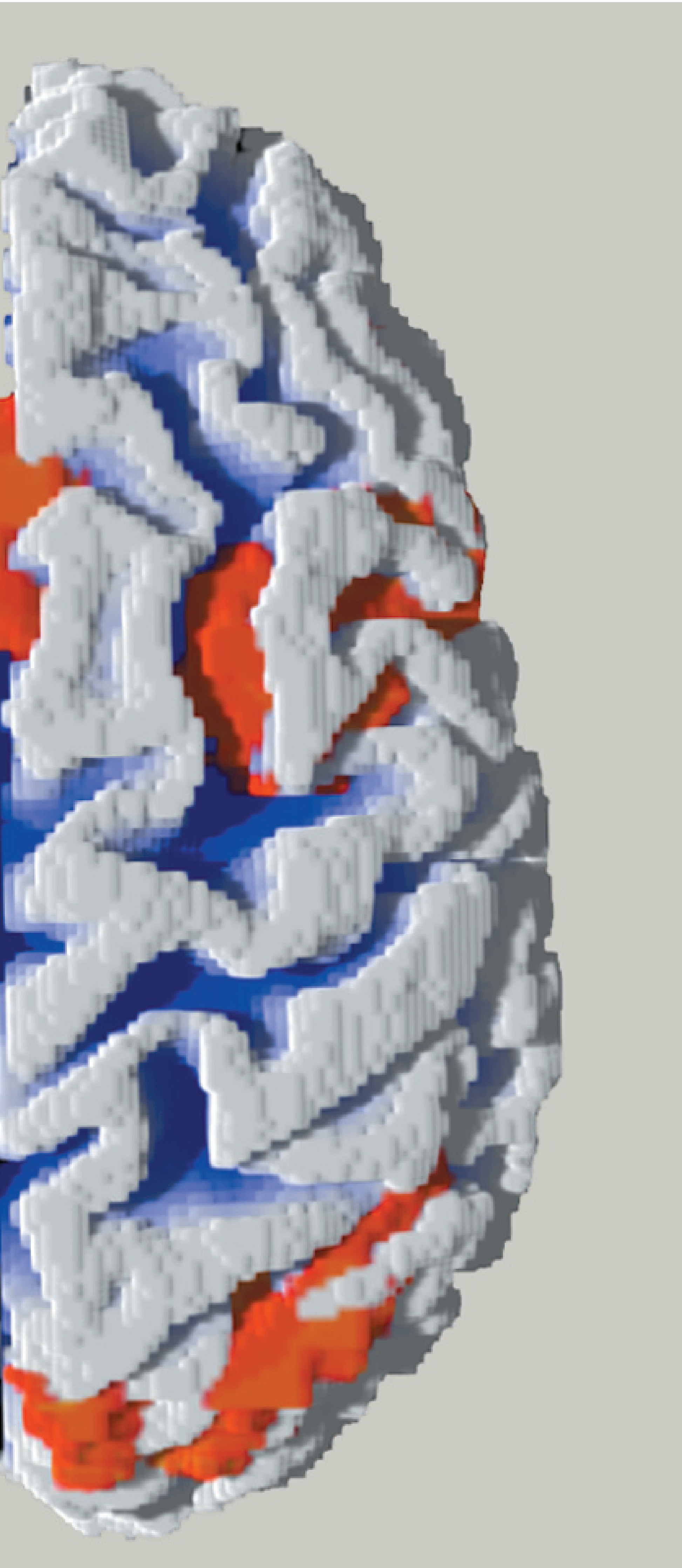

Annual Report 2004 · 2005

Max Planck Institute for
Human Cognitive and Brain Sciences

Leipzig · Munich

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Annual Report 2004 · 2005

The past two years have witnessed the merger of the two former Institutes, the Max Planck Institute for Psychological Research (Munich) and the Max Planck Institute of Cognitive Neuroscience in Leipzig into a new centre: the **Max Planck Institute for Human Cognitive and Brain Sciences**. In 2004, it was still a merger on paper, but in 2005 it turned into reality. The Munich group, headed by Wolfgang Prinz, moved to Leipzig and resumed its work at the Institute. A number of exciting new collaborations are starting.

Research at the centre addresses human cognitive and brain processes with particular emphasis on language, music, action and executive functions. During the period covered by this report – 2004/2005 – research has been flourishing at both places, Leipzig and Munich, and is now flourishing even more after the Munich branch has moved to Leipzig. The new Leipzig centre provides unique conditions for joint interdisciplinary research into the behavioral and neurobiological bases of human cognition.

The merger is the first link in a chain of major changes and extensions we anticipate to see in the near future. Most importantly, we will soon be implementing two novel departments, one in Imaging Science and another one in Behavioral Cognitive Science. Further, to house the enlarged centre, an annexe will be raised on a plot adjoining our present building. Last but not least, a 7 Tesla Magnetic Resonance Tomograph will soon be installed in a further special annexe. The system will add to the two 3 Tesla NMR systems that are already under operation.

On a smaller scale, new research groups are coming and going. With regard to Independent Junior Research Groups, the present report covers two new groups – one on Neurotypology (headed by Ina Bornkessel), and another one on Cognitive Psychophysiology of Action (headed by Edmund Wascher). Besides Independent Junior Research Groups this report also covers the work of four Research Groups from our Munich branch. Furthermore, Hans-Joachim Heinze from the University of Magdeburg, who was recently appointed Max Planck Fellow at the Institute, has started building up a new research group on Attention and Awareness. Finally, Yves von Cramon was appointed Managing Director of the Max Planck Institute for Neurological Research at Cologne.

D. Yves von Cramon
Angela D. Friederici
Wolfgang Prinz

Leipzig, February 2006

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Our research addresses relationships between cognition and action. The focus of our agenda is on cognitive processes involved in action planning, action control and action perception as well as interactions between cognition, volition and action in experimental task contexts. One of the central theoretical intuitions that guides our research is that cognition, volition and action are much more intimately related to each other than traditional theories in these domains believe. Notably, we hold that perception and action (i.e., perceived and intended events) share common representational resources.

Our research program can be seen from two perspectives. In one perspective we adopt a functional stance on cognition, that is we view cognitive functions in the service of voluntary action and study their role for the planning, execution and perception of action. In the other perspective, we adopt a cognitive stance on action. Here we view action in the service of cognition and study its impact on cognitive operations. Accordingly, there are two major lines of research. In one line, studies are concerned with the cognitive underpinnings of action control and task control (2.1). In the other line, studies focus on contributions of representational resources for the control of action to the cognitive processes involved in understanding actions and intentions (2.2).

ACTION AND TASK CONTROL 2.1

Projects from this domain are devoted to the study of cognitive underpinnings of action planning and action control (projects 2.1.1 – 2.1.9) and cognitive mechanisms involved in task control (projects 2.1.10 – 2.1.13). The central issue addressed by studies in the first group of projects concerns the functional role of anticipatory mechanisms involved in the formation of goals and intentions and their impact on action performance. This issue is addressed in paradigms involving choice reactions (2.1.1, 2.1.4, 2.1.6), musical performance (2.1.2, 2.1.6), action synchronization (2.1.2, 2.1.3), posture control (2.1.5), tool transformations (2.1.6, 2.1.8) and bimanual coordination (2.1.7, 2.1.8). A further, more theoretical, project puts psychological views on voluntary action in the broader context of philosophical, historical and sociological perspectives on will and free will (2.1.9). The second group of projects studies mechanisms of task control, i.e., the impact of episodic task contexts on action control and action performance. These projects address mechanisms of task-set competition and selection (2.1.10, 2.1.11, 2.1.13), formation of episodic S-R-bindings (2.1.13) and sequencing of actions and tasks (2.1.12).

2.1.1 Intention-based and stimulus-based mechanisms in action selection

Waszak, F., Herwig, A., Keller, P.E., Wascher, E., Müller, V., Brass, M. & Prinz, W.

Humans interact with their environment in two principle ways: They carry out movements to manipulate the environment in order to produce desired effects, or they move to accommodate externally imposed environmental demands. The first kind of movement, which may be referred to as voluntary, is selected on the basis of the agent's intentions. The second kind is performed as a reaction to an often uncontrollable stimulus event. In this project, we investigated the different neural substrates controlling these two kinds of actions by comparing the EEG profiles of physically identical movements performed either in an intention-based or stimulus-based mode (Waszak et al., 2005; Keller et al., in press).

In each block of our experimental paradigm, a series of 35 visual stimuli appeared with a fixed inter-stimulus interval (1200 ms). Participants performed keypress movements so as to 'bisect' the intervals between consecutive stimuli. In the 'intention-based' condition, participants were free to select which of two keys (left or right) to press during each interval, with their selections determining the position of the next stimulus on the computer screen. In the 'stimulus-based' condition, participants were instead required to press the key corresponding to the position of the *preceding* stimulus (see Figure 2.1). To keep the degree of action alternation constant in both conditions, the actions in a given stimulus-based run were yoked (in a disguised fashion) to the actions produced in a preceding intention-based run. We collected both behavioral (movement timing) and EEG data.

In the behavioral data, we observed temporal attraction effects in the timing of movements. Intention-based actions occurred relatively close in time to their effects, whereas stimulus-based actions occurred closer to their triggering stimuli. This result is consistent with the idea that the perceptual representation of a given environmental event (trigger or effect) is bound together with the representation of the motor processes that drive behavior related to that event.

The EEG results evidenced two different modes of processing. In the stimulus-based mode, processing worked in a stimulus-driven fashion, as demonstrated by various stimulus-locked EEG components. In this mode, stimulus- and attention-related processes (P3) and response-related processes (e.g., stimulus-locked lateralized readiness potential [S-LRP]) ensured that a given stimulus elicited an appropriate response (Figure 2.2). In the intention-based mode, response-locked ERPs (readiness potentials) showed that other cortical structures mediated the execution of actions selected by the agent (Figure 2.3).

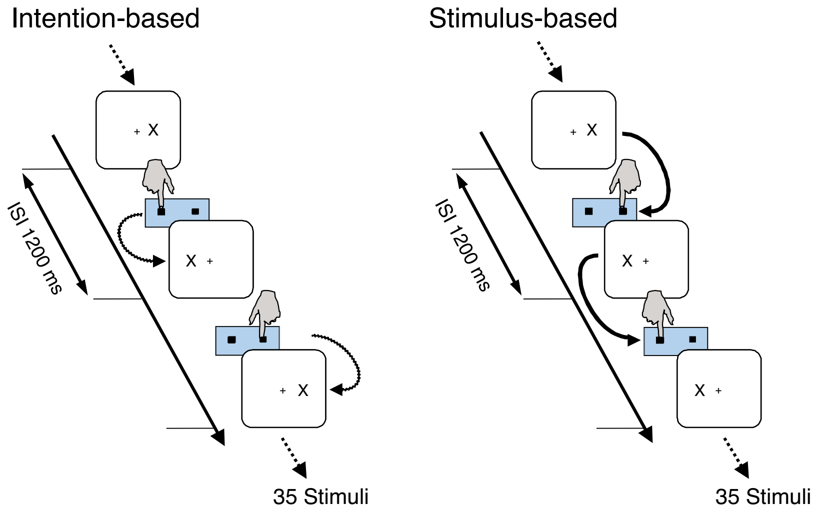

Figure 2.1 Illustration of the sequence of events in intention-based and stimulus-based conditions.

Our current research strategy is twofold. On one hand, we complement the EEG data (high temporal resolution) by running experiments with functional magnetic resonance imaging (fMRI; high spatial resolution). This allows us to identify the neural generators of the outlined EEG activity. On the other hand, we also try to describe the differences between the two movement modes in functional terms in more detail.

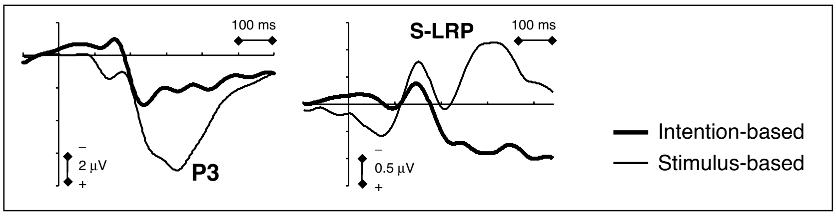

Figure 2.2 The P3 (left) and S-LRP (right) EEG components are present for stimulus-based actions, but not for intention-based actions.

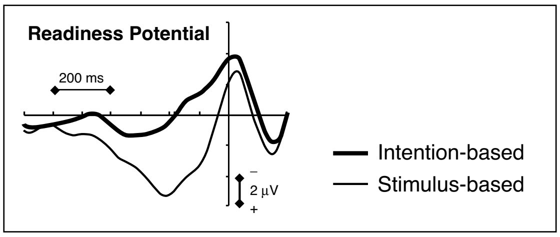

Figure 2.3 The readiness potential (reflecting cortical preparation for voluntary movement) is stronger for intention-based actions than for stimulus-based actions.

2.1.2 Anticipatory auditory images and temporal precision in music performance

Keller, P.E.[1], Koch, I.[1,2], Knoblich, G.[1,3] & Prinz, W.[1]

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[2] Department of Psychology, RWTH Aachen University, Germany
[3] Psychology Department, Rutgers University, Newark, NJ

Musicians strive to produce ideal sounds through the precise execution of body movements. How important are anticipatory auditory images in this process? Experimental tasks that manipulate the compatibility between manual response sequences and their auditory effects (see Koch et al., 2004) suggest that musicians anticipate upcoming sounds while planning the performance of short melodies. Unlike most instances of musical performance, however, these tasks are usually conducted under 'speeded' conditions, where movements are carried out as quickly as possible. In such speeded tasks, action planning (indexed by reaction times to 'go' signals), but not action execution (indexed by movement duration), is typically faster when responses and their effects are compatible than when they are incompatible (in terms of spatial height and pitch height, for example).

In this project (Keller & Koch, in press), we tested whether response-effect compatibility affects the execution of music-like sequential actions that require temporal regularity rather than rapidity. We were specifically interested in whether response-effect compatibility affects timing accuracy for the first (pre-auditory feedback) movement of each sequence, because this would provide evidence that action-effect anticipation plays a role in the control of temporally precise movements.

In our experimental task (see Figure 2.4), musicians responded to each of four color-patch stimuli by producing a unique sequence of three taps on three vertically aligned keys. The stimulus in each trial flashed three times with a 600 ms inter-onset interval, and participants tapped their responses as regularly as possible at this tempo after a further three flashes of a neutral stimulus. Each tap triggered a tone. Response-effect mapping was either compatible (taps on the top, middle, and bottom keys triggered high, medium, and low pitched tones, respectively) or incompatible (key-to-tone mapping was scrambled or reversed).

We found that tap timing was more accurate with compatible than with incompatible mappings, both for taps produced before (tap 1) and after (taps 2 and 3) the onset of auditory feedback (see Figure 2.5). Thus, the observed influence of response-effect compatibility on action execution was not due exclusively to actual auditory feedback.

Our results suggest that the anticipation of auditory action-effects plays a role in planning the dynamics of temporally precise movements. This implies that in musical contexts the degree to which movement trajectories are optimal (i.e., conducive to producing a desired timing pattern) may be affected by the performer's ability to imagine forthcoming sounds.

In recent work with Bruno Repp (Haskins Laboratories, New Haven, CT), we have extended the study of anticipatory auditory imagery to the domain of musical duet performance (Keller et al., in press).

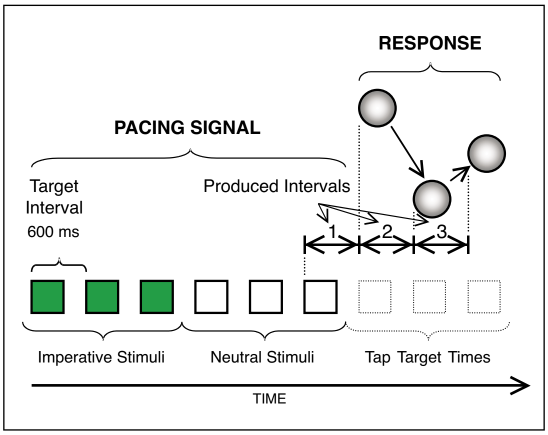

Figure 2.4 An example of the experimental procedure in a single trial. A visual pacing signal with 600 ms inter-onset intervals was presented, wherein three flashes of a colored imperative stimulus (green, yellow, pink or blue) were followed by three flashes of a neutral (white) stimulus. Participants responded to the pacing signal by making three consecutive finger taps on three vertically aligned response keys at a rate that continued the tempo set by the signal. The response keys were tapped in four different orders, with each order being associated with a different colored imperative stimulus. Each tap triggered a tone, and key-to-tone mapping was manipulated between blocks to be either compatible or incompatible in terms of spatial height and pitch height.

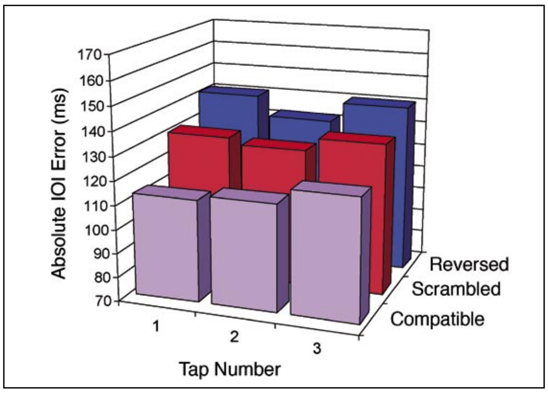

Figure 2.5 Timing accuracy indexed by average absolute inter-onset interval error (produced interval minus target interval) across the three sequential taps for each condition.

2.1.3 Action timing

Aschersleben, G.[1], Cole J.[2], Drewing, K.[3], Gehrke, J.[1], Li, S.-C.[4], Pollok, B.[5] & Prinz, W.[1]

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In this series of studies, we analyzed the functional sources subserving the timing of simple repetitive actions. In Aschersleben et al. (2004) we proposed a model suggesting that the timing of an action in a synchronized tapping task is determined by the perceived time of that action. We were able to validate that model by manipulating, among others, the intensity of tap-related feedback. Results suggest that the perceived time of an action is strongly determined by the sensory information arising from its execution.

Central processes underlying the performance in a synchronization task were investigated using a 122-channel whole-head neuromagnetometer (MEG). Three neuromagnetic sources localized in the primary sensorimotor cortex were found contralateral to the tapping hand (see Figure 2.6). A first source peaking clearly before tap-onset most likely represents activation of the primary motor cortex due to the motor command, a second source localized in the primary somatosensory cortex peaking around taponset might be due to kinesthetic feedback of the finger movement, and a third source peaking clearly after taponset is localized inferior to the first S1 source in the primary somatosensory cortex. This third source probably represents the neuromagnetic correlate of tactile-kinesthetic feedback due to finger-taps and movements (Pollok et al., 2004a; 2004b).

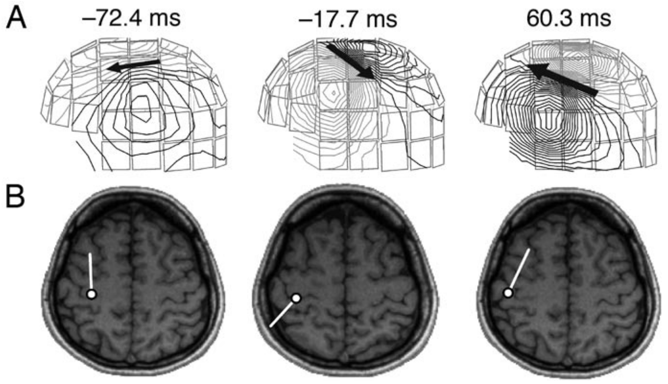

Figure 2.6 (A) Magnetic field distributions at local field maxima (at three different points in time before and after tap-onset). Arrows depict size and orientation of the current dipoles. (B) Anatomical localization of the sources. Symbols demonstrate the localization, while tails show the direction of the current flow.

