperger, M.

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International Conference on "Errors, Conflicts, and the Brain: Current Opinions on Performance Monitoring", Dortmund, Germany, July 2003.

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Friederici, A.D.

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3rd International Workshop on Mismatch Negativity and Auditory Functions and Dysfunctions, Lyon, France, May 2003.

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Institute of Cognitive Neuroscience Workshop "Speech and complex sound processing", London, United Kingdom, June 2003.

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International Society for Behavioral Neuroscience (ISBN)-Meeting, Prague, Czech Republic, July 2003.

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Friederici, A.D.

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Workshop on "Perception, Action, Syntax and the Brain: Broca's Area and Ventral Premotor Cortex in Sensorimotor Mapping and Language", Leipzig, Germany, September 2003.

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11th European Conference on Developmental Psychology (ECDP), Milan, Italy, August 2003.

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16th Conference of the Fachgruppe Entwicklungspsychologie der Deutschen Gesellschaft für Psychologie (EPSY), Mainz, Germany, September 2003.

Gruber, O.

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Conference of the Arbeitskreis Kinder- und Jugendpsychiatrie der Gesellschaft für Neuropsychologie (GNP)/ Society for Neuropsychology, Flehingen, Germany, May 2003.

Gruber, O.

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Güllmar, D., Flemming, L., Anwander, A., Dümpelmann, M., Knösche, T.R., Eiselt, M., Reichenbach, J.R. & Haueisen, J. (2003).

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Gunter, T.C.

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Guthke, T., Sandmann, A. & Ferstl, E.C.

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Heim, S. & Friederici, A.D.

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Hofmann, M., Höhle, B. & Weissenborn, J.

The prosody-syntax interface in the acquisition of word order in German.

25th Annual Meeting of the Deutsche Gesellschaft für Sprachwissenschaft (DGfS), Munich, Germany, February 2003.

Höhle, B., Luther, C. & Weissenborn, J.

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Child Language Seminar, Newcastle-upon-Thyne, United Kingdom, July 2003.

Hruska, C., Steinhauer, K. & Alter, K.

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Discourse, Information Structure, Semantics, and Prosody", Leipzig, Germany, August 2003.

Hund-Georgiadis, M.

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Annual Meeting of the Deutsche Gesellschaft für Neurologische Rehabilitation (DGNR), Weimar, Germany, November 2003.

Hüttner, T., Drenhaus, H., van de Vijver, R. & Weissenborn, J.

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28th Annual Boston University Conference on Language Development, Boston, MA, USA, November 2003.

Ischebeck, A.K.

Event-related fMRI: Experimentelles Design.

3rd Austrian fMRI Workshop, University of Innsbruck, Innsbruck, Austria, December 2003.

Jochimsen, T.H., von Mengershausen, M., Mildner, T., Norris, D.G., Freude, D., Kärger, J. & Möller, H.E. Separating the contributions of the intravascular signal change in spin-echo fMRI at 3 Tesla. 25 Annual Meeting of the Fachgruppe Magnetische Resonanzspektroskopie der Gesellschaft Deutscher Chemiker, Leipzig, Germany, September/October 2003.

Knösche, T.R.

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HFSP Workshop on Music and Language Processing, Sydney, Australia, April 2003.

Knösche, T.R., Neuhaus, C., Haueisen, J. & Alter, K.

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Körber, M., Jochimsen, T.H., Riemer, T. & Möller, H.E.

¹H NMR spectroscopy of the human brain using segmented spatially 2D-selective excitation pulses at 3 T. 25th Annual Meeting of the Fachgruppe Magnetische Resonanzspektroskopie der Gesellschaft Deutscher Chemiker, Leipzig, Germany, September/October 2003.

Kotz, S.A.

Introduction to event-related brain potentials: Investigations in patients and healthy controls. 48th Annual Meeting of the Deutsche Gesellschaft für klinische Neurophysiologie und funktionelle Bildgebung, Freiburg, Germany, October 2003.

Lindner, D., Trantakis, C., Preul, C., Tittgemeyer, M. & Meixensberger, J. (2003).