It has been argued that, although timing of each hand is controlled by independent timekeepers, during bimanual tapping both signals might be integrated. To determine the oscillatory network associated with a simple bimanual synchronization task, neuromagnetic activity as well as surface EMG of the first dorsal interosseus of both hands was recorded. Data demonstrate that an oscillatory network coupling at 8–12 Hz subserves task execution. Moreover, our data indicate strong coupling between both cerebellar hemispheres, substantiating the hypothesis that cerebellar signals are integrated during temporal bimanual coordination (Pollok et al., 2005). This finding is supported by a study with a deafferented person (Drewing et al., 2004). This patient showed a more pronounced bimanual advantage (reduced variability when tapping bimanually instead of single-handedly) than healthy controls suggesting that bimanual timing profits from the averaging of different central control signals that relate to each effector's movements.
As part of a large-scale cross-sectional life-span study (Li et al., 2004), we investigated the contribution of general processing resources to the life-span development of sensorimotor synchronization (Drewing et al., in press). The results provided the first direct life-span evidence showing that performance in these tasks improves substantially during childhood, and remains relatively stable until old age. This pattern of life-span age gradient holds for measures of different component processes of sensorimotor synchronization, such as basic timekeeping and error correction processes, suggesting a complex interaction between general resources and more specific factors in the life-span development of sensorimotor synchronization.

2.1.4 Unattended stimuli fail to induce the Simon effect

Grosjean, M.

Inattentional Blindness (IB) refers to the absence of awareness of events that appear in unattended regions of the visual field. Prior studies that have employed IB as an operational definition of *unattended* have shown, among other things, that unattended stimuli can be grouped on the basis of similarity and support the completion of partially visible surfaces. In the present study (Moore et al., 2004), we combined IB with an online measure of processes that lie at the interface between perception and action: The Simon effect. One variant of this effect refers to the finding that people are faster to respond to a stimulus that is accompanied by an accessory stimulus that matches the location of the required response than an accessory stimulus that does not match the location of the response. The results of our study revealed that, unlike various early perceptual processes, unattended accessory stimuli failed to engage the processes that underlie the Simon effect.

2.1.5 The effects of movement amplitude and frequency on postural variability

Grosjean, M.

The effect of spatial and temporal constraints on movement variability has mainly been studied in the context of aimed hand movements. In the current study (Danion et al., in press), we sought to extend this line of research to the control of whole-body movements. To do so, we asked participants to perform reciprocal aiming movements with their center of pressure (COP) at varying amplitudes (As) and frequencies (Fs) while standing on a force platform. An analysis of both spatial and temporal variability of COP trajectories revealed that absolute variability, as assessed with standard deviations, had a tendency to increase with A and F, whereas relative variability, as indexed by coefficients of variation, decreased with A and F. Moreover, there was no correlation between variability in the time and space domains. When taken together with the results of other studies, it could be concluded that the influence of spatial constraints is relatively task independent, whereas the effects of temporal constraints depend on the nature of the movement that is performed.

2.1.6 Action goals in action control

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One important aspect of the relationships between cognition and action is that actions are performed in order to attain desired goals. In the following, three projects will be described, in which the role of action goals was investigated.

Fitts law: Tool transformation. If actions are controlled in reference to extracorporal space, action kinematics should differ depending on the visual context in which an action occurs. To investigate this, participants performed a Fitts' task, in which different gains between movement space and visual space were introduced. For example, participants perform the same movement in all conditions, but the visual context differs (see Figure 2.7). According to Fitts' law, movement times should be equal in all conditions. Results showed that movements with higher gain were slower and had lower peak velocity than movements with lower gain. Thus, extracorporeal space has an effect on movement kinematics. Fitts' law does not hold across different transformations between movement space and visual space (Rieger et al., 2005).

Music: Action induction by action effects. The strength of action-effect associations should directly depend on the amount of learning, and, therefore, be most pronounced in motor experts. Using an interference paradigm, it was investigated whether evidence for such representations can be demonstrated in expert

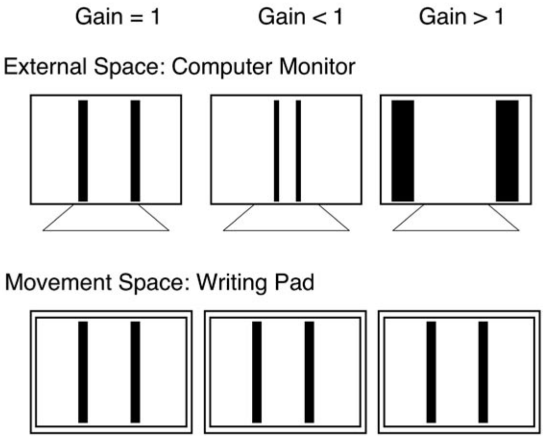

Figure 2.7

pianists. Participants were required to play chords on a keyboard in response to imperative visual stimuli. Concurrently, task-irrelevant auditory stimuli ("potential" action effects) were presented that were congruent or incongruent with the chords to be played. We found evidence that expert pianists, as compared to non-musicians, have acquired such action-effects representations. For the most part, interference occurs on the response level rather than on an abstract level (Drost et al., 2005). It was further examined whether perceived action effects have the capacity to induce the corresponding actions. Using a similar paradigm that required the playing of two-tone sequences (intervals), it was found that in expert pianists potential action effects are able to induce corresponding actions. (Drost et al., in press).

Typewriting: Effector dependent and spatial representations. In this project, it was investigated whether seeing letters activates the corresponding action of keypressing in people skilled in typewriting in the 10-finger-system. Participants responded to the color of letters (congruent condition: Responding finger was the one usually used to type the letter). Skilled participants showed a congruency effect, unskilled participants did not. Responding with crossed hands on an external response device provided evidence for effector-dependent representations only, whereas responding on a keyboard resulted in evidence for effector-dependent and spatial representations (Rieger, 2004).

The control of bimanual actions 2.1.7

Weigelt, M.

The ability to grasp and manipulate objects in a purposeful way is essential to solve everyday tasks, such as when using a knife to spread butter over bread or operating a cork screw to open a bottle of wine. Given the seemingly endless number of situations, in which we have to grasp and manipulate objects, it is astonishing that we appropriately select our grip postures nearly every time we perform a particular action. From a behavioral perspective, the selection of grip postures provides an interesting field of study for researchers interested in the principles and mechanisms underlying human action control. We investigate the influence of action goals on the production of bimanual actions and provide strong evidence for the notion that the simultaneous coordination of two movements is largely constrained by the congruency of anticipated, perceptual goal states (Weigelt et al., in press).

Bimanual object manipulation. Similar to a bar tender putting two glasses simultaneously on a shelf, participants placed two objects either into congruent or incongruent orientations by carrying out either mirror-symmetrical or mirror-asymmetrical rotation movements of the bilateral forearms (Kunde & Weigelt, 2005). The results demonstrated strong goal-congruency effects as participants initiated their actions faster under conditions, in which the two objects had to be rotated into the same orientations – irrespective of whether this afforded mirror-symmetrical or mirror-asymmetrical rotations.

Movement-symmetry effects were only observed when the movements themselves became the goal of the action. We conclude that performance in bimanual object manipulation is constrained by the creation and maintenance of goal codes rather than by properties inherent in the neuromuscular system that carries out these responses. These goal codes can relate to either body-intrinsic states or body-extrinsic states according to the actors' current intentions.

Bimanual end-state comfort effects. The notion of end-state comfort describes the sensitivity to avoid awkward hand- and arm-postures at the final position of a movement. We investigated end-state comfort effects in bimanual object manipulation (Weigelt et al., in press). Participants were required to simultaneously reach for two bars and to place the objects' ends into two target discs on the table. The design of the experiment allowed dissociation of the relative roles of initial means (e.g., the selection of grips) and final postures (e.g., the anticipation of end-states). The question of interest was whether affording different grip patterns for the two hands would introduce a bias away from reaching end-state comfort. Results revealed a strong sensitivity for end-state comfort independent of the required grip patterns. In particular, end-state comfort was preferred, even if this meant selecting different initial means (i.e., different grips) for the two hands. Hence, end-state oriented action planning appears to dominate interaction costs that may result from motor-related, intermanual interference. We infer that movement planning is constrained by action goals (e.g., a comfortable end-posture for both hands), but largely unaffected by the type of motor actions necessary to achieve these goals.

2.1.8 A psychological approach to voluntary actions

Mechsner, F.

How is it possible that we move fluently and smoothly according to our ever-changing intentions, in an abundantly flexible, creative and thereby perfectly adapted way? Our working hypothesis says that the key to understanding human motor performance lies in the abundant flexibility, creativity and adaptability of our psychological system (Mechsner, 2004a; 2004b). That means, the critical problem for the controlling system lies in the construction of task-adequate perceptual and conceptual movement representations. Coordinative training is about such psychological movement schemes and strategies, and not about motor commands. The latter are automatically tuned accordingly in every situation.

Bimanual multi-finger tapping. We investigated stability characteristics in bimanual multi-finger tapping (Mechsner & Knoblich, 2004). Participants periodically tapped with four fingers altogether with two pre-selected fingers of each hand tapping in alternation. The selected finger pairs could be congruent (i.e., identical pairs were selected in both hands) or incongruent (i.e., different pairs were selected in both hands). In earlier experiments we had shown that the symmetry tendency is independent of the selected finger pairs and thus certainly not a tendency towards co-activation of homologous muscle portions as has widely been suggested. The present experiments revealed that the finger-independent symmetry tendency was also independent of whether the hands were visible or hidden from view. Visual cues to facilitate the perception of symmetrical or parallel movement patterns were not able to change the stability characteristics. When the hands were put in non-symmetrical positions the main stability characteristics of the finger movement did again not change. We conclude, first, that the stability characteristics, including the symmetry tendency, originate in connection with planning and monitoring the movements as perceptual events, and second, that the primary perceptual medium for planning and controlling the investigated tapping patterns is somatosensoric rather than visual in nature.

Complex athletic movements. If movement control is psychological in nature, perceptual and conceptual representations must provide a suitable basis for solving the functional and biomechanical problems of the task. We investigated perceptual-conceptual representations of the tennis serve (Schack & Mechsner, 2006). We revealed representational networks of so-called basic action concepts in long-term memory of skilled athletes. These networks corresponded well to the functional and biomechanical demands of the task. We infer that such perceptual-conceptual networks might form the representational basis for action control in skilled movements.

Voluntary action

2.1.9

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Goschke, T.[1,2], Maasen, S.[1,3], Prinz, W.[1], Vossenkuhl, W.[4], Splett, T.[4], Vierkant, T.[1,5] & Walde, B.[6]

This interdisciplinary project aims at an understanding of voluntary action. Investigating voluntariness seems very important not only for the progress of our scientific understanding of human action control, but also because the willing subject is a practical assumption in most discourses of social life.
The research project started off with the provocative question whether there might be a cognitive illusion.
One philosophical project attempted a direct answer to that question. According to this project, when one asks whether the will exists one should consider the question of what this thing called *the will* is. To characterize it, one has to examine the ways we deal with it in our various discourses and practices. The will is what statements about the initiation of action are about. Some of those statements are wrong, others are true. The true ones differ in what is making them true. Some of them are true, because they express natural features, which play important functional roles in action initiation, independent of our social practice of attributing volitional attitudes (these were investigated in the psychological subprojects). But some of them may not aim at the natural features, but at something that is dependent on or even constituted by the social practice. In this respect, the discourse on the will is made true partly by itself (although under some natural constraints), like a trail is made just by people walking on it. The project concluded that we can take the will partly as a social construction without denying its existence (the changes in the constituting discourse on the will were the topic of the sociological subproject). One would not dismiss paper money although its value is dependent of our taking it as valuable. Of course, not all of our common statements dealing with attributing volitional attitudes are true. Insofar as important features of the will are expressed by those false statements, it is justified to call the will an illusion.
Working from this result, our discourse on the will can, but does not have to be illusory, another philosophical subproject explored the practical philosophical consequences of our improving knowledge and changing discourse on the will. Neuroscience might be able to show that consciousness cannot fulfill the role, which we take to be essential for it to fill, in order to allow for proper willed actions. The subproject devised a strategy that could integrate a semi-compatibilist proposal for responsibility with the findings of cognitive science. This general account has enabled the project to understand why consciousness has to play a central role in justified responsibility ascription. Consciousness is the place where the narrative evaluation of behavior takes place. Only through consciousness is it possible for the individual to evaluate whether the constraints that have been implemented into the functional machinery after prior reasoning are influencing *current* behavior in a way that is consistent with the moral self.
All in all, the interdisciplinary project was highly successful. Using the expertise from the different sub-disciplines, enabled a new perspective to be acquired on the problems in the sub-disciplines. What is more, taking on board the different perspectives of the other disciplines made it easier to see how complex our everyday notion of willed action is and to make sense of it in scientific discourse without being either overly defensive or dismissive about its value.

2.1.10 Cognitive task representations and task-set selection

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One aim in cognitive psychology is to explore which processes are necessary to perform different tasks. A related question that, however, has been largely neglected so far is the question of what actually defines a task. In the present project, we examined which response-related factors are relevant in the cognitive representation of tasks.

One possible method to examine both questions is the task-switching paradigm. Here, participants are introduced to different tasks and are required to execute them in a changing sequence. When participants perform a sequence of different tasks, it is assumed that the engagement in one task leads to the inhibition of the previous task. This inhibition persists and impairs performance when participants switch back to this (still inhibited) task after only one intermediate trial.

Previous task-switching studies have defined different tasks at the level of stimulus categorization (e.g., categorizing a digit as odd or even vs. categorizing a digit as greater or less than 5). However, there is no consensus as regards how a "task" can be defined. We assume that a task-set (i.e., the cognitive representation of a task) consists of different components like stimulus modality, stimulus categorization, stimulus-response mapping and so on. Whereas the role of stimulus-related task-set components has been studied previously, the role of response-related components was largely neglected. In the present project, we were able to specifically show the relevant role of response-related task-set components. On the one hand, we demonstrated inhibition on the level of response modes (i.e., choice-response vs. simple response; Koch et al., 2004). On the other hand, we provided evidence for the role of response modalities in cognitive task representations (Philipp & Koch, 2005). In the later experiments, participants always used the same stimulus categorization (e.g., categorize a digit as odd or even), but had to give a vocal-, finger- or foot-response (A, B or C). Our results showed a higher reaction time and error rate in ABA sequences (e.g., vocal/finger/vocal) than in CBA sequences (e.g., foot/finger/vocal), indicating n-2 repetition cost as a marker for persisting task inhibition (see Figure 2.8). We conclude that different response modalities can define a task and are inhibited in a "task switch" in the same way as stimulus categories are inhibited. Thus, the results provide evidence that the same cognitive processes underlie switching between response modalities and switching between stimulus categories.

In a different research project, following an earlier study of Schuch and Koch (2003), we could support the finding that response-related processes play an important role in task switching (Koch & Philipp, 2005). The activation of the relevant task set as well as the inhibition of competing task sets strongly depends on response-related processes (e.g., response-selection). We further suppose that different task-set components like stimulus categories or response modalities have to be integrated into one single task representation before subjects can perform a "task". Thus, even components that are often classified as motor-related processes (e.g., the response modality) need to be specified and integrated into a cognitive task representation before the selection of a response.

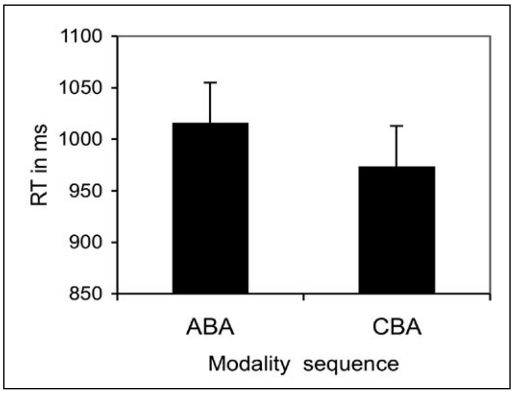

Figure 2.8

The role of task competition and inhibitory processes in the control of task set

2.1.11

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[2] *Department of Psychology, RWTH Aachen University, Germany*

Gade, M.[1] & *Koch, I.*[1,2]

This project aims to explore the mechanisms underlying task-set control. Current models assume that task set is controlled by both activation and inhibition mechanisms (Schuch & Koch, 2003). Our project seeks a better functional characterization of task inhibition mechanisms. Inhibition of abandoned tasks in task switching can be inferred when finding worse performance in n-2 task repetitions (ABA sequences) compared to non-repetitions (CBA sequences). In a recent study, we used temporal manipulations to vary the degree of task competition assumed to determine inhibitory processes (Gade & Koch, 2005).
Recent evidence has shown that inhibition effects (i.e., n-2 task repetition costs) decrease with long inter-trial intervals (i.e., response to task-cue intervals/RCI). Two alternatives have been proposed to account for this decrease. One alternative attributes the observed decrease to the decay of inhibition itself. The other alternative proposes that decay of the activation of competing tasks reduces the interference and leads to less inhibition. To decide between these alternatives, we manipulated RCI trialwise. The results favor the decay-of-activation account as explanation for the decreased inhibition effect. This links the amount of inhibition to the activation level of the competing tasks, whereas evidence for the decay of inhibition remains weak.
Taken together, the findings suggest that task competition is the major determinant of inhibitory processes in task-set control. Task competition can vary as a function of several variables, such as decay-time interval and response set. Future studies will explore the role of response-set overlap and stimulus-set overlap in task-set control.

Sequencing of actions and tasks

2.1.12

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Koch, I.[1,2]

In a series of interrelated projects, we investigated the cognitive bases of action control at various levels. The first two projects were concerned with learning and performing basic action sequences, whereas two further projects aimed at exploring how actions are coded in a context-sensitive and task-specific manner.
Processes of action sequencing were investigated using a serial reaction-time (RT) task paradigm, contrasting motor performance with random stimulus sequences with that with predictable, structured sequences. In this paradigm, learning is indicated by a sequence-specific decrease of RT relative to random sequences. Sequence learning was found to reduce stimulus-induced interference effects (i.e., S-R compatibility effects), suggesting that learning leads to the formation of motor programs that can control action in a memory-based rather than stimulus-based fashion. This, however, occurred only for subjects who acquired an explicit, verbalizable sequence representation. Using hierarchically organized stimulus material, we sought to induce an explicit chunking strategy, and we found in a neuropsychological study that performance of explicitly learnt action sequences is not disrupted in patients with lesions of the prefrontal cortex. This suggests that chunks are represented in a motor program-like format that can control action in a very basic and robust way.
Action sequences are typically embedded in a "higher-order" task context. Tasks determine required actions, and actions can acquire task-specific meanings. Learning of such higher-order sequences of tasks was examined using the sequence-learning methodology described above (see Koch, 2005). We found learning of task sequences, but only those subjects who developed an explicit representation of the task sequence showed evidence of chunking. This evidence was indirectly indicated by a modulation of a task inhibition effect, which was not modulated in implicit learning (Koch et al., in press).

We investigated task-specific processes of action coding also using a dual-task methodology (Schuch & Koch, 2005). In a dual-task trial, two stimuli are presented in close temporal succession. We manipulated the task-context, in which each of the two stimuli had to be processed, and we used instructions to induce a grouping of the two manual responses into an action sequence. We found that action sequencing was more successful (i.e., shorter inter-response intervals) when both actions belonged to the same task context as compared to different task contexts ("task switching"). This suggests that actions are coded in a task-specific way and that the task-specific "meaning" of each action needs to be recoded in a time-costly way, if two sequential motor actions need to be assigned to different task contexts (see also Schuch & Koch, 2004).
Taken together, the interrelated projects were aimed at understanding the sequencing mechanisms governing human performance better, ranging from chunking processes in motor performance to more complex sequencing processes at the higher-order level of tasks.

2.1.13 The role of episodic S-R bindings in task-switch costs

Waszak, F.[1], Hommel, B.[2], Allport, A.[3], Herwig, A.[1] & Prinz, W.[1]

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The retrieval account of task shift costs (TSC) assumes that previously appropriate task sets may be automatically retrieved from memory when stimuli recently associated with these sets are presented again, thereby creating a conflict with the currently appropriate set. In emphasizing the role of stimulus repetition and bindings between the stimulus and task set, this approach contrasts with other accounts that consider TSC to reflect a kind of task-set reconfiguration needed to intentionally prepare the cognitive system for the new task.

In the project "The role of episodic S-R bindings in task-switch costs", we examined stimulus-driven aspects of cognitive control in more detail, and refined the retrieval account of task shift costs. The general procedure of the paradigm we used is as follows: Participants named pictures and read words in response to incongruent picture-word Stroop stimuli (see Figure 2.9), switching between the tasks every two trials. Some of the stimuli were presented in both tasks, picture-naming (prime task) and word-reading (probe task), whereas other stimuli were presented only for word-reading. The common outcome of this kind of experiment is that stimuli presented in both tasks show significantly larger shift costs than stimuli presented in word-reading only.

Using bivalent Stroop stimuli, there are two different ways in which previous experience with a given stimulus, in the context of picture naming, might affect later word reading performance. Naming the picture in the presence of a word distractor may have required suppression of the competing (word-reading) response, and it could be this prior suppression of the previously irrelevant response that impairs later response to the same stimulus (negative priming, NP). On the other hand, naming the picture also results in a memory trace linking the stimulus and the picture naming response. If the same stimulus is presented again in the context of word reading, it may trigger involuntary retrieval of this earlier, picture-naming episode, reactivating the (now inappropriate) picture-naming process (competitor priming, CP). In the study by Waszak and coworkers (2005), NP and CP were manipulated independently. We demonstrated that both factors influence reaction times. Importantly, both types of interference interacted with task readiness: The word reading task showed priming effects on switch trials only (thereby increasing shift costs,

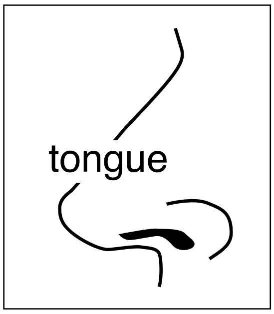

Figure 2.9 Typical picture-word Stroop stimulus.

see Figure 2.10). Thus, the retrieval of previous processing episodes has a selective impact on situations, in which task competition is high.

In another series of experiments (Waszak et al., 2004), we showed that task switching is also impaired for stimuli that are only semantically related to previously picture-named stimuli. Hence, stimulus-task bindings generalize semantically suggesting that possibly most or all residual shift costs reflect some sort of generalized proactive interference from previous stimulus-task episodes.

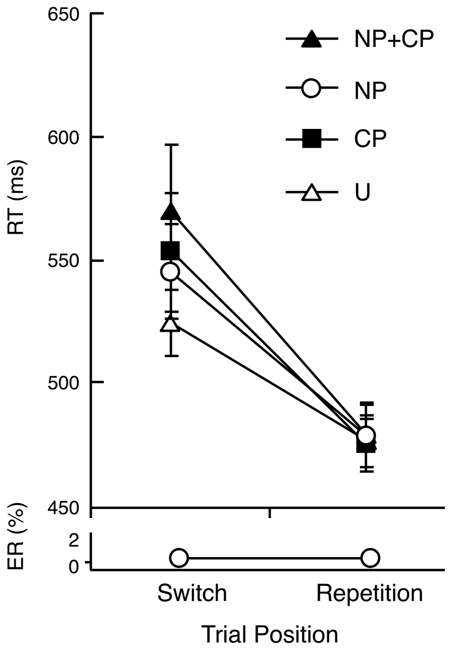

Figure 2.10 Data from Waszak et al. (2005, Experiment 1): Mean RTs for word-reading as a function of trial (switch, repetition) and priming (unprimed [U], competitor primed [CP], negative primed [NP], negative and competitor primed [NP+CP]).

Projects from this domain of research study the impact of representational resources for action planning and action control on the perception and understanding of intention and action. One of the basic ideas here is that action perception relies on action simulation, i.e., that, in order to understand other individuals' actions and intentions, individuals make use of their own resources for action planning and control. These projects address such diverse domains like spatial and functional interactions with objects (2.2.1, 2.2.5), perception of speech and musical performance (2.2.2, 2.2.3), imitation (2.2.6) and action perception in shared task environments (2.2.4). Major theoretical issues concern the importance of spatial, temporal and functional information for action understanding (2.2.1, 2.2.3), mechanisms of co-representation (2.2.2, 2.2.4, 2.2.6) and the role of own action for understanding others' action (2.2.2, 2.2.5, 2.2.6).

2.2.1 Action understanding: The role of spatial and functional relations

Bach, P.[1,2], *Knoblich, G.*[1,3], *Gunter, T.C.*[1], *Friederici, A.D.*[1] & *Prinz, W.*[1]

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In order to understand instrumental actions, we need to analyze functional and spatial relations between actions and objects. For instance, in order to successfully perform a cutting action, we need an appropriate tool (scissors) and this tool needs to be in a specific spatial orientation relative to the target object (Figure 2.11A). Mismatches in the spatial or functional relationship preclude successful action. For instance, if the spatial relationship between instrument and target object does not match (Figure 2.11B), the tool cannot be applied to the target object. Similarly, if the functional relationship between tool and target object is mismatching, no meaningful action is possible (Figure 2.11C). Obviously, the action will also not be successful, if spatial and functional relation mismatch (Figure 2.11D).

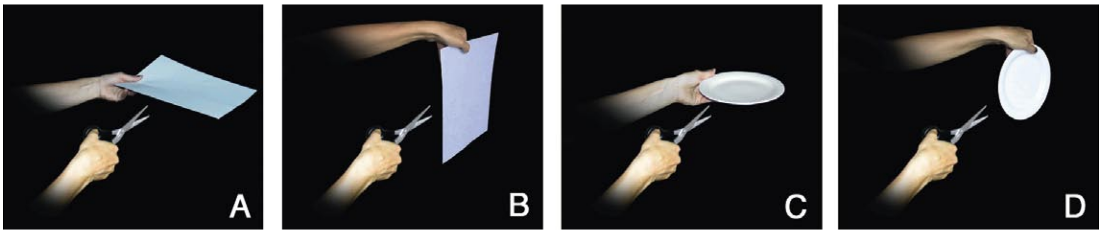

Figure 2.11 Examples for possible functional and spatial relations in a cutting action. (A) Full match: Spatial and functional match. (B) Spatial mismatch and functional match. (C) Spatial match and functional mismatch. (D) Spatial match and functional mismatch.

In a recent series of experiments (Bach et al., 2005), we used an interference paradigm to determine whether action understanding involves automatic processing of such spatial and functional relations. Participants observed action displays such as the ones displayed in Figure 2.11. In one experiment, we asked participants to judge whether the spatial relation between tool and target was matching or mismatching and to ignore the functional relation. The results showed that judgments were slower when there was a functional mismatch between tool and target object. Thus, irrelevant functional mismatches interfered with judging the spatial relation. In another experiment, we asked participants to judge whether the functional relation was matching or mismatching and to ignore the spatial relation. This time, spatial mismatches interfered with judging the functional relation. Together, these results imply that action understanding involves automatic processing of both, spatial and functional relations.

In further studies, we will address the question of whether two separate processes support deriving spatial and functional relations. So far, results from behavioral and EEG experiments seem to support the two-systems hypothesis. The analysis of reaction time distributions indicates that spatial and functional relations are processed independently and in parallel. The EEG data provide a first hint that a premotor network (mirror system) derives spatial relations, whereas temporal areas derive funtional relations.

How musicians recognize their own playing

2.2.2

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Previous research on the self has often stressed knowledge about one's past and presence such as autobiographical memories or ascribing certain personality traits to oneself. Less attention has been paid to the fact that individuals have different ways of performing actions, and that particular ways of performing actions might also be part of a person's identity. Musical expertise, such as playing the piano, provides a good example. Skilled pianists do not just mechanically reproduce the score of a musical piece. Rather, they deviate from the score in particular ways. Previous research has shown that a pianist's style can be described in terms of expressive dynamics and expressive timing. Expressive dynamics refer to the fact that skilled piano players put different emphasis on the different notes in the score. Expressive timing refers to subtle timing deviations from the notated score, e.g., holding a note a little bit longer or playing it a little bit too late.

Do pianists recognize their own performances based on expressive dynamics and expressive timing? We addressed this question in a collaborative research project with Bruno Repp at Haskins Laboratories (Repp & Knoblich, 2004). Twelve expert pianists studying or taking lessons at the Yale School of Music (New Haven, CT) were recorded, while they played musical excerpts they were mostly not familiar with (from Bach's Preludes from the Well-Tempered Clavier, Beethoven's Sonata movements, and Mozart's Sonata movements). Half of the pieces were performed on a silent keyboard, so that the pianists could not hear their playing. Several months later, we played these performances back to the pianists and asked them to rate whether they heard their own or somebody else's performance. The ratings showed that they could recognize their own performances well. In two follow-up tests, we presented edited performances that had been equated in the overall tempo and dynamics, leaving only expressive timing for recognition. Pianists recognized their own performances as well as before. This means that the remaining expressive timing information was sufficient for self-recognition. Surprisingly, the absence of sound during recording had no significant effect. Whether or not pianists heard themselves play the piece did not affect self-recognition.

How can these results be explained? It is unlikely that episodic memory of the recording session informed self-recognition. Otherwise, there should have been a large difference in self-recognition between pieces that were heard and pieces that were not heard during production. We suggest that pianists recognize their own performances, because listening to a piano performance leads to an activation of the same action representations a pianist would use to perform the heard piece. The activation of these representations, in turn, results in a prediction of what should be heard next. In other words, the pianist runs an action simulation of what the piece would sound like if s/he played it her/himself and compares it to the heard piece (cf. Wilson & Knoblich, 2005). If the heard piece sounds like the internally simulated piece, it is perceived as self-produced, if there are mismatches, it is perceived as other-produced. In further studies, we plan to investigate the effects of action simulation in duet performances (Keller et al., in press). Finally, it should be mentioned that recognition of one's own actions based on idiosyncratic timing patterns is not restricted to musical experts. Individuals who are not musically trained can recognize the rhythm of their own clapping even if the sound of clapping is replaced by simple beeps (Flach et al., 2004).

2.2.3 Hand movements can reveal the time course of phonological processing

Grosjean, M.

A variety of models of spoken-language processing assume a continuous intake and accrual of acoustic-phonetic information and a dynamic competition between concurrently active lexical representations. In a recent study (Spivey et al., 2005), we provided further evidence for this notion by analyzing the trajectories of goal-directed hand movements performed during spoken-word recognition in a visual context. The task of the participants was to move their hand to one of two simultaneously presented objects that was indicated by the acoustic presentation of a word. Evidence for graded activation of and continuous competition between lexical representations was revealed in the difference between hand trajectories recorded during conditions in which the distractor object did and did not have a name that phonologically overlapped with that of the target object. These findings suggest that the recording of hand movements may provide a new method of visualizing the dynamics of language processing.

2.2.4 Action and task co-representation: Predicting what others will do

Sebanz, N.[1,2], Knoblich, G.[1,2], Wascher, E.[1,3], Stumpf, L.[4] & Prinz, W.[1]

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Research in social cognitive neuroscience suggests that the cognitive and neural processes underlying perception and action cannot be fully understood without taking into account how they are shaped by social context. Previous studies have provided evidence that processes related to the planning and performance of goal-directed actions are modulated by observing others' actions, suggesting that action perception and execution are tightly linked. These studies focused on social settings in which an individual either merely observed another's actions, or performed certain actions while concurrently perceiving actions. In a series of new studies, we employed behavioral and electrophysiological techniques to investigate how the planning and control of actions is shaped by *acting together with* another individual rather than just *observing* another's actions.

Replacing the usual observer-actor context with a setting in which two participants performed a task together, it was shown that others' actions can become part of one's own action plan, and that acting in turns places special demands on action control. In an ERP study (Sebanz et al., in press), participants performed a go-nogo task, responding whenever a ring on the index finger of a hand was red or green, while ignoring the pointing direction of the hand (see Figure 2.12, left). The same task was performed alone and in a group, with the other participant responding to the other color. Although there was no need to take the other's actions into account, RTs in the group were slowed when individuals responded to a stimulus referring to the other's action (a hand pointing towards the other). Thus, an action selection conflict occurred when the stimulus activated a representation of the other's action, suggesting that participants represented their own and the other's action in a functionally equivalent way. Analysis of the nogo trials showed that the Nogo-P3, an electrophysiological component associated with response inhibition, was more pronounced when participants had to withhold an action while the other was acting, compared to when they were alone and no-one acted on nogo trials (see Figure 2.12, right). Most likely, anticipating the other's action caused a tendency to act which had to be suppressed.

The results of two further studies provide evidence that each participant represented not only the spatial position of the other's action, but formed a representation of the other's task, i.e., the specific stimulus conditions under which the other was supposed to act (Sebanz et al., 2005). Surprisingly, even individuals with autism, who had difficulties understanding others' beliefs, formed a representation of the other's task, suggesting that forming shared task representations is a basic and ubiquitous phenomenon that occurs despite theory of mind deficits (Sebanz et al., 2005). It can be concluded that the ability to form shared representations of tasks is a cornerstone of social cognition allowing individuals to act in anticipation of others' actions rather than just responding.

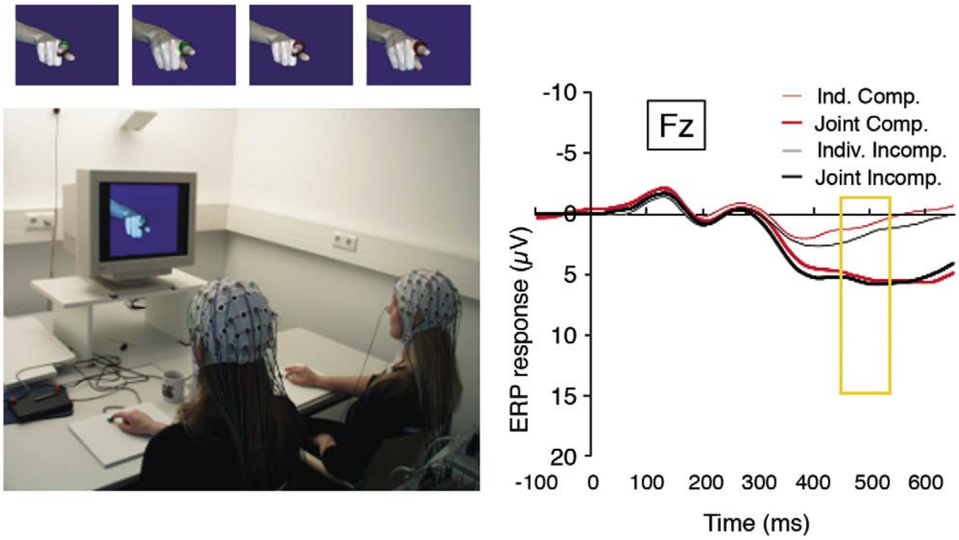

Figure 2.12

What we cannot do ourselves, we cannot understand in others

2.2.5

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Bosbach, S.[1,2], Cole, J.[3], Prinz, W.[1] & Knoblich, G.[1,4]

Successful social communication critically depends on the ability to understand the actions of other people. A growing body of evidence suggests that in order to understand others' actions we have to remap what we observe onto an internal representation of our own actions. But what happens if there is a deficit in the knowledge of one's own body? Simone Bosbach, Jonathan Cole, Wolfgang Prinz und Günther Knoblich showed that patients without the senses of cutaneous touch and proprioception are impaired in extracting some information from others' actions.

The authors investigated two patients with the extremely rare condition of selective haptic deafferentiation due to sensory neuropathy resulting in a complete loss of touch and proprioception from their body. Bosbach et al. (2005) were interested whether these deficits affected their ability to interpret the action of other's.

Both patients were confronted with videos showing a person lifting a box of varying weights (cf. Figure 2.13) and were asked to estimate the weight of the box. Both patients performed this task as well as a group of healthy controls. Thus, they could deduce the box's weight purely from observing a person's lifting movement.

In a second task, the patients and controls were asked to guess whether the person lifting the box had prior to lifting received correct or incorrect information about its weight. Again, the only source of information for making this judgment was the movement of the lifter. It turned out that the patients did much worse than the controls, indicating that they had a deficit in deducing someone else's expectation from their action.

Finally, the authors reversed the task. They asked one of the patients to pick up the box himself, and then showed him and a group of controls videos of his actions. The patient was no more accurate at judging his own weight expectations than those of others. Also, the controls did worse at deciding whether the patient had correct or incorrect information about the weight of the box; his movement kinematics during picking up boxes of unknown weight did not differ depending on whether he expected a correct or false weight. In other words, the deafferented patient was not able to attune his movements to his expectations. Therefore, he was not able to deduce the expectation of others from their movements.

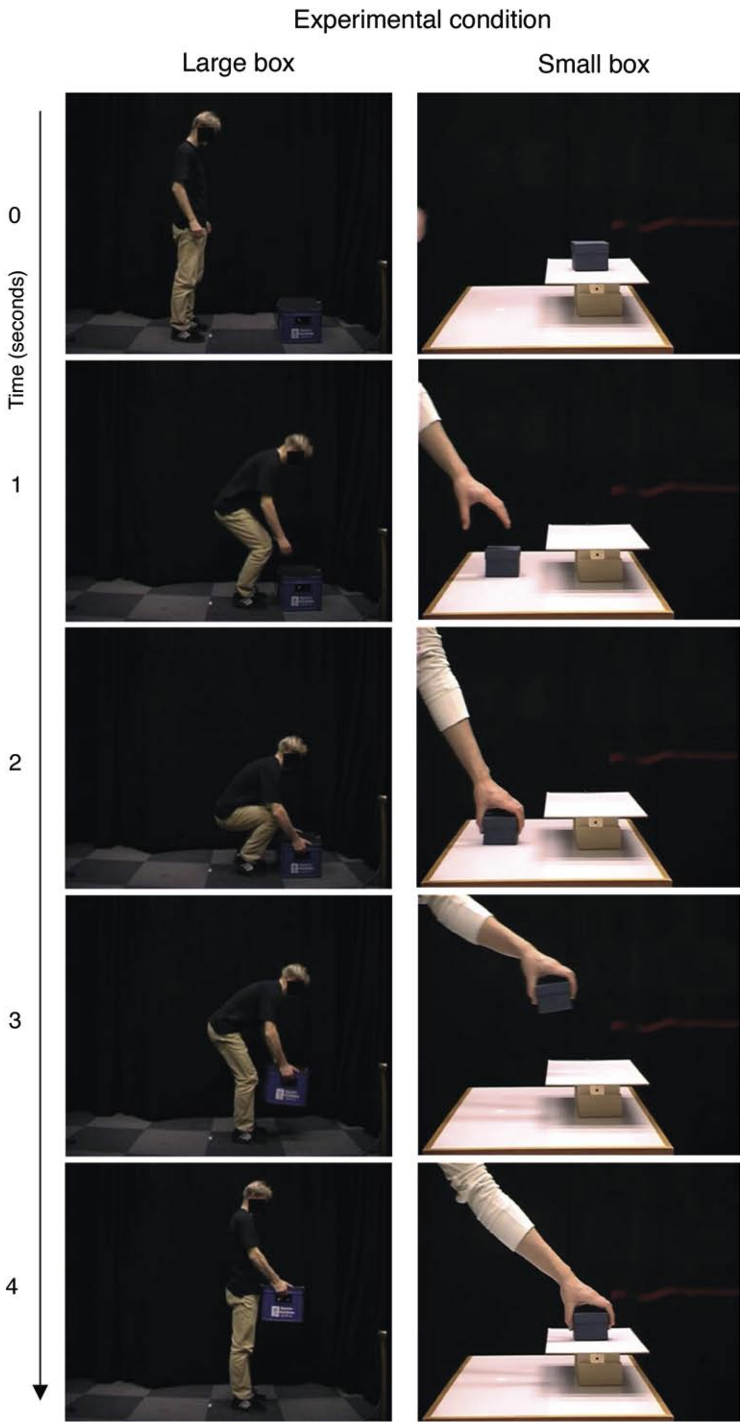

Figure 2.13 Frames of the video clips: Normal subjects are lifting boxes of various weights. Faces of actors were blacked out to ensure that facial expressions did not affect subject's judgments.

These results seem to suggest that the possibilities and limitations of our own body determine our understanding of other's actions. In other words, we understand in others what we can do ourselves and what we cannot do ourselves, we cannot understand in others.