Veränderung der Ventrikelgröße und Konfiguration nach Ventrikulostomie bei Okklusivhydrocephalus.

2nd Annual Meeting of the Deutsche Gesellschaft für Computer- und Roboterassistierte Chirurgie e.V. (CURAC 2003), Erlangen, Germany, November 2003.

Möller, H.E., Mildner, T. & Trampel, R.

Cerebral perfusion imaging by adiabatic spin inversion with separate labeling and imaging coils. 2nd International Conference on Biomedical Spectroscopy, London, United Kingdom, July 2003.

Möller, H.E., Kurlemann, G. & Pützler, M.

Magnetic resonance spectroscopy in patients with MELAS. 3rd International Congress on Vascular Dementia, Prague, Czech Republic, October 2003.

Müller, J., Hahne, A., Fujii, Y. & Friederici, A.D.

Implementing a second language in the brain: Electrophysiological correlates of the aqcuisition of a miniature language system.

14th Annual Meeting of the European Second Language Association, Edinburgh, United Kingdom, September 2003.

Müller, K. (2003).

Investigating the temporal dynamics in the human brain using spectral methods. 9th Annual German-American Frontiers of Science Symposium, Irvine, CA, USA, June 2003.

Nubel, K., Kruck, S., Höhle, B., Suhl, U., Weissenborn, J. & Gross, M.

Interaktion behavioraler und elektrophysiologischer Ergebnisse zur Phonemdiskrimination bei Säuglingen.

20th Scientific Annual Meeting of the Deutsche Gesellschaft für Phoniatrie und Pädaudiologie (DGPP), Rostock, Germany, September 2003.

Pannekamp, A., Toepel, U. Hahne, A. & Friederici, A.D.

The brain's response to hummed sentences.

"Syntax and Beyond": International Workshop on "Syntactic Processing and its Relation to the Processing of Discourse, Information Structure, Semantics, and Prosody", Leipzig, Germany, August 2003.

Pollmann, S.

Neural correlates of visual dimension weighting.

Munich Visual Search Symposium, Holzhausen am Ammersee, Germany, June 2003.

Roehm, D., Schlesewsky, M., Bornkessel, I. & Haider, H.

Frequenzanalytische Dissoziation nicht dissoziierbarer EKP-Komponenten: Ein neuer Weg zur Untersuchung sprachlicher Verarbeitungsprozesse

12th German EEG/EP Mapping Meeting, Gießen, Germany, September 2003.

Rüschemeyer, S.-A., Fiebach, C.J., Hahne, A. & Friederici, A.D. (2003).

Cerebral representation of spoken language processing in bilinguals. 16th Annual CUNY Conference on Human Sentence Processing, Cambridge, MA, USA, March 2003.

Schauer, M., Maess, B. & Friederici A.D. (2003).

Pre-attentive auditory deviance detection in temporal complex stimuli. 3rd International Workshop on Mismatch Negativity and Auditory Dysfunctions (MMN03), Lyon, France, May 3003.

Schlesewsky, M. & Bornkessel, I.

Case and transitivity: Two determining factors in online language comprehension. Workshop on "Case, Valency and Transitivity", Nijmegen, The Netherlands, June 2003.

Schmitz, M., Höhle, B. & Weissenborn, J.

The influence of pause length on the perception of major syntactic boundaries. Child Language Seminar, Newcastle-upon-Thyne, United Kingdom, July 2003.

Schmitz, M., Höhle, B. & Weissenborn, J.

How pause length influences the perception of major syntactic boundaries in 6-month-old German infants.

Generative Approaches to Language Acquisition (GALA), Groningen, The Netherlands, September 2003.

Schubotz, R.I. & von Cramon, D. Y. (2003).

Observation of action slips.

International Conference on "Errors, Conflicts, and the Brain: Current Opinions on Performance Monitoring", Dortmund, Germany, July 2003.

Senkowski, D., Talsma, D., Herrmann, C.S. & Woldorff, M.G.

Timing makes the difference: Effects of audio-visual stimulus onset-asynchrony on oscillatory gammaband responses.