2.2.6 Imitation in preschoolers and adults

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Imitation, or performing an act after perceiving it, guides the behavior of a remarkable range of species at all ages. Imitation also serves an important function in human development, offering the acquisition of many skills without the time-consuming process of trial-and-error learning. The common view on how perception and action are mediated in imitation postulates that a matching takes place between the perceptual input and existing motor programs in the observer. We, however, have argued that this matching does not take place at the motor level; rather, we suppose it to take place at the cognitive level of goal specification. That is, if we observe an action, we decompose the movement observed into its constituent components and later reconstruct an action from these components. Importantly, the de-

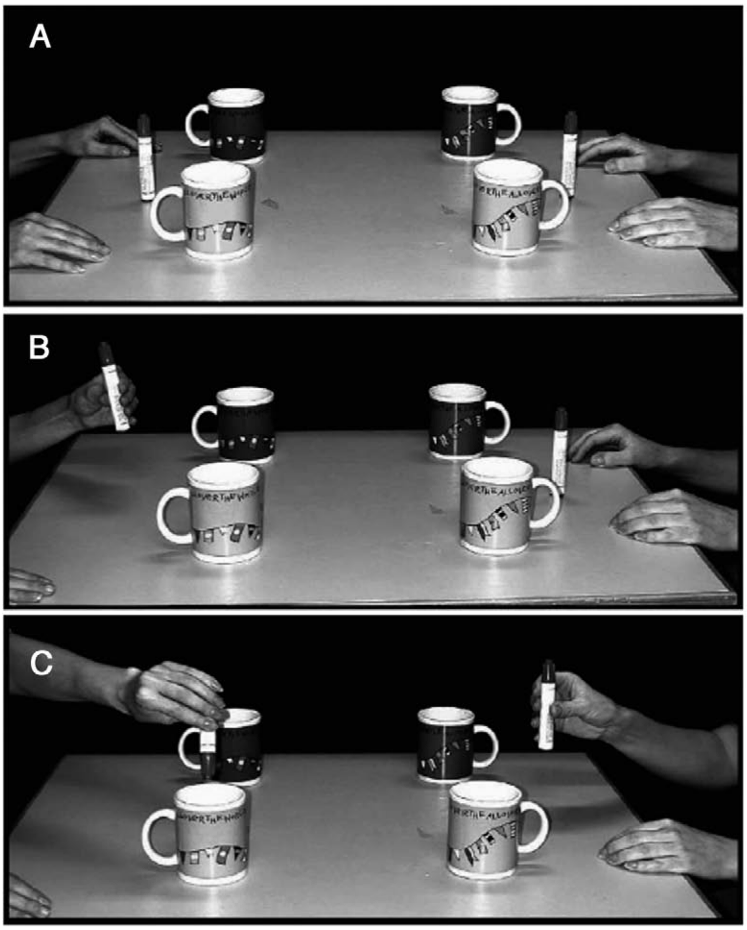

Figure 2.14 Example of the pen-and-cup imitation task. The subject is sitting opposite to the experimenter and they both have a blue cup, a green cup, and a pen on the table in front of them. The subject imitates the experimenter's movements as simultaneously and accurately as possible.

composition-reconstruction process is guided by an interpretation of the movements as a goal-directed behavior with some of the goals being dominant over others (Wohlschläger et al., 2004; Gattis et al., 2002; Bekkering & Wohlschläger, 2002).

More recently, we have tried to determine the nature of the goal hierarchy in more detail. In a series of experiments, adult subjects had to imitate a pen-and-cup action. The action modeled consisted of several components: There were two different objects, two possible locations, two treatments of what to do with the pen and the cup, two effectors (left or right arm), and two movements (clockwise or anticlockwise, see Figure 2.14). Participants were fully informed about the aspect they needed to imitate. In another experiment, they were asked to imitate spontaneously the action observed. Results were basically the same: As predicted by the goal-directed theory of imitation, the category of errors observed most frequently was the type of movements performed. The second and third most frequent types of errors were the effector chosen and the location, respectively. Almost no errors occurred for treatment, and the best-imitated component was the object. Taken together, these observations indicate that imitation is not about copying movements. Rather, it is the goal of the action observed that we imitate. The organization of these goals seems to be very functional. That is, the ends of an action are more important than the means (Wohlschläger et al., 2004).

NEUROCOGNITION OF LANGUAGE PROCESSING 3.1

While prior work focused on the functional neuroanatomy and the neural dynamics of lexical-semantic, syntactic and prosodic processes as different components, the goal of the research of the last two years was first, to test to what extent the effects observed for German can be found in other languages, be they natural or artificial, and second, to specify the neural basis of the interaction between these subcomponents.

In the three-phase neurocognitive model of language comprehension formulated in 2002 (Friederici, 2002), Phase 1 is defined as a phase during which the build-up of local phrases takes place. This phase is independent of Phase 2, during which hierarchical dependencies are established and thematic roles are assigned on the basis of morphosyntactic information (subject-verb agreement, verb-argument structure, case of the arguments) as well as lexical-semantic information.

Phase 3 is considered to cover integration processes. The neuroanatomy of the different aspects of syntactic processing, local phrase structure versus hierarchical dependencies, was investigated in an fMRI study using two types of artificial grammars. It was found that the processing of local transitional probabilities is supported by the left frontal operculum, whereas the processing of hierarchical dependencies additionally recruits Broca's area (3.1.1). In an ERP study with the same grammar types, we observed a late positivity (P600) for both grammar types, but an early negativity only for violations of local phrase structure (3.2.2). Early syntactic negativities followed by P600 have been reported for syntactic violations in natural languages as well. In a study using an MMN paradigm, the early syntactic negativity reflecting phase structure building was shown to be highly automatic (3.1.3). A study investigating syntactic processes in Chinese also found an early syntactic negativity for phrase structure violations, which preceded effects of semantic violations in time (3.1.4). The neural network supporting these processes across different languages was compared in native Russian and native German speakers and was found to be very similar in these typologically different languages (3.1.5). The relation between phrase structure and morphosyntactic processes was studied with sentences in which target items either carried single or double violations. An early syntactic negativity for phrase structure violations and later LAN-P600 for the argument violations support the assumed Phase 1 and Phase 2 in the model (3.1.6). The processing of case information was tested in two different languages. Case conflicts resulted in an N400-P600 pattern in German (3.1.7) and in Japanese (3.1.8, 3.1.9). A biphasic N400-P600 has also been observed for verb-argument structure violations. Here, we conducted an fMRI study to uncover its neural basis and show that the left superior temporal cortex plays a major role in verb-argument structure processing (3.1.10).

Earlier fMRI work from our laboratory demonstrated the right hemisphere to support syntax-relevant prosodic processes. In an ERP study, we found that prosodic violations elicit a right anterior negativity (RAN), and that a combination of a syntactic and a prosodic violation leads to an interaction in the P600 time window covering Phase 3 in the model (3.1.11). The on-line use of contrastive accent placements for syntactic parsing was demonstrated even in a reading study using contrastive constructions (3.1.12). Prosodic information and contextual information, moreover, interact at the level of dialogues (3.1.13).

Interaction between prosodic information and morphosyntactic information can be observed during auditory word processing (3.1.14). The neural basis of this interaction at the sentence level was specified in patients with lesions in the corpus callosum (CC). The results indicate that the posterior portion of the CC is the structure through supporting the interaction between syntactic and prosodic information (3.1.15).

3.1.1 The brain differentiates between human and non-human grammars: Functional localization and structural connectivity

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The human faculty to process hierarchical syntactic structures was claimed to be one core attribute that differentiates human from non-human language (Hauser et al., 2002). This human ability goes beyond the capacity to process sequences with simple transitional probabilities of adjacent elements observable in non-human primates (Fitch & Hauser, 2004). In the present study, an artificial grammar task was used in order to compare hierarchical structures (Phrase Structure Grammar, PSG) and simple transitional structures (Finite State Grammar, FSG) in humans. In a functional magnetic resonance imaging study, senseless, but well-structured consonant-vowel syllables, were applied to explore whether FSG and PSG recruit different brain areas. As a result, the processing of both artificial grammars (FSG and PSG) caused activity in the left frontal operculum. In addition, only in the PSG condition was the left pars opercularis (BA 44, Broca's area) engaged (see Figure 3.1). Tractography data revealing differential structural connectivity signatures for these two brain areas provide additional evidence for a segregation of two areas in the left inferior frontal cortex. These findings suggest that the processing of local transitions is subserved by the left frontal operculum, a region that is phylogenetically older than Broca's area, which specifically holds responsibility for the computation of hierarchical sequences.

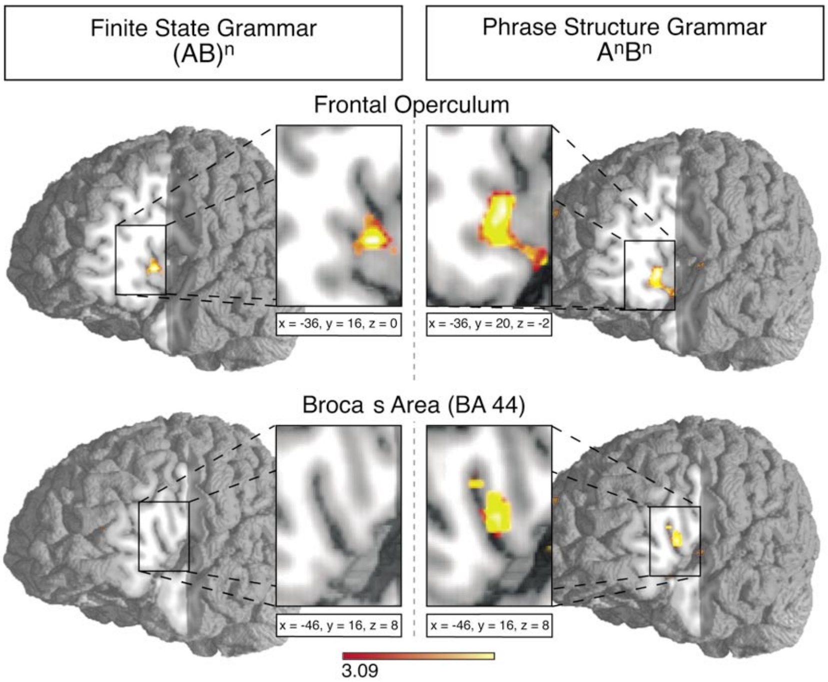

Figure 3.1 Brain activation pattern for the two grammar types. Statistical Parametric Maps of the group-averaged activation during processing of violations of two different grammar types ($p < 0.001$, corrected at cluster-level). Left panel shows the contrast of incorrect vs. correct sequences FSG, right panel shows the same contrast in the PSG for Broca's area (upper part) and the frontal operculum (lower part).

Hierarchical and linear sequence processing: An electrophysiological exploration of two different grammar types

3.1.2

Bahlmann, J., Gunter, T.C. & Friederici, A.D.

The present study investigated the processing of two types of artificial grammars by means of event-related brain potentials (ERPs). Two categories of meaningless CV-syllables were applied in each grammar type. The two grammars differed with regard to the type of the underlying rule. The Finite State Grammar (FSG) followed the rule $(AB)^n$, thereby generating local transitions between As and Bs (e.g., n = 2: ABAB). The Phrase Structure Grammar (PSG) followed the rule A^nB^n, thereby generating center-embedded structures in which the first A and the last B embed the middle elements (e.g., n = 2 [A[AB]B]). Two sequence lengths (n = 2, n = 4) were used. Violations of the structures were introduced at different positions of the syllable sequences. Early violations were situated at the beginning of a sequence, and late violations were placed at the end of a sequence. A posteriorly distributed early negativity elicited by violations was only present in FSG. This effect was interpreted as the possible reflection of a violated local expectation. Moreover, both grammar type violations elicited a late positivity. This positivity varied as a function of the violation position in PSG, but not in FSG (see Figure 3.2). These findings suggest that the late positivity could reflect difficulty with integration in PSG sequences.

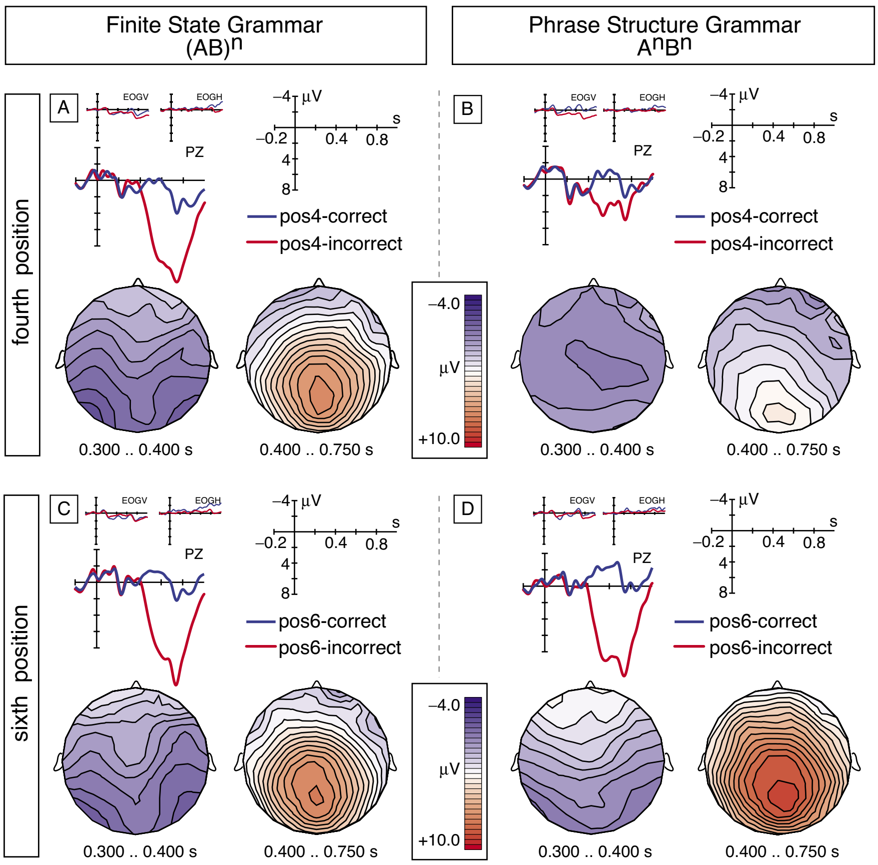

Figure 3.2 ERPs elicited by FSG (A, C) and PSG (B, D) at the fourth position (upper plot) and at the six position (lower plot) for correct sequences (blue line) and for incorrect sequences (red line) as shown by a selected electrode. Topographic maps of the differences between effects for correct and incorrect are shown for the two time windows that entered analyses. Red areas indicate positive differences between the conditions, and blue areas indicate negative differences.

3.1.3 Automatic processing of syntactic structure based on word category information: A mismatch negativity study

Hasting, A.S., Kotz, S.A. & Friederici, A.D.

Syntax processing has repeatedly been claimed to be automatic. Various ERP studies have gathered evidence that especially first-pass parsing processes are independent of attentional resources (e.g., Hahne & Friederici, 1999). These early processes of syntactic structure building are believed to operate on the basis of word category information (Friederici, 2002). This view implies that the identification of a word's syntactic category must take place very quickly and automatically.

The present study tested the assumptions listed above using a mismatch negativity paradigm. The mismatch negativity (MMN) is an ERP component indicating automatic deviance detection in the auditory modality. It has recently proven a useful tool for the investigation of automatic syntax processing as its amplitude has been shown to be modulated by the grammaticality of the deviant stimulus (Pulvermüller & Shtyrov, 2003; Shtyrov et al., 2003). In the current protocol, two pairs of syntactically correct phrases and phrases containing a word category violation served as standard and deviant stimuli in four MMN sequences. Importantly, the phrases in each pair were acoustically identical until the onset of their final syllable, which determined both the word category of the second word and the grammaticality of the phrase (i.e., *er faltet* – **er Falter* [he folds – *he butterfly]; *ein Falter* – **ein faltet* [a butterfly – *a folds]). The sequences were presented via headphones to 24 subjects who focused their attention on a silent movie while the EEG was recorded.

Based on the acoustic differences between standard and deviant phrase, each sequence produced a reliable MMN peaking at ~180 ms after the onset of the diverging syllable. The characteristics of these responses were modulated by the syntactic properties of the deviant phrase. In accordance with the findings from previous syntactic MMN studies, grammatically incorrect deviants produced larger MMN responses than grammatically correct deviants. Even prior to this grammaticality effect, both MMN amplitude and topography, were greatly affected by the word category of the deviant phrase. Starting ~100 ms after change onset, MMNs to verb deviants were much larger than MMNs to nouns. Additionally, the latter displayed a more posterior distribution. The current findings provide evidence for the view that word category information is accessed automatically as a primary step in syntactic analysis and that violations of syntactic structure are detected just as automatically on the basis of this information.

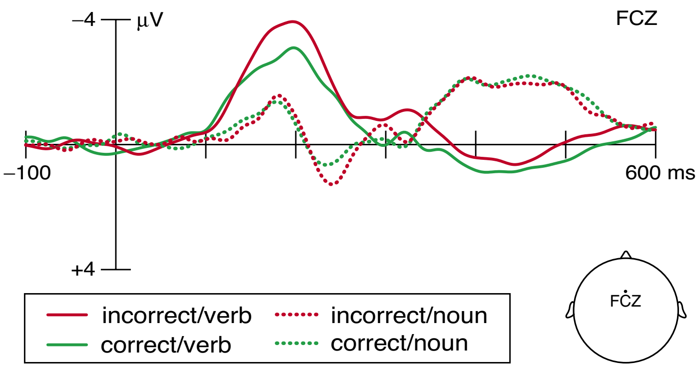

Figure 3.3 MMN difference waves (deviant – standard) at electrode FCz, where the MMN is usually largest.

Semantic and syntactic processing in Chinese sentence comprehension: Evidence from event-related potentials

3.1.4

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An ERP experiment was conducted to explore semantic and syntactic processes as well as their interplay in Chinese sentence comprehension. Participants were auditorily presented with Chinese *ba* sentences, which were either correct, semantically incorrect, syntactically incorrect or both semantically and syntactically incorrect. The syntactic violation, which was created by eliminating the object-noun phrase from a preposition-object phrase structure, elicited an early starting anterior negativity merging into a sustained negativity over anterior sites and a temporally limited centro-parietal negativity. The semantic violation elicited an early starting N400 effect. The combined violation, in which the syntactic phrase structure violation and the semantic violation were crossed, elicited an early starting sustained anterior negativity similar to the pure syntactic effect, and a centro-parietal negativity which was more negative than those of the syntactic condition and the semantic condition. No P600 was obtained neither for the syntactic, nor for the combined condition. The results suggest that the syntactic processes (at about 50 ms) appear earlier than the semantic processes (at about 150 ms). They are independent from each other in the early time window (150–250 ms) but interact in a later processing phase (250–400 ms) during Chinese *ba* sentence comprehension. The broadly distributed negativity, which occurred during the N400 latency range observed in the three violation conditions, is thought to reflect thematic integration processes in the sentence-final position.

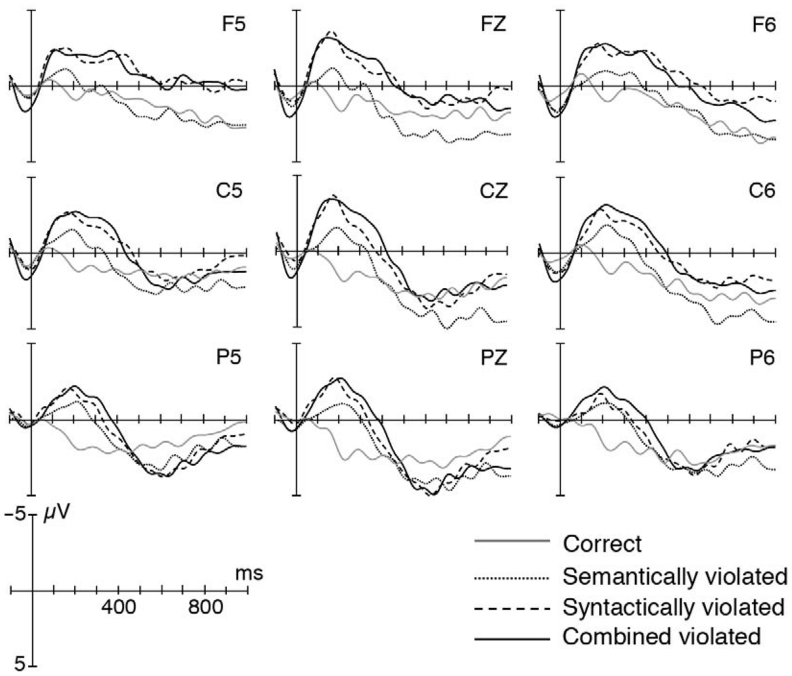

Figure 3.4 Grand average ERPs for the target verb in the semantic violation condition, the syntactic condition and the combined condition as opposed to the correct condition. Participants judged the *ba* sentences for overall correctness. The origin of the x-axis corresponds to the onset of the target verb and the negative voltage is plotted upwards.

3.1.5 Cross-linguistic investigation of semantic and syntactic processing in spoken sentences

Rüschemeyer, S.-A.[1], Fiebach, C.J.[1,2], Kempe, V.[3] & Friederici, A.D.[1]

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[3] *Department of Psychology, University of Sterling, Scotland, UK*

We used fMRI to investigate the neural correlates of syntactic and semantic processing in spoken sentences by native speakers of two typologically different languages. To this end, German and Russian participants listened to sentences in their respective native language while lying in the fMRI scanner environment. Sentences were either [1] well-formed and sensible, or they contained [2] a syntactic or [3] a semantic violation (see examples below).

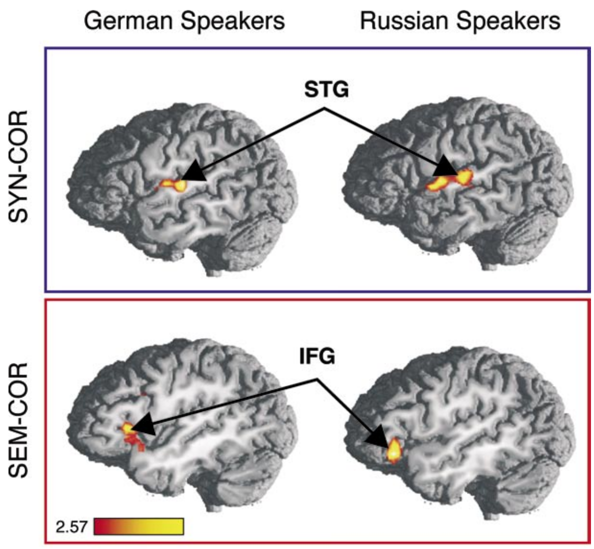

Figure 3.5

[1] *Das Brot wurde gegessen*. [The bread was eaten.]
[2] *Das Eis wurde im gegessen*. [The ice-cream was in-the eaten.]
[3] *Der Vulkan wurde gegessen*. [The volcano was eaten.]

The BOLD response of participants to each violation condition was compared to that elicited by correct sentences. The results show that the underlying neural response of participants to stimuli across different native languages is quite similar. Both groups of participants showed increased involvement of left superior temporal cortex (STG) in response to syntactic phrase structure anomalies. Both groups showed an increased involvement of left inferior frontal gyrus (IFG) in response to semantic anomalies. This study provides evidence for the idea that native speakers of typologically different languages rely on the same neural substrates to processes comparable linguistic information in their respective native language.

3.1.6 When word category information encounters morphosyntax: An ERP study

Rossi, S., Gugler, M.F., Hahne, A. & Friederici, A.D.

The present event-related brain potential (ERP) study aimed to investigate the relationship between two different syntactic information types, namely word category and morphosyntax, by using a combination paradigm. Previous studies (Hahne & Friederici, 2002; Friederici, et al., 2004) investigating word category violations combined with semantic violations found that combined violations showed the same ERP pattern as the pure word category violation. In the present study, the ERP pattern of acoustically presented

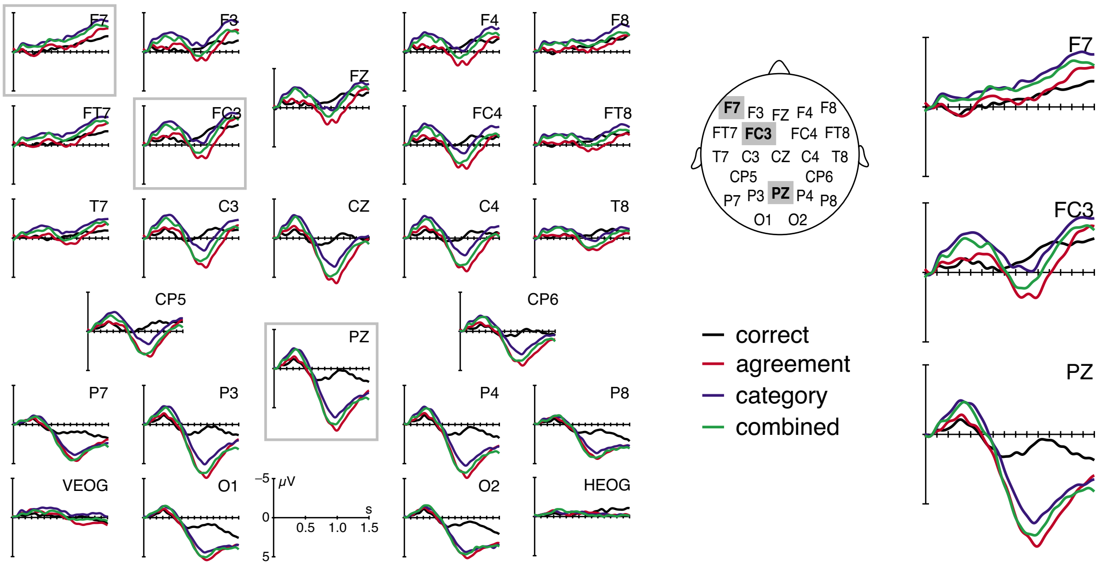

Figure 3.6 Grand average ERPs from 30 participants from verb onset up to 1500 ms for the four experimental conditions. Negative voltage is plotted upwards. Selected electrodes (F7, FC3, PZ) are enlarged on the right.

German sentences containing two syntactic anomalies (word category and subject-verb agreement) was compared to the ERP response to sentences containing a single violation. The ERPs for the agreement violation revealed a left anterior negativity (LAN) indicating the detection of the morphosyntactic error, followed by a P600 reflecting processes of reanalysis. The ERPs for both, the category and the combined violation, showed an early negativity reflecting processes of phrase structure building, followed by a P600 indicating syntactic reanalysis. Additionally, a broadly distributed negativity following the early negativity and preceding the P600 was observed. This ERP component is suggested to reflect reference specification processes arising from the specific sentence structure used in the present study (prepositional phrase that was part of the subject noun phrase). The ERP pattern for the combined violation suggests, on the one hand, no additivity or interaction between the two syntactic anomalies in the early time windows (early negativity, reference-related negativity, and LAN) indicating independent and autonomous syntax-first processes. On the other hand, the results further show that interactive mechanisms can take place at later processing stages (P600).
In sum, the present study provides evidence that word category information has a primacy not only over lexical-semantic processing, but also over other syntactic information types, such as morphosyntax.

3.1.7 The resolution of case conflicts from a neurophysiological perspective

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Especially in languages with overt morphological case marking and word order freedom (e.g., German, Russian, Polish, Finnish etc.), case is an important indicator as to how sentential arguments should be interpreted with respect to their underlying syntactic and semantic function. In two ERP experiments, we examined the resolution of language processing conflicts involving the multidimensional linguistic feature case, which determines sentence processing in both, syntactic and interpretive respects. We presented sentences such as (1) phrase-by-phrase and visually to our subjects: (1) *Welcher Kommissar* *lobte der Detektiv (…)?* [Which inspector (Nominative)commended the detective (Nominative) (…)?]. As we had shown in a previous study, ungrammatical German structures with two identically case-marked arguments (double subject constructions) lead to a biphasic N400-P600 response on the second (mismatching) argument in ERPs (Frisch & Schlesewsky, 2001). As could be also shown, the N400 effect is associated with problems of semantic-thematic integration, since it becomes unclear who is doing what to whom in (1). By contrast, we interpreted the P600 effect as reflecting the syntactic ill-formedness of a double case ungrammaticality. In the present study, we not only tested double nominative structures, but we also included structures in which both arguments were marked with dative (indirect object) case (Experiment 1) or accusative (direct object) case (Experiment 2), respectively. As the results revealed, all three types of double case ungrammaticalities elicited the expected N400-P600 pattern compared to correct sentences. However, double datives differed from double nominatives in that they induced a larger P600 component. Double accusatives, by contrast, elicited a larger N400 compared to double nominatives. We argue that the differences nicely reflect the multiple underlying properties of case in German, being spelled out slightly differently by the specific cases nominative, dative and accusative. Obviously, individual cases are specifically affected by the different types of information on which the conflict is based.

The larger P600 for double datives suggests that the structural problems induced in this condition have a greater syntactic impact on the processing system than in double nominative (and double accusative) structures. This is due to markedness differences between dative as an exceptional case in German transitive constructions on the one hand, and nominative (as well as accusative) as the default case on the other.

The larger N400 for double accusatives compared to double nominatives (and datives) suggests that the thematic integration problem is more salient in the former. This can be explained by the fact that accusative is in principal thematically dependent on a second, thematically higher argument. Nominative and dative, by contrast, can both co-occur with either a thematically higher or a thematically lower argument in a clause. In other words, both double nominatives and datives allow for some kind of "interpretive resort" in a construction with two identically case marked arguments, but not accusatives.

3.1.8 Processing of case information in Japanese: A cross-linguistic characterization

Mueller, J.L. & Friederici, A.D.

Previous ERP research has shown that violations of case information can lead to an N400-P600 pattern with the N400 reflecting processes of thematic hierarchizing and the P600 reflecting syntactic processes (Frisch & Schleswsky, 2001; 2005). Furthermore, Frisch and Schlesewsky (2005) have shown that different cases in German can modify the N400-P600 complex distinctively. Double accusatives, for example, led to a larger N400 than double nominatives in German, which has been interpreted as being related to specific linguistic properties of those cases.

The present study tested if double nominative and double accusative violations would elicit similar patterns in Japanese, which, like German, allows a relatively free word order. There are differences between Japanese and German, however, with respect to the occurrence of multiple case markings within a clause. In Japanese, double nominatives can legally occur within a simplex clause, while double accusatives are prohibited as is described in the well-known "double-*o* constraint" (Harada, 1973). Thus, it was expected that double accusatives would elicit a stronger violation effect than double nominatives at the syntactic level in Japanese.

The results of the present ERP experiment are similar to the findings in German as double case violations elicited a general N400-P600 pattern. However, in Japanese double accusatives led to an enhanced P600 effect compared to double nominatives, but not to a larger N400 as has been reported for German. This cross-linguistic difference may be a reflection of the "double-*o* constraint" existing in Japanese which renders double accusative constructions more obviously ungrammatical than double nominative constructions. While a double nominative can be repaired, in principle, by the choice of a different verb

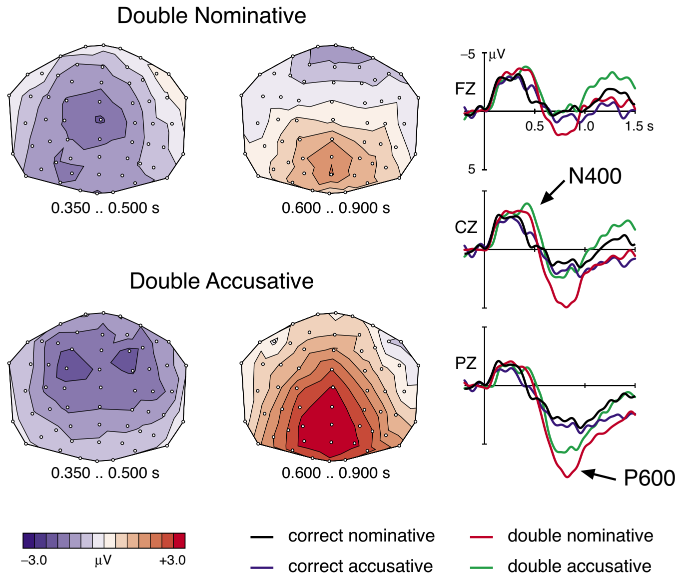

Figure 3.7

type, double accusatives cannot. Thus, language-specific constraints regarding the use of case information are possibly related to the different modulations of ERP effects across German and Japanese.

3.1.9 Generalization of language rules: The influence of lexical knowledge on syntactic and thematic processing mechanisms

Mueller, J.L. & Friederici, A.D.

In previous studies, we showed that, after less than ten hours of training, initially native German learners of a miniature version of Japanese (Mini-Nihongo) developed ERP patterns in response to word category and case violations, which were remarkably similar to those observed for Japanese native speakers (Mueller et al., 2005).

The aim of the present study was to test which of the acquired language processing mechanisms could be applied when participants were presented the same violation conditions with new items. In the experiment, trained German participants listened to sentences of Mini-Nihongo which were either correct or contained a case violation (marked on the noun) or a word category violation (indicated by the verb). Half of the sentences the participants heard were familiar and the other half contained either a new noun or a new verb. In both cases, grammaticality judgments could be given based on (morpho)syntactic cues in the sentences.

On the behavioral level, learners had difficulties in distinguishing correct and incorrect sentences if new words were present, although the performance was above chance level. ERPs in the case violation condition showed an N400-P600 pattern in familiar-word sentences. The N400 probably reflects difficulties in the thematic ordering of the arguments, while the P600 indicates controlled syntactic processes of repair (cf. Frisch & Schlesewsky, 2001). In unfamiliar-word sentences, only the P600 was observed. Thus, the lexical difficulties affected thematic processes, while controlled syntactic repair processes were unimpaired. Word category violations elicited an early negativity and a P600 in familiar-word sentences. The early negativity was related to the unexpected prosody of incorrect sentences and the P600 to processes of syntactic repair (cf. Mueller et al., 2005). In sentences with unfamiliar verbs, both the early negativity and the P600, were observed. The P600, however, was largely reduced.

In sum, the results suggest that controlled syntactic processes as reflected in the P600 can in principle be generalized to lexically new material by learners of a miniature language. This does not seem to be the case for the N400 related to thematic processing. The lexical difficulties induced by the unfamiliar lexical item may block or slow down the thematic processes reflected in this component.

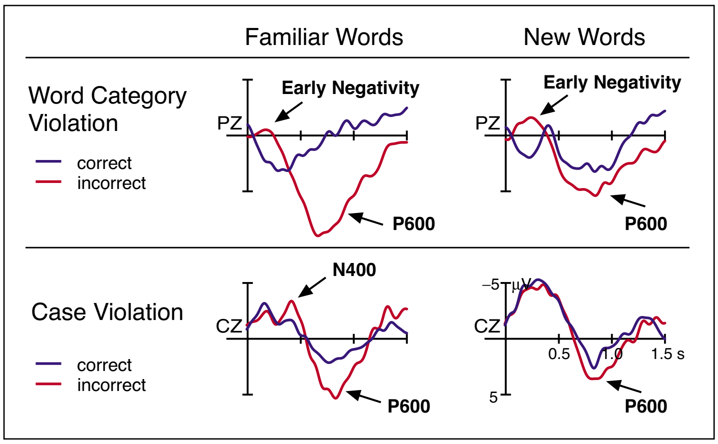

Figure 3.8

3.1.10 Neural correlates of verb-argument structure and semantic processing: An fMRI study

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[2] *Day Clinic of Cognitive Neurology, University of Leipzig, Germany*
[3] *Institute of Linguistics, University of Potsdam, Germany*

In the present study, we set out to elucidate the cognitive processes underlying two different linguistic components of verb-argument structure processing, that is, semantic and syntactic processing aspects. Empirically, the claim that there are actually two such components, has received considerable support from ERP studies: Frisch and Friederici (2000), Frisch et al. (2004), and Friederici and Meyer (2004) all report a biphasic N400-P600 pattern for verb-argument structure violations, the N400 commonly being associated with semantic integration difficulty, and the P600 generally being interpreted as a marker of syntactic reanalysis. Our study aimed at extending the knowledge on temporal properties of semantic and syntactic aspects of verb-argument structure processing by adding information about the spatial realization of such components.

Fifteen participants (8 female) were tested in an auditory grammaticality judgment task. The sentences presented during each session were either correct or belonged to one of three violation conditions: syntactically incorrect sentences with a mandatory past participle replaced by an infinitive, semantically incorrect sentences containing an object NP which did not fit the selectional restrictions imposed by the verb, and sentences in which verb-argument-structure was incorrect containing both an intransitive verb and a direct object. Sentences were equally distributed across conditions and presented in pseudo-randomized order. Functional images (18 slices, 3*3 mm in-plane, thickness = 3 mm, gap = 2 mm) were acquired using a 3 T Bruker system.

With regard to the processing of verb-argument structure and morphosyntactic violations, our initial expectations concerning the neural substrates involved were partly confirmed: For morphosyntactic

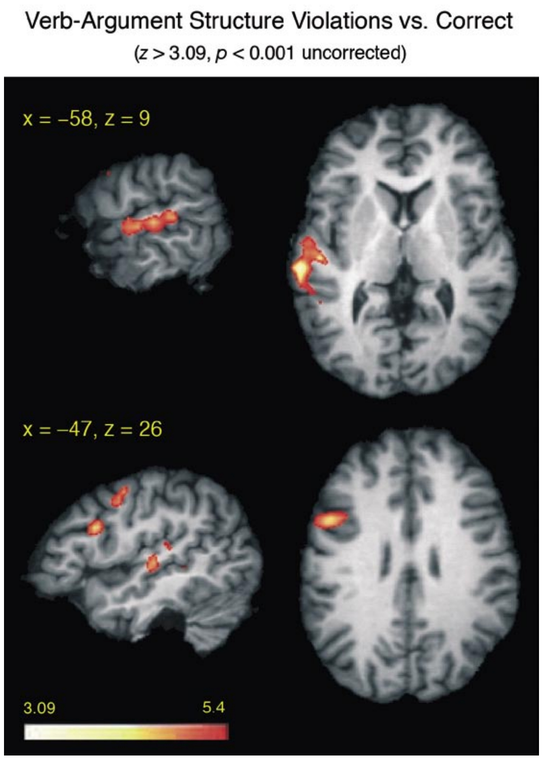

Figure 3.9

as well as for verb-argument structure violations, large parts of the left superior temporal gyrus were active. The activation pattern was not identical for both conditions: For morphosyntactic violations, two distinct regions in the bilateral superior temporal gyrus showed an increase in activation (BA 13, 22, 41, 42). For verb-argument structure violations, only one continuous (and quite extensive) area in the left superior temporal gyrus (BA 42) was active. Concerning verb-argument structure and selectional restriction violations, we found an overlapping area of activation in the left inferior frontal gyrus. This is in accordance with our hypothesis. However, this particular subregion of the IFG (BA 9) is not commonly associated with semantic processing.

In conclusion, verb-argument structure processing seems to be mainly syntactic in nature recruiting large parts of a left superior temporal network in addition to inferior frontal regions commonly implicated in non-linguistic processes such as response inhibition and working memory operations.

3.1.11 Late interaction of prosody and syntax during speech comprehension

Eckstein, K. & Friederici, A.D.

A multitude of behavioral research supported the assumption of an interaction between prosody and syntax in sentence processing. However, the exact time course of this interaction remains still to be depicted. To gain further insight into this question, the following ERP study was conducted.
We used eight experimental conditions, in which we contrasted correct conditions with sentences containing mere prosodic, mere syntactic, or combined prosodic-syntactic violations at two different positions of German sentences (penultimate vs. final word).
First, a word in penultimate position, which was prosodically marked for sentence end, gave rise to an N400 that corresponded in time to the unexpected sentence final word. This effect depended on the sentences' grammatical correctness as it was present in syntactically correct sentences only. Second, unfulfilled prosodic expectations raised by a sentence final word, which was marked for sentence continuation, resulted in a right anterior negativity (RAN) (see Figure 3.10). The RAN peaked at around 150 ms after the unexpected sentence offset and was observed for both the mere prosodic incongruity condition and the combined prosodic-syntactic violation. As the RAN showed up independently of the grammatical correctness of the sentences, it is therefore considered as a pure prosodic effect. We suggest that the RAN is a reflection of a mismatch between expectancies built up on basis of prior prosodic information and the prosodic properties of the actual input.