33rd Annual Meeting of the Society for Neuroscience (SfN), New Orleans, LA, USA, November 2003.

Stolterfoht, B., Friederici, A.D., Alter, K. & Steube, A.

The difference between the processing of implicit prosody and focus structure during reading: Evidence from event-related brain potentials.

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"Syntax and Beyond": International Workshop on "Syntactic Processing and its Relation to the Processing of Discourse, Information Structure, Semantics, and Prosody", Leipzig, Germany, August 2003.

Toepel, U.

The influence of prosody in processing information structure.

GLOW-Workshop on Information Structure in Generative Theory vs. Pragmatics, Lund, Sweden, April 2003.

Toepel, U.

On the independence of information structural processing from prosody.

"Syntax and Beyond": International Workshop on "Syntactic Processing and its Relation to the Processing of Discourse, Information Structure, Semantics, and Prosody", Leipzig, Germany, August 2003.

Trampel, R., Jochimsen, T.H., Mildner, M., Norris, D.G., Ernst, H., Kärger, J. & Möller, H.E.

Simulation of adiabatic spin inversion for local surface coils.

25th Annual Meeting of the Fachgruppe Magnetische Resonanzspektroskopie der Gesellschaft Deutscher Chemiker, Leipzig, Germany, September/October 2003.

Ullsperger, M.

Monitoring performance in different situations: Action slips and errors in underdetermined situations. 2nd Dutch Endo-Neuro-Psycho Meeting, Doorwerth, The Netherlands, June 2003.

Ullsperger, M. & von Cramon, D.Y.

Response uncertainty and external feedback: Hemodynamic and electrophysiological findings. International Conference on "Errors, Conflicts, and the Brain: Current Opinions on Performance Monitoring", Dortmund, Germany, July 2003.

Ullsperger, M. & von Cramon, D.Y.

Performance monitoring based on external feedback: Hemodynamic and electrophysiological findings. Charité Conference on Emotional Neuroscience: Brain Imaging of the Human Reward System, Berlin, Germany, August 2003.

Ullsperger, M.

Kognitive ereigniskorrelierte Potentiale in der Rehabilitation.

Annual Meeting of the Deutsche Gesellschaft für Neurologische Rehabilitation (DGNR), Weimar, Germany, November 2003.

Volz, K.G., Schubotz, R.I. & von Cramon, D.Y.

Brain correlates of uncertain decisions. International Conference on "Errors, Conflicts, and the Brain: Current Opinions on Performance Monitoring", Dortmund, Germany, July 2003.

Volz, K.G., Schubotz, R.I. & von Cramon, D.Y.

Brain correlates of decisions in well-defined problems: Types and degrees of uncertainty. Arbeitstreffen des Schwerpunktprogramms (SPP) "Exekutive Funktionen" der Deutschen Forschungsgemeinschaft (DFG), Fulda, Germany, July 2003.

Volz, K.G., Schubotz, R.I. & von Cramon, D.Y.

Brain correlates of uncertain predictions: Degrees and types of uncertainty investigated by functional Magnetic Resonance Imaging (fMRI).

9th Conference of the Fachgruppe Sozialpsychologie, Heidelberg, Germany, September 2003.

Volz, K.G., Schubotz, R.I. & von Cramon, D.Y.

Brain correlates of uncertain predictions: Degrees and types of uncertainty investigated by functional Magnetic Resonance Imaging (fMRI).

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Weber, C.

Der Spracherwerb in den ersten Lebensjahren.

Fortbildungsveranstaltung am Staatlichen Seminar zur Lehrerausbildung, Leipzig, Germany, May 2003.

Weber, C., Hahne, A., Friedrich, M. & Friederici, A.D.

Processing of different stress patterns in 4- and 5-month-old infants. 3rd International Workshop on Mismatch Negativity and Auditory Functions and Dysfunctions (MMN03), Lyon, France, May 2003.

Weber, C., Hahne, A., Friedrich, M. & Friederici, A.D. Impaired stress pattern discrimination in infants at risk for SLI.

International Workshop on Neurophysiology of Developmental Disorders in Children, Freiburg, Germany, December 2003.