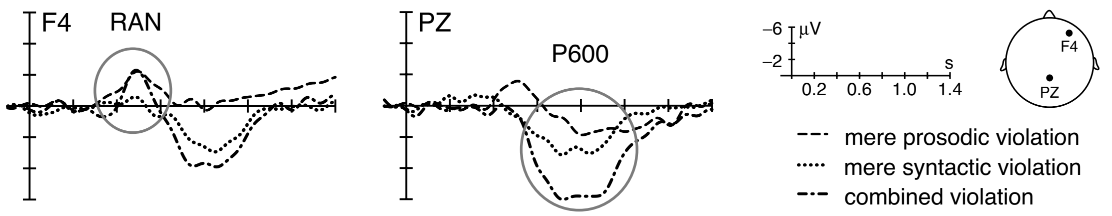

Figure 3.10 ERP difference waves obtained at the critical word in sentence final position. Each difference wave was calculated by subtracting the ERP for the correct condition from the ERPs for the respective violation condition.

In a later time window, a P600 was present after a mere syntactic violation, which is in line with the general notion of the P600 as a marker of syntactic repair and integration. Interestingly, a P600 was also observed following the RAN in a mere prosodic incongruity. This finding suggests an extension of the interpretation of the P600 to apply also to prosodic processing. Finally, for the combined violation, an enhanced P600 effect was observed, which was found to be greater than the sum of mere prosodic P600 and mere syntactic P600. This result shows that an interaction between prosody and syntax takes place during a late integrative stage of speech processing.

3.1.12 Syntactic predictions on the basis of contrastive accent placement: An ERP study

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It has been shown in a series of experiments that prosodic phrasing influences syntactic processing in hearing (e.g., Marslen-Wilson et al., 1992; Warren et al., 1995, Steinhauer et al., 1999) and reading (e.g., Fodor, 1998; 2002; Steinhauer & Friederici, 2001). Fewer studies looked at the interaction of syntactic processes and accent placement (Grabe & Warren, 1995; Schafer et al., 1996; 2000; Bader, 1998).
We used elliptic constructions to find out whether the position of a contrastive pitch accent in the first part of the sentence leads to syntactic predictions about the ellipsis site (see examples in [1]). In the correct sentences, the remnant (*der/den Onkel*) constitutes a correction or replacement of a constituent that bears a contrastive pitch accent in the related clause (focus structure is indicated by brackets and pitch accent by capitals). In the related sentences of the incorrect conditions [1b] and [2b], the constituent that bears a contrastive pitch accent does not contrast with the remnant.

Subject contrast, correct (SK) / incorrect (SI)

[1a] *Am Freitag hat [der VAter]$_{CF}$ den Neffen beleidigt, <u>und nicht [der/den ONkel]</u>$_F$*
[On Friday has the father$_{nom}$ the nephew$_{acc}$ insulted, and not the uncle$_{nom/acc}$]

Object contrast, correct (OK) / incorrect (OI)

[1b] *Am Freitag hat der Vater [den NEffen]$_{CF}$ beleidigt, <u>und nicht [den/der ONkel]</u>$_F$*
[On Friday has the father$_{nom}$ the nephew$_{acc}$ insulted, and not the uncle$_{acc/nom}$]
'On Friday, the father insulted the uncle, and not the nephew.'

Using the method of event-related brain potentials (ERPs), we tried to answer the following question: *Does the position of the pitch accent in the related sentence lead to different expectations with regard to the ellipsis site?*

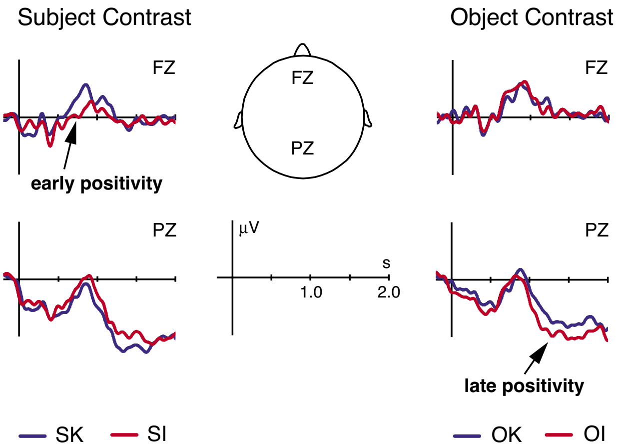

Figure 3.11 Grand average ERPs for the ellipses (underlined part of the sentences in [1]), subject and object contrast, correct (blue line) and incorrect (red line).

Our results showed clear differences with regard to the position of the contrastive pitch accents. A contrastive accent on the subject in the related clause showed an early fronto-central positivity on the last DP, whereas a contrastive accent on the object resulted in a late posterior positivity (see Figure 3.11).

Our explanation of this difference refers to the number of possible structural predictions depending on the accent positions: If the subject bears the contrastive accent, there exists only one possible structure for the correction by the ellipsis. The ellipsis site has to be a subject remnant. If the object bears the contrastive accent, there exists more than one possible syntactic structure for a continuation. Not only the contrastive object remnant is a possible continuation, but the correction could also contrast other parts of the related clause, for example the whole sentence. The reason for these multiple possibilities is the ambiguity of an focus accent on the object.
To sum up, we found clearly different ERP effects for the processing of elliptic constructions dependent on the position of contrastive accents in the related clause.

3.1.13 Pragmatics and prosody in conflict: The Closure Positive Shift (CPS) in information structural processing

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Information exchanges constantly require interlocutors to update their state of knowledge. In particular, speakers have to evaluate which pieces of knowledge are commonly known to their dialog partner, and which are not. As a consequence, speakers tend to produce verbal information in a way that helps listeners to extract novel or corrective foci of knowledge. In German, for example, the prosodic realization and the contextual embedding of an utterance support this communication goal.
Two event-related potential (ERP) studies were conducted exploring the relevance of context and prosody for information retrieval in spoken dialogue interaction.
In the first experiment, contextually established (pragmatic) novelty and correction foci were presented to volunteers with either a matching or non-matching prosody. The ERP data show that a Closure Positive Shift (CPS; Steinhauer et al., 1999) is evoked depending on the context of an utterance but irrespective of the prosodic realization of a focus (see Figure 3.12). Furthermore, the prosodic mismatch effect is reflected by a sustained ERP with negative amplitude preceding the CPS (not evident in Figure 3.12).

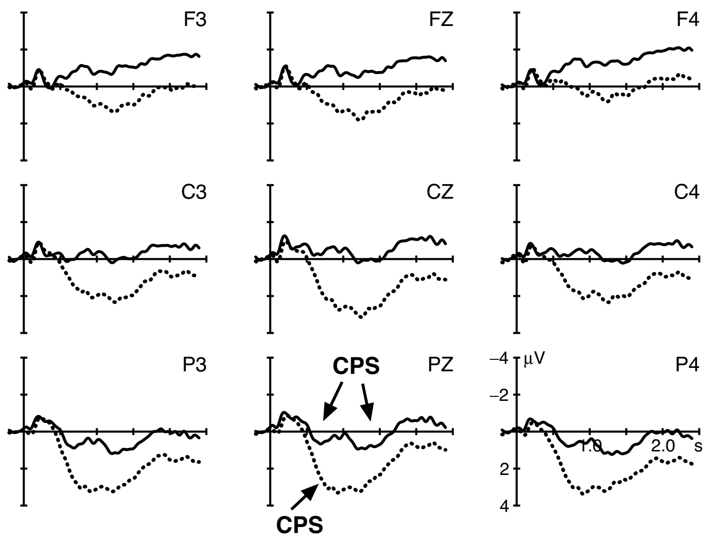

Figure 3.12 ERPs to identical utterance prosodies solely diverging in the context preceding them. The solid line illustrates the ERPs when the prosody is congruent with the preceding context (pragmatic and prosodic novelty focus). The dotted line shows the ERPs when context and prosody are incongruent (pragmatic correction focus + prosody of novelty).

In a second experiment, the dependence of the CPS on contextual requirements was explored in further detail. Volunteers were presented with dialogues where contexts either established a pragmatic correction focus or no focus at all (all-given information). Again, these information types were presented with a matching or non-matching prosody. The ERP data indicate that the context implying a correction focus again evokes a CPS in the positions of pragmatic foci independent of their prosodic realization (see Figure 3.13). On the other hand, the context which indicates no-focus induces a CPS response to the major prosodic boundary preceding the sentence position without knowledge in focus. Moreover, an ERP with negative amplitude is elicited prior to the CPS response when a focus position is presented with the prosody of no-focus (all-given information).

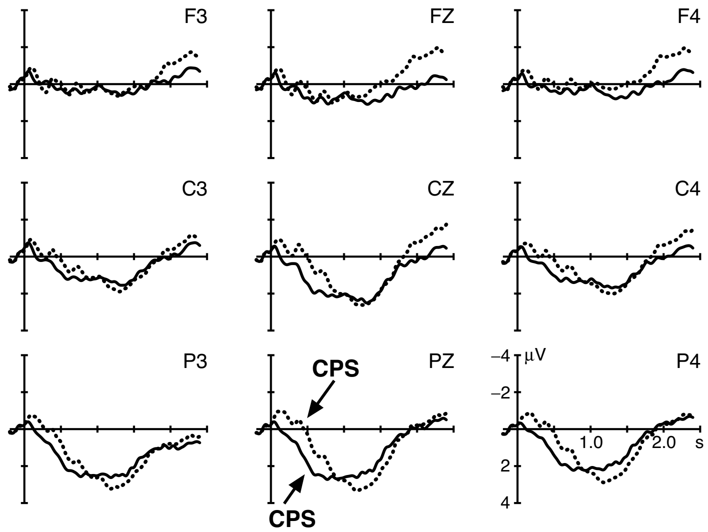

Figure 3.13 ERPs to identical utterance realizations solely diverging in the context preceding them. The solid line illustrates the ERPs when the prosody is congruent with the preceding context (pragmatically and prosodically no-focus). The dotted line shows the ERPs when context and prosody are incongruent (pragmatic correction focus + prosody of no-focus).

In summary, when utterances beyond sentence level (i.e., dialogues) comprise contextually derivable knowledge foci for listeners, these foci are used to structure the auditory input as reflected by the CPS pattern. However, when utterances do not convey any focused information for listeners, major prosodic boundaries again serve to structure spoken utterances as in single sentence processing.

3.1.14 Morphosyntax, prosody, and linking elements: The auditory processing of German nominal compounds

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The morphosyntactic decomposition of German compound words and a proposed function of linking elements were examined during auditory processing using event-related brain potentials (ERPs). In Experiment 1, the syntactic gender agreement was manipulated between a determiner and the initial compound constituent (the *nonhead* constituent), and between a determiner and the last constituent (*head*). Although only the head is (morpho)syntactically relevant in German, both constituents elicited a left-anterior negativity if gender incongruent. This strongly suggests that compounds are morphosyntactically decomposed. Experiment 2 tested the function of those linking elements which are homophonous to plural morphemes. Previously, it has been suggested that these indicate number of nonhead constituents. The number agreement was manipulated for both constituents analogous to Experiment 1. Number incongruent heads, but not nonhead constituents, elicited an N400 and a subsequent broad negativity, suggesting that linking elements are not processed as plural morphemes. Experiment 3 showed that prosodic cues (duration and fundamental frequency) are employed to differentiate between compounds and single nouns and, thereby, between linking elements and plural morphemes. Number incongruent words elicited a broad negativity if they were produced with a single noun prosody; the same words elicited no ERP effect if produced with a compound prosody. A dual-route model can account for the influence of prosody on morphosyntactic processing.

The neural basis of the prosody-syntax interplay: The role of the corpus callosum

3.1.15

Friederici, A.D.[1], von Cramon, D.Y.[1,2] & Kotz, S.A.[1,2]

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For the processing of spoken language, the left and the right hemisphere have to work in concert to process segmental and suprasegmental information on-line. This suggests a crucial involvement of the corpus callosum (CC) during speech processing. The literature provides some evidence for that. In a case study, a patient with a lesion in the anterior portion of the CC suffers from impairment in the processing of affective and linguistic prosody (Klouda et al., 1988). Recent imaging studies as well as lesion studies, however, indicate that the posterior quarter of the CC may be relevant for the interhemispheric transfer of auditory information (Rumsey et al., 1996; Pollmann et al., 2002), and for the development of verbal abilities (Nosarti et al., 2004).
Here, we investigated the role of the corpus callosum (CC) in the interhemispheric interaction of prosodic and syntactic information in patients with lesions of the posterior CC, of the anterior part of the CC, and normal controls. The crucial sentences material consisted of sentences in which the target verb either correctly matched the prior prosodic and syntactic structure [1] or, due to a prosodic manipulation, did not [2].

[1] Prosodically correct, intransitive verb
[Peter verspricht Anna zu arbeiten]$_{IPh1}$ *[und das Büro zu putzen.]*$_{IPh2}$
[Peter promises Anna to work] [and to clean the office.]

[2] Prosodically incorrect, intransitive verb
* *[Peter verspricht]*$_{IPh1}$ *[Anna zu arbeiten]*$_{IPh2}$ *[und das Büro zu putzen]*$_{IPh3}$.
[Peter promises] [to work Anna] [and to clean the office.]

Using event-related brain potential (ERP) measures, it was shown that patients with lesions in the anterior part of the CC, similar to controls, demonstrated an N400 effect for the mismatching condition. This effect is taken to indicate a prosody-induced mismatch between a given verb and its expected syntactic verb-argument structure. In contrast, patients with lesions in the posterior part of the CC did not show the prosody-induced N400 effect, but a prosody-independent semantic N400 effect. The present data indicate that the posterior part of the CC is crucial for the interplay of suprasegmental prosodic information and syntactic information.

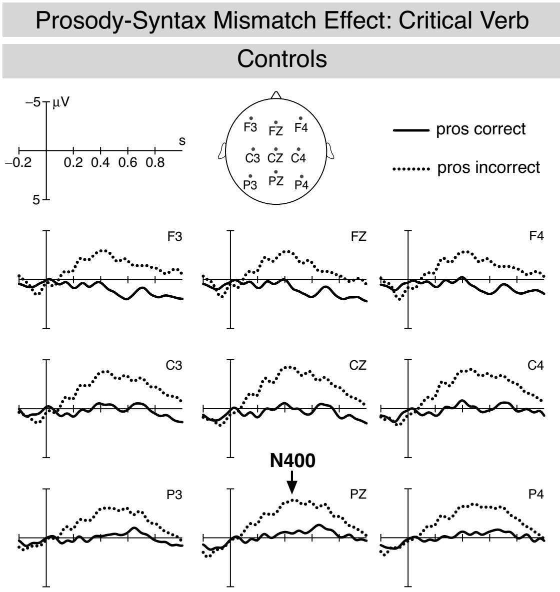

Figure 3.14 Verb-specific ERPs for normal age-matched controls. Solid line indicates prosodically correct verb, dotted line the prosodically-guided incorrect verb.

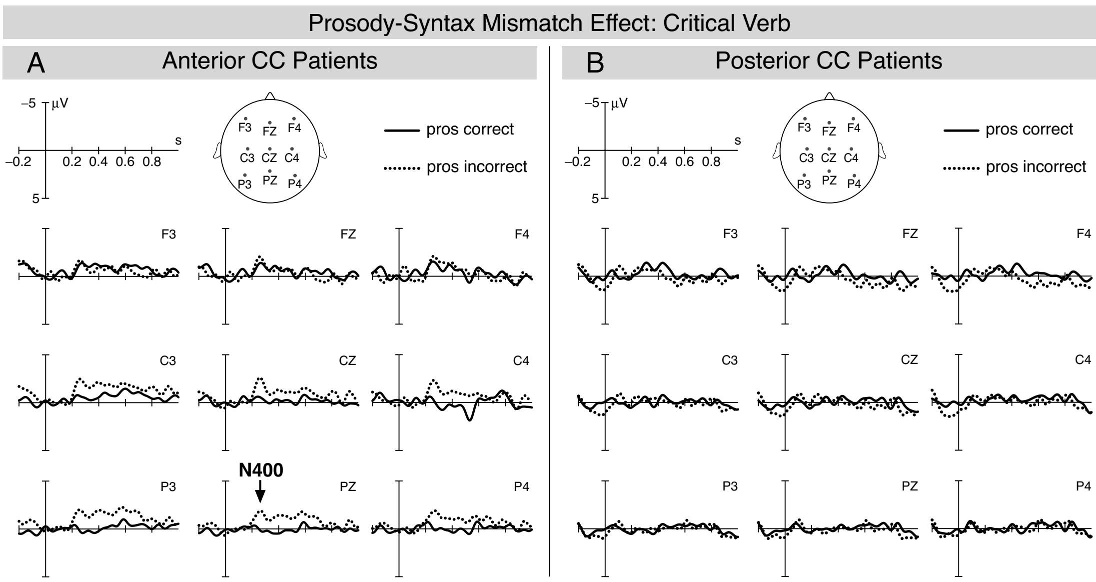

Figure 3.15 Verb-specific ERPs for CC patients. Figure 3.15A displays the anterior CC group, Figure 3.15B the posterior CC group. Solid line indicates prosodically correct verb, dotted line the prosodically-guided incorrect verb.

The research program focused on first and on second language learning.

First language learning has been investigated covering the first months and years of life (see also Annual Report 2003). On the basis of these experiments, we were able to describe the main developmental stages and the neurophysiological markers of them in an overview published in Trends in Cognitive Sciences (Friederici, 2005; see Figure 3.16). The infants' acquisition of word meaning was documented in a series of experiments describing the mechanisms underlying the mapping from phonological-lexical form to meaning at the word level (3.2.1). The development of processing semantic relations between nouns and verbs in a sentence and the related N400 effects is described in 3.2.2. Processing syntactic information at the sentences level was investigated by using sentences containing phrase structure violations. For active sentences, the ERP revealed an ELAN-P600 pattern similar to adults by the age of 2;8 years (3.2.3). When passive sentences had to be processed, adult-like patterns for syntactic processes are only observed at the age of 7 years suggesting that processing demands required by the syntactic structure (passive sentences) interacts with the detection of phrase structure violations during development (3.2.4).

Studies prosodic processing revealed an early sensitivity to this information type. It was shown that 7-month-old infants discriminate emotional prosody (3.2.5) and that 9-month-olds demonstrate an ERP pattern to the processing of intonational phrase boundaries which is similar to adults.

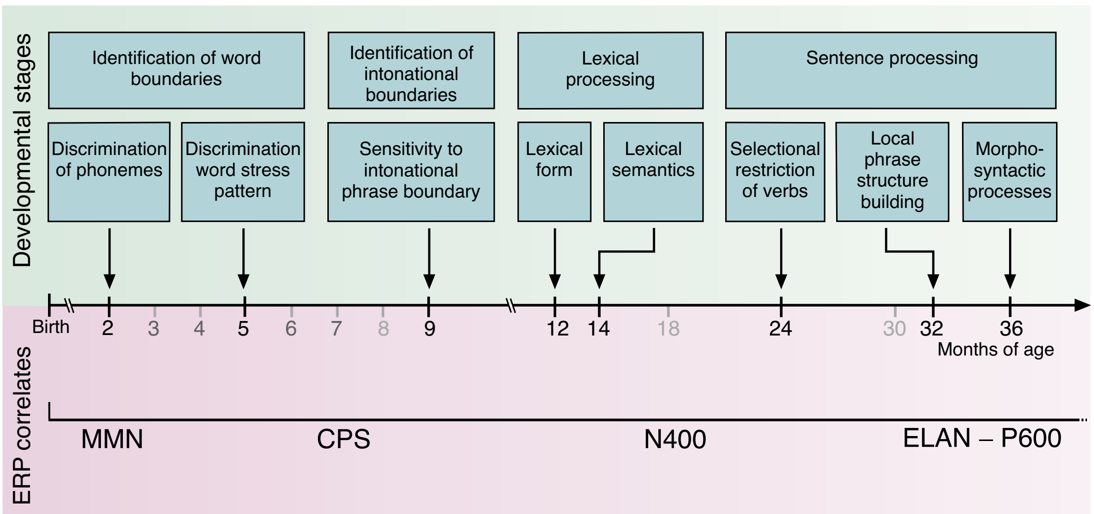

Figure 3.16

Second language processing studies evaluated the neural network supporting semantic and syntactic processes during auditory (3.2.6) and reading (3.2.7) comprehension. Generally, we observed a very similar network for natives and non-natives though with a generally higher degree of activation in second language processing. When using two languages, we can observe interference effects of the first language on the second are observable during an initial stage after language switch. The system's ability to adjust to the target language, however, was found to be quite remarkable (3.2.8).

3.2.1 Phonotactic knowledge, lexical priming and semantic integration in one-year-old children

Friedrich, M. & Friederici, A.D.

Using a cross-modal picture-word ERP paradigm, we investigated phonological-lexical and semantic processing mechanisms as well as phonotactic knowledge and its impact on semantic processing in one-year-olds. While looking at pictures of known objects (e.g., a sheep), children listened to congruous words that correctly named the pictures at the basic level (*sheep*), to incongruous words that named an unrelated basic level concept (*ball*), to legal pseudo-words (*fless*), or to phonotactically illegal non-words (*rlink*). In 19-month-olds, both incongruous words and pseudo-words, elicited an N400. The group of 14-month-olds also displayed an N400 in response to incongruous words. In contrast, 12-month-olds did not show an N400, neither on incongruous nor on pseudo-words. In addition, all groups displayed a phonological-lexical priming effect for congruous words, and a phonotactic familiarity effect for legal pseudo-words. The results imply that lexical priming and phonotactic familiarity affects the acoustic-phonological processing of words or word-like stimuli even in 12-month-olds. N400 mechanisms of semantic integration mature around 14 months of age. These mechanisms develop in response to words and legal pseudo-words, but not to phonotactically illegal non-words. This indicates that one-and-a-half-year-old children treat pseudo-, but not non-words, as potential word candidates. Post-hoc grouping of 19-month-olds according to their production performance in a language test performed at 2;6 years suggests that the emergence of an N400 early in development is associated with the children's later language skills.

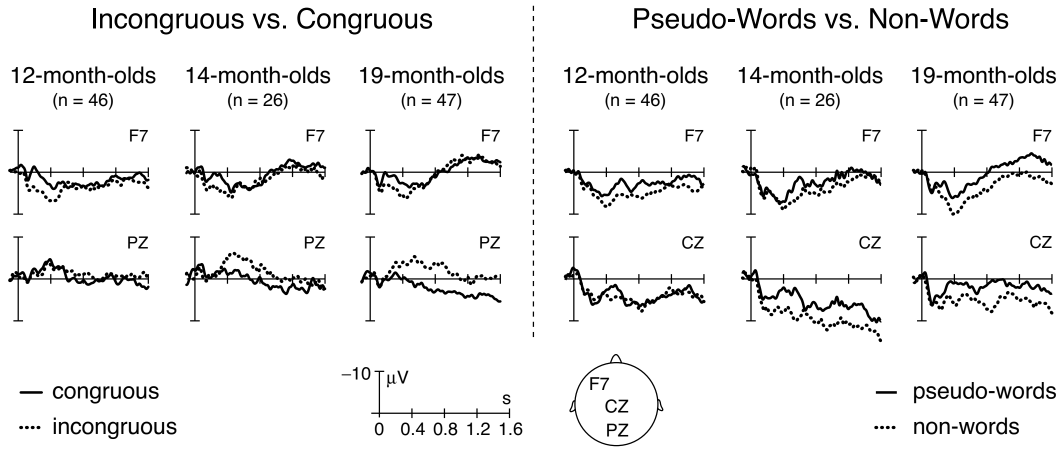

Figure 3.17

3.2.2 Semantic sentence processing in one- and two-year-old children

Friedrich, M. & Friederici, A.D.

As the N400 is in principle present during early developmental stages (Friedrich & Friederici, 2004; 2005a; 2005b), it can be used as a methodological tool for studying children's early cognitive and language development. Here, we investigated the children's early ability to integrate the meaning of words in sentential contexts. Children at the age of either 19 or 24 months listened passively to semantically appropriate sentences (e.g., *The child rolls the ball*) and to sentences in which the object noun violates

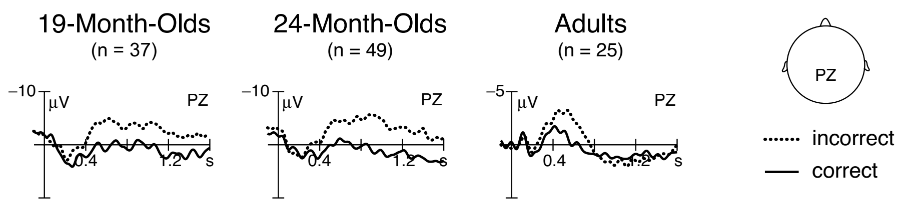

Figure 3.18

the selection restriction of the verb (e.g., *The cat drinks the ball*). The ERPs of both age groups revealed an N400 on inappropriate object nouns, which indicates that even 19-month-old children are able to semantically integrate words during the processing of simple subject-verb-object sentences. The result, moreover, implies that selection restrictions are part of the children's first verb representations.

3.2.3 Neural correlates of syntactic processing in two-year-olds

Oberecker, R., Friedrich, M. & Friederici, A.D.

Numerous event-related brain potential (ERP) studies on sentence processing in adults have reported a biphasic ERP pattern on phrase structure violations. This pattern consisted of an early left anterior negativity (ELAN) and a P600 on phrase structure violations (e.g., Hahne et al., 2004; Hahne & Friederici, 1999). While the ELAN is assumed to be functionally related to early automatic processes of structure building, the P600 is interpreted to reflect late processes of syntactic integration.

The aim of the present study was to find out whether children beyond the age of three years process phrase structure violations similarly to adults. Therefore, we investigated children at a mean age of 2;8 years and adults. Children as well as adults listened passively to short active sentences that were either correct or contained a phrase structure violation. For the syntactically incorrect condition, the ERP pattern of adults displayed an ELAN, which was followed by a P600. The ERP pattern of children also demonstrated a biphasic ERP pattern on phrase structure violations consisting of an early left hemispheric negativity and a late positivity. The observed ERP components in children, however, started later and persisted longer than those observed in adults. The left lateralization of the early negativity suggests that this negativity can be interpreted as a child-specific counterpart of the ELAN observed in adults. The appearance of the early negativity indicates that the neural mechanisms of syntactic parsing are, in principle, installed very early during development.

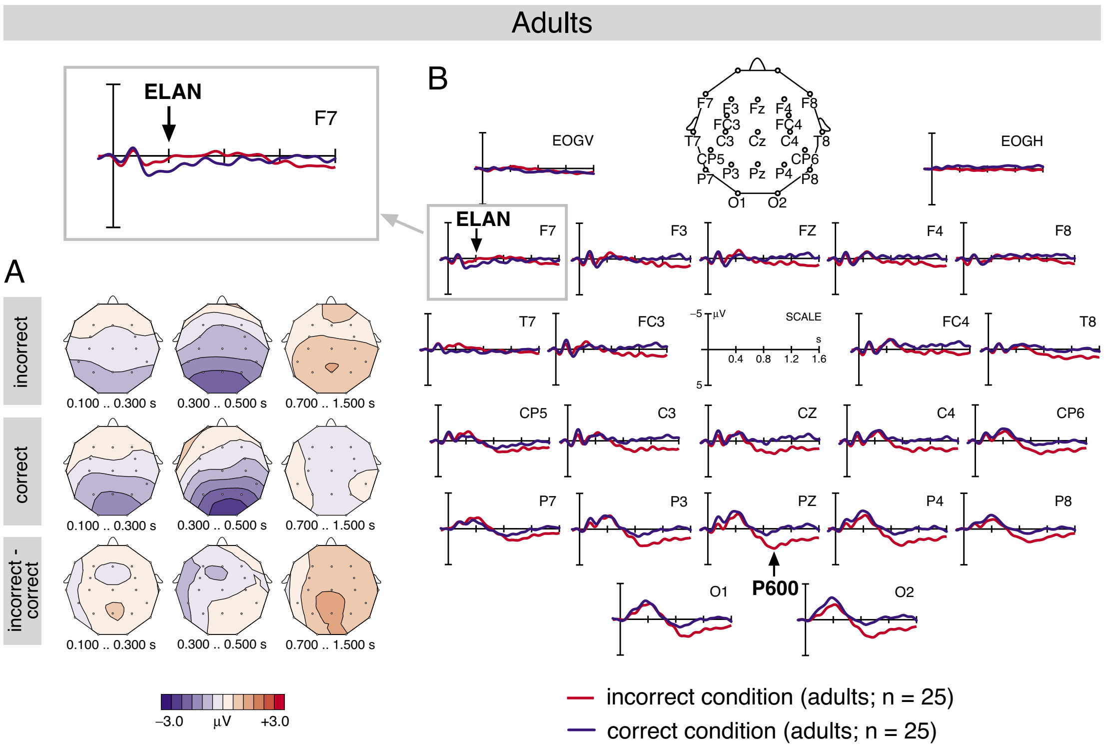

Figure 3.19 (A) Distribution of effects and difference waves for the ERPs of adults for the critical word in the syntactic violation condition versus the correct condition. (B) Grand average ERPs of adults for the critical word in the syntactic violation condition versus the correct condition. The incorrect condition (solid line) is plotted against the correct condition (dotted line). The vertical line indicates the onset of the critical word; negative voltage is plotted upwards.

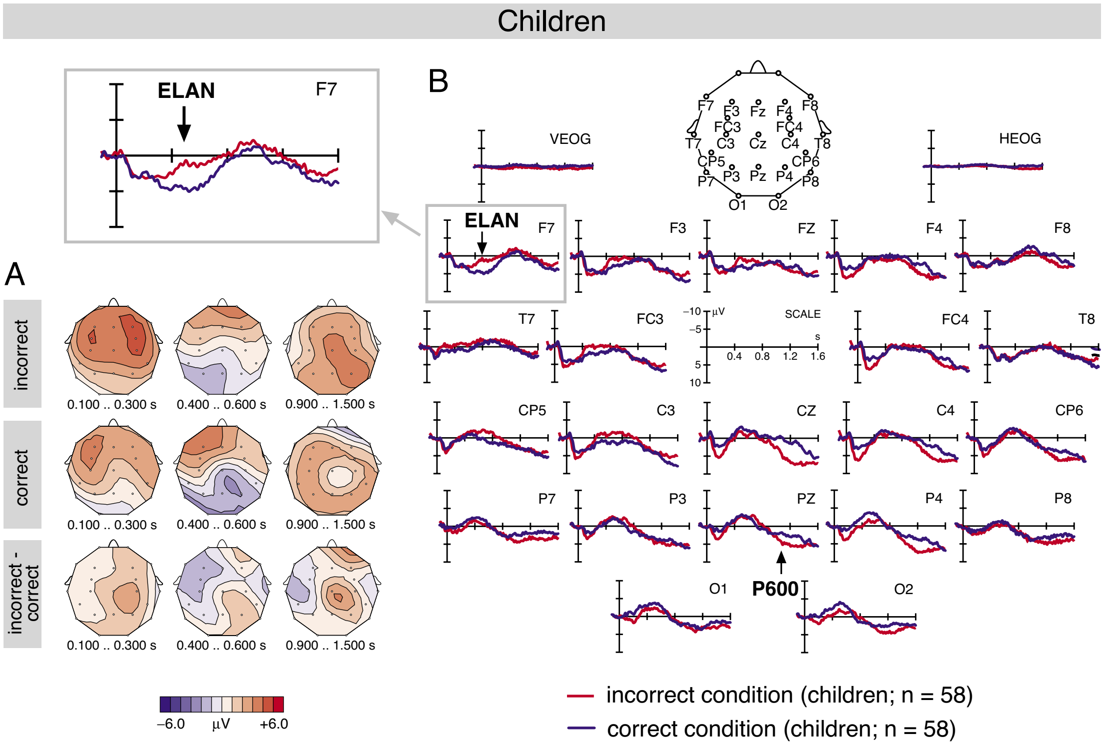

Figure 3.20 (A) Distribution of effects and difference waves for the ERPs of two-year-olds for the critical word in the syntactic violation condition versus the correct condition. (B) Grand average ERPs of two-year-olds for the critical word in the syntactic violation condition versus the correct condition. The incorrect condition (solid line) is plotted against the correct condition (dotted line). The vertical line indicates the onset of the critical word; negative voltage is plotted upwards.

3.2.4 Comprehension of passive sentences in children aged 6 to 13: An ERP study

Hahne, A., Eckstein, K. & Friederici, A.D.

We examined developmental aspects of language comprehension using ERPs in children between the ages of 6 and 13 years. Children listened to passive sentences that were either correct, semantically incorrect, or syntactically incorrect, and data in each condition were compared to those of adults. For semantic violations, adults demonstrated a negativity (N400), as did children, but the latency decreased with age.

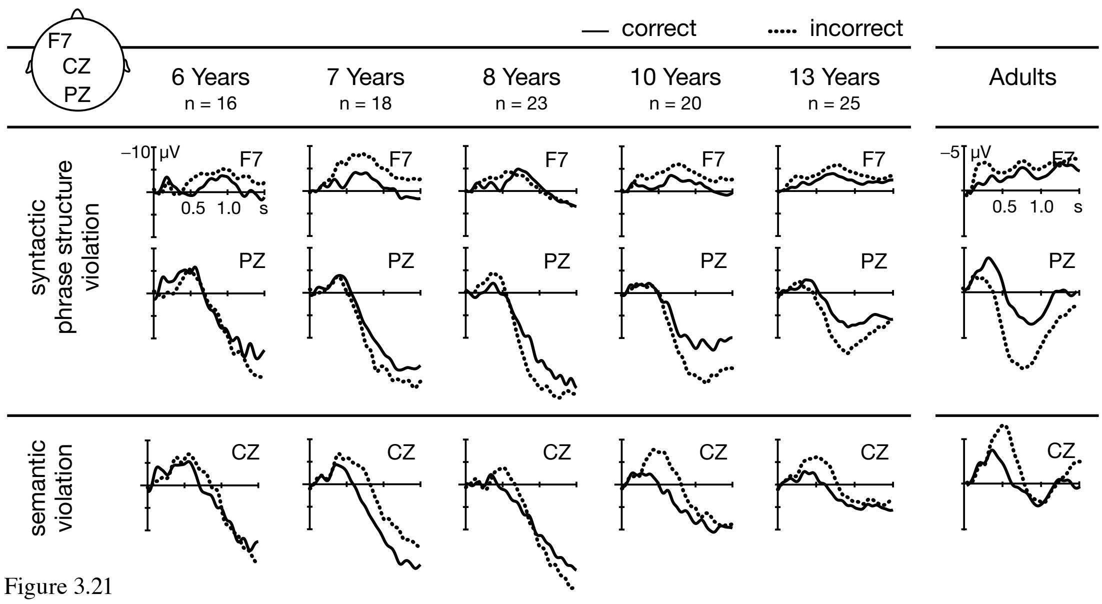

Figure 3.21

For syntactic violations, adults displayed an early left anterior negativity (ELAN) and a late centroparietal positivity (P600). A syntactic negativity as well as a late positivity were also present for children between 7–13 years, again with latency decreasing with age. Six-year-olds, in contrast, did not demonstrate an ELAN effect, but a late, reduced P600 pattern for the syntactic violation condition. In the early time window, the 6-year-olds displayed a widely distributed negativity that was larger for the correct than for the syntactically incorrect condition. These data indicate that the neurophysiological basis for semantic processes during auditory sentence comprehension does not change dramatically between early childhood and adulthood. Syntactic processes for passive sentences appear to differ between early and late childhood, at least with respect to those processes reflected in the ELAN component. These processes are not yet established at age 7, but gradually develop toward adult-like processing during late childhood.

Crossmodal integration of emotion in the infant brain

3.2.5

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The way that emotions are perceived when communicated either by the face or the voice has been extensively studied in each modality separately. In most social interactions, emotional information is communicated simultaneously by different modalities such as the face and voice. Event-related brain potentials (ERPs) have been found to be sensitive to infants' crossmodal recognition of objects, and have proven to be a valuable tool in assessing the underlying mechanisms of infants' processing of emotional information conveyed by face and by the voice. However, to date, the underlying electrophysiological processes for crossmodal integration of emotion in infancy have not been examined.
We assessed 7-month-old infants' processing of emotionally congruent and incongruent face-voice pairs using ERP measures. Infants (n = 18) watched facial expressions (happy or angry) and, after a delay of 400 ms, heard a word spoken with a prosody that was either emotionally congruent or incongruent with the face being presented.
The ERP data revealed that the amplitude of a negative component and a subsequent positive component in infants' ERPs varied as a function of crossmodal emotional congruity (Figure 3.24). An emotionally incongruent prosody elicited a larger negative component in infants' ERPs than did an emotionally congruent prosody ($F\ (1,17) = 9.59$, $p < 0.01$). Conversely, the amplitude of infants' positive component was larger to emotionally congruent than to incongruent prosody ($F\ (1,17) = 14.63$, $p < 0.01$).
Previous work has shown that an attenuation of the negative component and an enhancement of the later positive component in infants' ERPs reflect the recognition of an item. Thus, emotionally congruent face-voice pairs in the current study elicited similar ERP effects as recognized items in a previous study. This suggests that 7-month-olds integrate emotional information across modalities and recognize common affect in the face and voice. Since the face-voice pairs presented to the infants were novel to them, the current data not only indicate that these infants recognized common affect, but, moreover, that they applied their knowledge about emotions in face and voice to draw inferences about what might be appropriate emotional face-voice associations when encountering novel bimodal events. Since we used static facial expressions, there was no amodal information (e.g., temporal synchrony between face and voice) available to the infants. Thus, infants could not simply determine that a face and voice belonged together by detecting amodal audio-visual relations; instead, they had to draw inferences based on their prior knowledge. Furthermore, extending behavioral findings, the current ERP data reveals insights into the time course and characteristics of the processes underlying the integration of emotional information from face and voice in the infant brain.

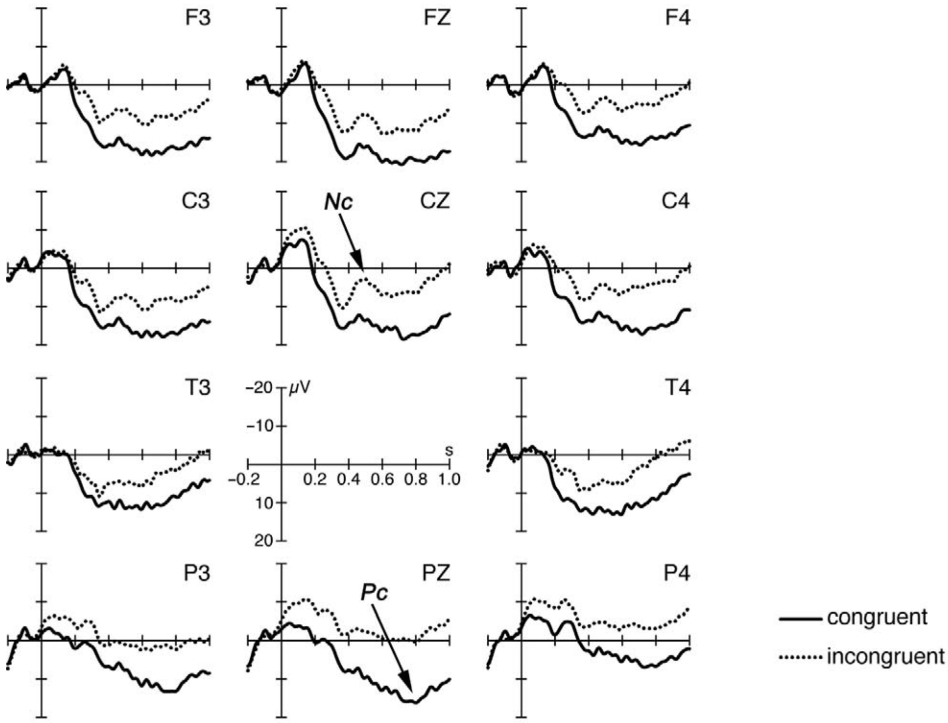

Figure 3.22 ERPs in response to congruent (solid) and incongruent (dotted) face-voice pairs in 7-month-old infants.