Wolfensteller, U., Schubotz, R.I. & von Cramon, D.Y. (2003).

Encoding of serial visual stimuli with and without motor implication: an fMRI-study. Workshop "Aspects of Working Memory" of the DFG Research Group "Arbeitsgedächtnis", Leipzig, Germany, July 2003.

Alter, K.

Influences des frontiéres prosodiques et de l'accentuation sur la segmentation.

Journée Scientifique de la Société de Linguistique de Paris, Paris, France, January 2003.

Alter, K.

Segmentation in speech and music.

University of Saarbrücken, Saarbrücken, Germany, February 2003.

Alter K.

Brain responses to speech segmentation.

Institute of Neurology, Neurobiology, and Psychiatry, Medical School, University of Newcastle, Newcastle upon Tyne, United Kingdom, May 2003.

Augurzky, P.

Verarbeitung von syntaktischen Ambiguitäten im Zweitspracherwerb.

Institute of Linguistics, University of Leipzig, Leipzig, Germany, May 2003.

Augurzky, P.

Syntaxverarbeitung crosslinguistisch: Relativsatzverarbeitung im Zweitspracherwerb. Klausurtagung des Graduiertenkolleg "Universalität und Diversität: Sprachliche Strukturen und Prozesse",

Großbothen, Germany, July 2003.

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A

Alter, K. 66-68, 70, 72-78, 161, 181 Anwander, A. 142, 146, 151, 152 Arnold, T. 183 Astésano, C. 75 Augurzky, P. 66, 181

B

Bach, P. 37, 38, 158
Besson, M. 75
Bohn, S. 142
Bornkessel, I. 24, 26, 28, 30, 45, 163, 164, 184
Brass, M. 115-117, 163, 164
Bücheler, M.M. 88, 93
Busch, N.A. 153, 155

С

Cappa, S.F. 22 Chen, H.C. 35

D

Danielmeier, C. 114 De Baene, W. 78 de Greck, M. 112 Debener, S. 155 Derrfuss, J. 116 Driesel, W. 132, 133, 137

E

Elston-Güttler, K.E. 49, 52, 54 Engel, A.K. 155

F

Ferstl, E.C. 123-125, 181 Fiebach, C.J. 20-22, 30, 163, 181, 184 Fiehler, K. 119-121 Fink, G.R. 33 Flemming, L. 152 Forstmann, B.U. 117
Friederici, A.D. 18-22, 24, 25, 28, 30-32, 37, 42-47, 49, 52, 60, 67, 68, 70, 72, 74, 76, 78, 82, 153, 158, 159, 161, 163-165
Friedrich, C.K. 76, 183
Friedrich, M. 42, 44
Frisch, S. 163
Fritz, T. 62
Fujii, Y. 46, 47

G

Goerke, U. 130, 134, 184 Goschke, T. 118 Grasedyck, L. 150 Grigutsch, M. 61, 121, 144, 145 Grube, M. 102 Gruber, O. 98, 118 Güllmar, D. 152 Gunter, T.C. 29, 32, 35, 37, 38, 60, 73, 158, 163, 164 Guthke, T. 181

H

Haase, G. 151 Hackbusch, W. 150 Hagert, A. 142 Hahne, A. 25, 36, 42, 46, 47, 67 Haider, H. 26 Hantsch, A. 183 Haueisen, J. 152, 161 Heim, S. 18, 19, 73, 181, 183 Heinke, W. 87 Hernandez, A.E. 51, 52 Herrmann, C.S. 153, 155, 156, 163, 165 Hetzer, S. 137 Hofmann, J. 31 Hruska, C. 68, 70, 72, 181 Hübsch, T. 95 Hugdahl, K. 104 Hummelsheim, H. 164 Hund-Georgiadis, M. 83, 85-87, 96, 97 Huttner, H.B. 183

6

I

Ischebeck, A. 74, 163, 181 Isel, F. 25

J

Jacobsen, T. 77 Jentschke, S. 58, 59 Jescheniak, J. 183 Jochimsen, T.H. 128, 129, 131, 136 Junge, S. 152

K

Karch, S. 118 Kasper, E. 60 Knoblich, G. 37 Knösche, T.R. 152, 153, 158, 161, 165 Koch, I. 117 Koelsch, S. 58-163 Körber, M. 136 Köster, D. 32 Kotz, S.A. 22, 23, 31, 51, 52, 54, 82, 163, 164, 181 Krainik, A. 86 Kranczioch, C. 155 Kruck, S. 78 Krumbholz, K. 33 Kühn, A. 183 Kupka, T. 90

L

Lattner, S. 35, 159 Lenz, D. 153 Lepsien, J. 104, 183 Leuckefeld, K. 45 Lex, U. 183 Lindner, D. 100, 184 Lingel, S. 181 Lohmann, G. 88, 96, 97, 142-147, 164

Μ

Maess, B. 153, 158-161
Manthey, S. 183
Martin, E.M. 83
McElree, B. 24, 28
Meixensberger, J. 99, 100, 184
Merkle, H. 137
Mildner, T. 90, 94, 128, 131, 132, 144, 145
Möller, H.E. 94, 102, 128-132, 134-137, 146, 164, 165, 184
Monaghan, P. 106
Mottweiler, E. 183

Müller, H.J. 103 Müller, J. 46, 164 Müller, K. 88, 142, 144, 145 Müsseler, J. 114

N

Naganawa, S. 85 Nakamura, A. 153, 158 Neuhaus, C. 161 Neumann, J. 142-145 Norris, D.G. 85, 128-131, 133

0

Obrig, H. 88 Olthoff, D. 87

P

Pannekamp, A. 43, 67 Paulmann, S. 52, 54 Pechmann, T. 66 Penney, T.B. 35 Pollmann, S. 103-106, 164, 181, 182 Preul, C. 96-100, 184 Prinz, W. 37

R

Regenbrecht, F. 181 Reinholz, J. 105 Reitzinger, S. 151 Riemer, T. 136, 137, 139 Rinck, M. 123 Rübsamen, R. 33, 102 Rüschemeyer, S.-A. 164, 184

S

Sakreida, K. 111 Sammler, D. 60, 61 Schäfer, A. 135 Schauer, M. 160 Scheid, R. 97, 98 Schirmer, A. 23 Schlesewsky, M. 24, 26, 28, 30 Schlumm, T. 139 Schniedel, O. 92 Schönwiesner, M. 33 Schriefers, H. 181 Schroeter, M.L. 88, 90, 92, 93 Schröger, E. 77, 78, 163, 164 Schubotz, R.I. 108, 110-112, 122, 181 Schulze, K. 60 Schwarzbauer, C. 130 Senkowski, D. 156 Siebörger, F.T. 125 Sivonen, P. 158 Steinhauer, K. 68 Stolterfoht, B. 73, 181 Szameitat, A.J. 78

Т

Talsma, D. 156 Tervaniemi, M. 78 Tewes, A. 112 Tittgemeyer, M. 88, 94, 95, 99, 100, 184 Toepel, U. 67, 181 Trampel, R. 131, 132 Trantakis, C. 100, 184

U

Ullsperger, M. 80, 119-121, 184 Uludağ, K. 88, 90

V

Villringer, A. 88 Volz, K.G. 122 von Cramon, D.Y. 23, 33, 80, 82, 83, 85-88, 92-100, 102-104, 108, 110-112, 114-124, 142, 144, 145, 184, 164, 168, 184 von Mengershausen, M. 128, 133, 146 Vonk, W. 181 Vos, S.H. 20

W

Wagner, S. 29 Weber, C. 42, 43 Weidner, R. 103 Weskott, T. 181 Wetzel, T. 136 Wiggins, C. 98 Winkler, D. 99 Witte, O.W. 161 Woldorff, M.G. 156 Wolf, A. 36, 184 Wolfensteller, U. 110, 112 Wollny, G. 99, 184 Wolters, C.H. 150-152, 184

Z

Zilles, K. 33 Zysset, S. 23, 83, 85-87, 94, 114, 137, 142, 164