3.2.6 Processing of semantic and syntactic information in spoken sentences by native and non-native speakers

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In a previous functional Magnetic Resonance Imaging (fMRI) experiment, we showed that native speakers of German and Russian demonstrate comparable neural responses to specific language violations in their respective native language. We, therefore, were interested in how native Russian speakers (highly proficient, but non-native speakers of German) would respond on the neural level to German sentences. To this end, we presented both native and non-native German speakers (native speakers of Russian) with [1] correct, [2] syntactically incorrect, and [3] semantically incorrect sentences in German (see examples below).

[1] *Das Brot wurde gegessen*. [The bread was eaten.]
[2] *Das Eis wurde im gegessen*. [The ice-cream was in-the eaten.]
[3] *Der Vulkan wurde gegessen*. [The volcano was eaten.]

The averaged BOLD response of participants from each group (native and non-native speakers) to each sentence condition was compared. Within group contrasts of the BOLD response to the different sentence conditions showed a similar pattern of activation increase between native and non-native speakers in response to semantic violations, but not in response to syntactic violations. Specifically, the left inferior frontal gyrus was seen in both native and non-native speakers, to respond selectively to semantic anomalies, whereas the left superior temporal gyrus was seen to respond selectively to syntactic anomalies in native speakers alone. Secondly, the between group contrast showed that non-native speakers employed specific portions of the fronto-temporal language network differently than native speakers for language processing in general (i.e., in all sentence conditions). These regions included the inferior frontal gyrus (IFG), superior temporal gyrus (STG) and subcortical structures of the basal ganglia. This study demonstrated two things. First, the difference between processing semantic violations and correct sentences is comparable in native and non-native speakers, whereas the difference between processing syntactic violations and correct sentences is not. Secondly, non-native speakers rely on specific language-relevant brain areas to process non-native language stimuli to a greater degree than native speakers. These additional resources may reflect greater effort in processing phonological information in spoken language stimuli.

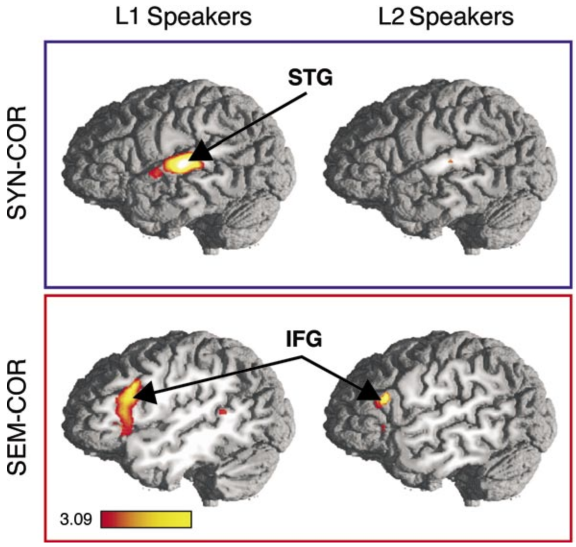

Figure 3.23

Processing of semantic and syntactic information in written sentences by native and non-native speakers

3.2.7

Rüschemeyer, S.-A., Zysset, S. & Friederici, A.D.

The processing of syntactic and semantic information in written sentences by native (L1) and non-native (L2) speakers was investigated in a functional Magnetic Resonance Imaging (fMRI) experiment. This was done by means of a violation paradigm, in which participants read sentences containing either [1] no violation, [2] a syntactic violation, or [3] a semantic violation.

[1] *Das Brot wurde gegessen*. [The bread was eaten.]
[2] *Das Eis wurde im gegessen*. [The ice-cream was in-the eaten.]
[3] *Der Vulkan wurde gegessen*. [The volcano was eaten.]

The results indicate that the processing of syntactic errors elicits greater activation in L1 speakers, but not in L2 speakers, in the left superior temporal gyrus (STG). The processing of semantic errors, on the other hand elicited comparable activation in the left inferior frontal gyrus (IFG) in both, L1 and L2

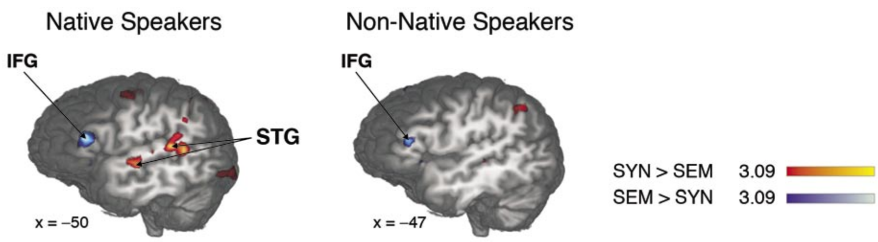

Figure 3.24

speakers. The results of this study were compared to a previously conducted fMRI study, which made use of identical sentence stimuli in the auditory modality. Results from the two studies are in general agreement with one another, although some differences in the response of brain areas very proximal to primary perceptual processing areas (i.e., primary auditory and visual cortex) were observed in conjunction with presentation in the different modalities. The combined results provide evidence that L1 and L2 speakers rely on overlapping cortical networks to process language (in particular semantic information), although with a higher level of activation in some regions for L2 processing.

3.2.8 Zooming in: How language mode and context adjustment affect processing of interlingual homographs in sentences

Elston-Güttler, K.E., Gunter, T.C. & Kotz, S.A.

We tested the "zooming in" process of adjusting from one language to another by using German-English homographs such as *gift* (German = "poison", English = "present") in sentence contexts using a joint reaction time (RT)/event-related brain potential (ERP) measure. Native German speakers with advanced knowledge of English (n = 48) performed an experiment in English where sentences such as "The woman gave her friend an expensive *gift*" (control prime: *item*) were presented, followed by targets (i.e., *boss*) for lexical decision (stimulus-onset asynchrony = 200 ms). If the L1 German influences the L2 during word recognition, then semantic priming in the N400 ERP component (unrelated targets more negative than related) and in RTs should be obtained. We aimed to test whether two main factors influence such activations during L2 processing. First, to test the role of *previous language context*, we presented half of the participants (n = 24) with a 20-minute silent film (*The Vampires*, Louis Feuillade, 1915) narrated in German and half (n = 24) with the film narrated in English right before the experiment. Second, to address the question of *task effects over time*, we analyzed the first and second halves of the experiment. The results showed a significant interaction between Priming, Film, and Block in both the RTs and ERPs. Thus, significant semantic priming in the RTs and in the N400 at 300–500 ms post-stimulus was observed *only* for participants who viewed the German movie (compare Figure 3.25, A and B), and *only* during the first block of that version (compare Figure 3.25, C and D). These results suggest: (1) that previous language context (in this case the English film before the English experiment) affected sentence processing by raising decision thresholds high enough to eliminate measurable influence of the L1 on the L2, and (2) that the bilingual word recognition system is recalibrated over time, allowing for the L1 influence from the German film to disappear in the second half of the experiment.

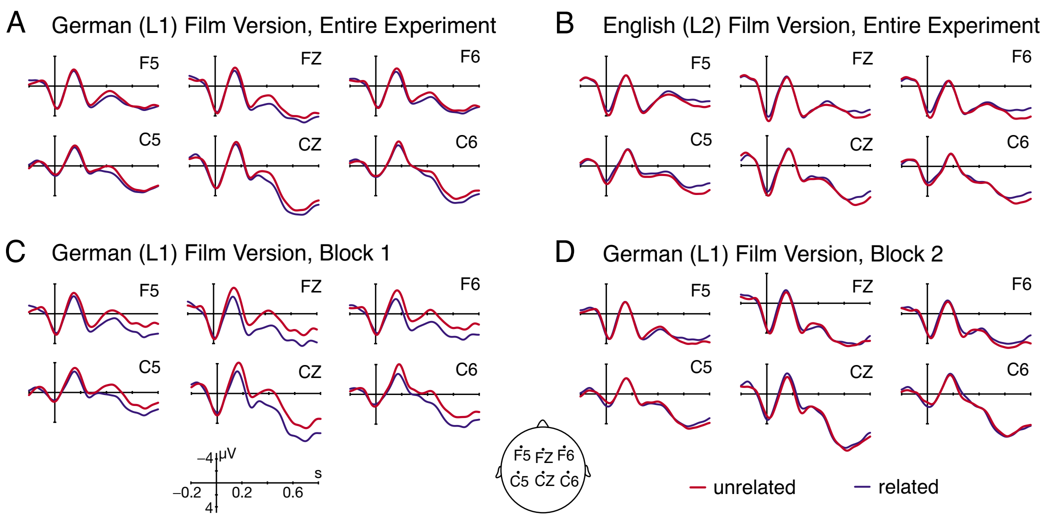

Figure 3.25 N400 priming effects showing the interaction between Priming, Film, and Block, in which significant priming was obtained for the German film version (A), but not the English film version (B). For the German film version, Block 1 (C) yielded significant priming, while in Block 2 (D), L1 influence disappeared.

CLINICAL NEUROPSYCHOLOGY 4.1

During the last years, the projects of the Clinical Neuropsychology (CNPS) group have exploited all techniques and methodological achievements available in the institute to further characterize the pathological state of both 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 for Human Cognitive and Brain Sciences. Others resulted from cooperations with different departments at the University Clinic of Leipzig, in particular with the Clinics of Neurosurgery, Neurology, and Psychiatry, with the Department of Anaesthesiology as well as with the Paul Flechsig Institute for Brain Research.

Since 2004, 337 patients from the Day Clinic and 68 patients from collaborative projects with other clinical institutions were submitted to MRI diagnosis at the institute. Our database now consists of a pool of more than 1350 patients with brain injuries of various aetiologies. In addition to the disease-specifically acquired MR modalities, each patient is characterized by a detailed analysis of his/her medical history, neuropsychological and linguistic profile.

This data base offers an excellent opportunity for a better insight into the basic understanding of cognitive neurology, in terms of description of structural brain damage as well as to its functional correlates. The data pool is the basis for all CNPS projects. For instance, for a project aiming on a better characterization of the cognitive sequelae of diffuse axonal injury (4.1.1), for the quantification of structural brain damage (e.g., 4.1.2) as well as for several functional studies that are performed applying event-related brain potentials (ERP), functional magnetic resonance imaging (fMRI), or functional near-infrared spectroscopy (fNIRS), or for the assessment of the relation of behavioral and imaging data.

The functional role, for instance, of the frontostriatal circuits in error processing was addressed in an ERP study in a group of patients with focal basal ganglia lesions (4.1.3), whereas the question of whether this kind of lesions result in a selective or general emotional deficit was tested in a behavioral experiment (4.1.4). The results of this latter study suggest that patients with lesions in the basal ganglia rely more on semantic than on emotional prosodic information. Indeed, language comprehension was a focus of several patient studies. To investigate aphasic language deficits, for instance, some studies were performed. An ERP approach focused on the interaction between distinct language processing and components of phonological short-term memory. This study was explored in patients suffering left-sided ischemic stroke of the prerolandic artery (4.1.5). Based on a behavioral design, story comprehension was assessed after left-hemispheric vs. right-hemispheric damage (4.1.6). Text comprehension has been the specific focus of some projects, e.g., of a behavioral experiment addressing the recognition of text words with increasing age (4.1.7).

As functional NIRS is particularly sensitive to the microvasculature, this method has gained attraction in studying normal and pathological aging. During recent years, various CNPS projects have focused on the sensitivity of fNIRS as to the decline in the fNIRS response associated with normal aging or, e.g., to the accelerating effect that cerebral microangiopathy seems to have (4.1.8).

4.1.1 Cognitive sequelae of diffuse axonal injury

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The results of recent reports on cognitive disability after traumatic brain injury (TBI) associated diffuse axonal injury (DAI) are inconsistent. In these studies, the diagnosis of DAI relied on CCT. In the current study, we aimed to further clarify the extent and severity of a possibly DAI-associated cognitive impairment by the use of MRI and detailed neuropsychological testing. For this purpose, eighteen patients (age range 17–50 years, median initial Glasgow Coma Scale score 5) were identified out of a databank with 299 TBI patients who showed an MRI lesion pattern compatible with pure DAI. All patients had undergone MRI on a 3 T system. Pure DAI was defined by the findings of traumatic microbleeds (TMBs) on T_2*-weighted gradient-echo images in the absence of otherwise traumatic or non-traumatic MRI abnormalities. Main outcome measures were neuropsychological performance in the categories attention and psychomotor speed, executive functions, spans, learning and memory, and intelligence 4–55 months (median 9 months) after TBI.
In summary, all patients showed impairments of one or more cognitive subfunctions, and no cognitive domain was fundamentally spared. Memory and executive dysfunctions were most frequent, the former reaching a moderate to severe degree in half of the patients. In comparison, deficits of attention, executive functions, and short term memory were mostly mild. Correlations between the amount of TMBs and specific or global cognitive performance were absent. We, therefore, conclude that a MRI lesion pattern compatible with isolated DAI is associated with persistent cognitive impairment. However, the TMB-load is no sufficient parameter for the assessment of DAI-severity or functional outcome.

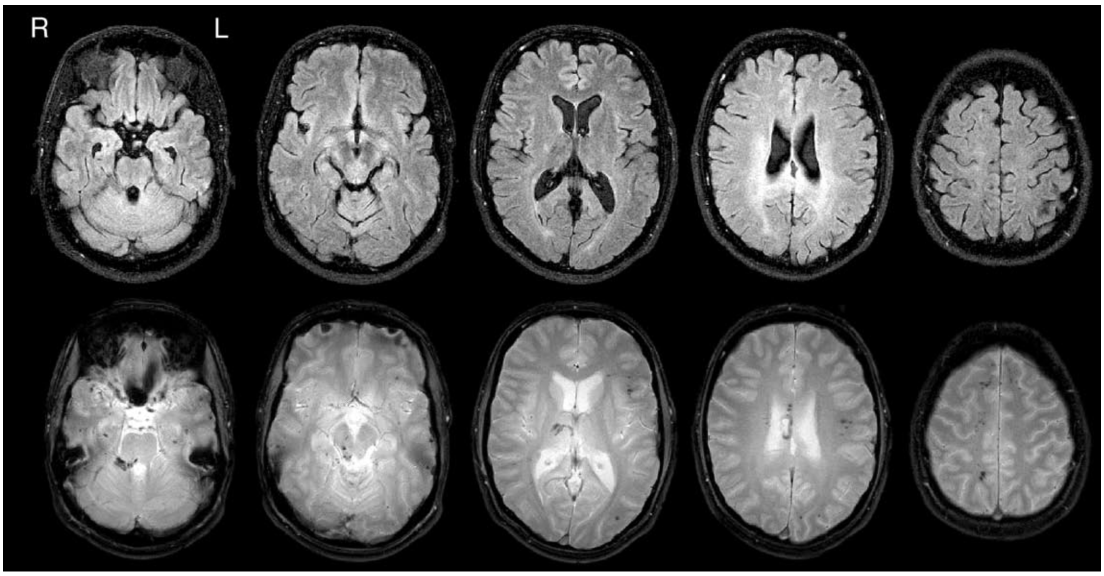

Figure 4.1 Examplary MRI findings of one patient. Comparison between FLAIR images (upper row) and T_2*-weighted gradient-echo images (lower row). Depicted are axial view sections of exactly corresponding levels. Multiple traumatic microbleeds are shown on the T_2*-weighted gradient-echo images.

How does the ventricular system adjust to intracranial pressure alterations and what are the possible mechanisms of ventricular change in hydrocephalus?

4.1.2

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The mechanisms of ventricular adjustment to alterations of intracranial pressure were analyzed in two studies in cooperation with the department of neurosurgery. In the first study, the case of a subacute obstructive hydrocephalus was evaluated in time-series MR examinations regarding the pattern of ventricular re-adaptation to intracranial pressure relief after surgery, i.e., third ventriculostomy. A vector field analysis was employed to visualize regional adaptational processes of the segmented ventricles referenced to the co-registered preoperative image. The vectors show a non-uniform pattern of ventricular decrease with a pronunciation at the ventricular roof, the temporal horns and the third ventricular floor (Figure 4.2). In the second study, the question was raised of what regional textural properties of the surrounding tissue allow or impede the ventricular system to react to the changes of intracranial pressure. The ventricular systems of patients with hydrocephalus of different etiology were modeled by means of spherical harmonic basis functions. The surface details of the segmented ventricles were simplified in a stepwise fashion to their underlying geometrical shape, a spheroid. It could be shown that distinct difference between chronic and subacute hydrocephalus appears in this theoretical approach that mimics the development of fine structural superficial details of the ventricles. More precisely, this algorithm revealed a very different underlying geometry in chronic vs. subacute hydrocephalus (Figure 4.3). These results show that the pattern of decrease or increase in ventricular volume depends on the etiology of hydrocephalus and has to be interpreted in the context of the surrounding white matter texture that allows or impedes regional adaptation.

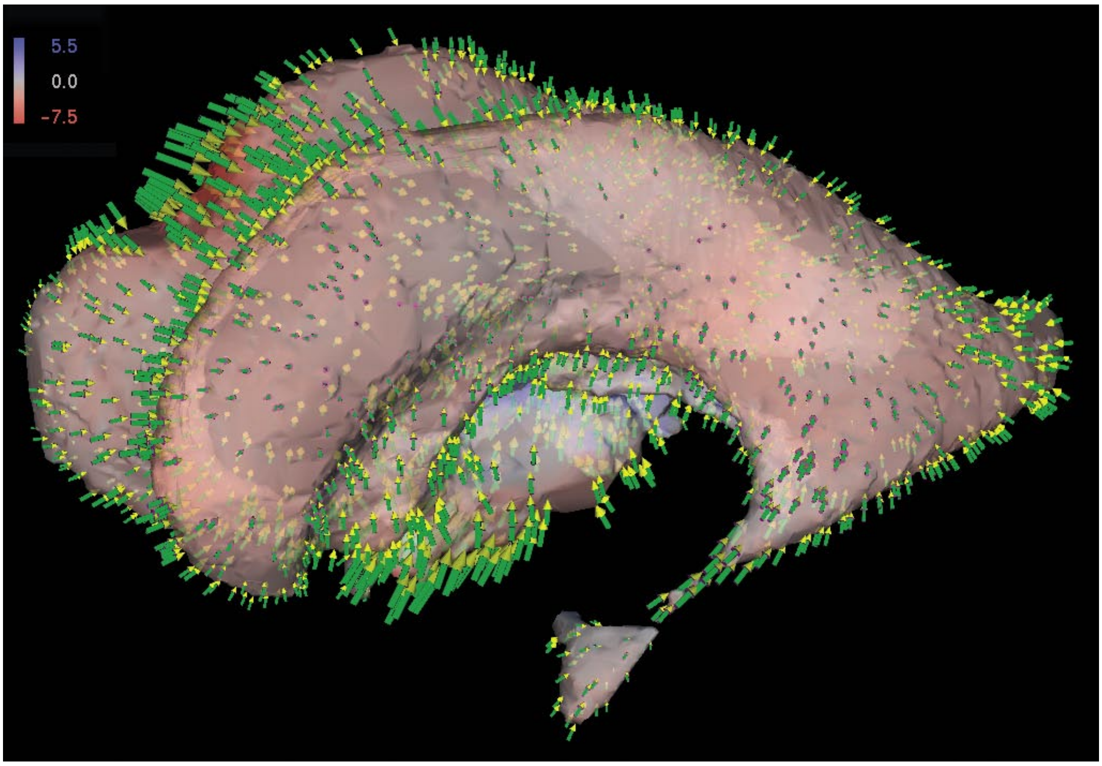

Figure 4.2 Changes in morphology are visualized by colors: Red and blue indicating inward and outward pointing directions, respectively, and the magnitude of shape change perpendicular to the surface of the ventricular system: Arrows indicate the displacements.

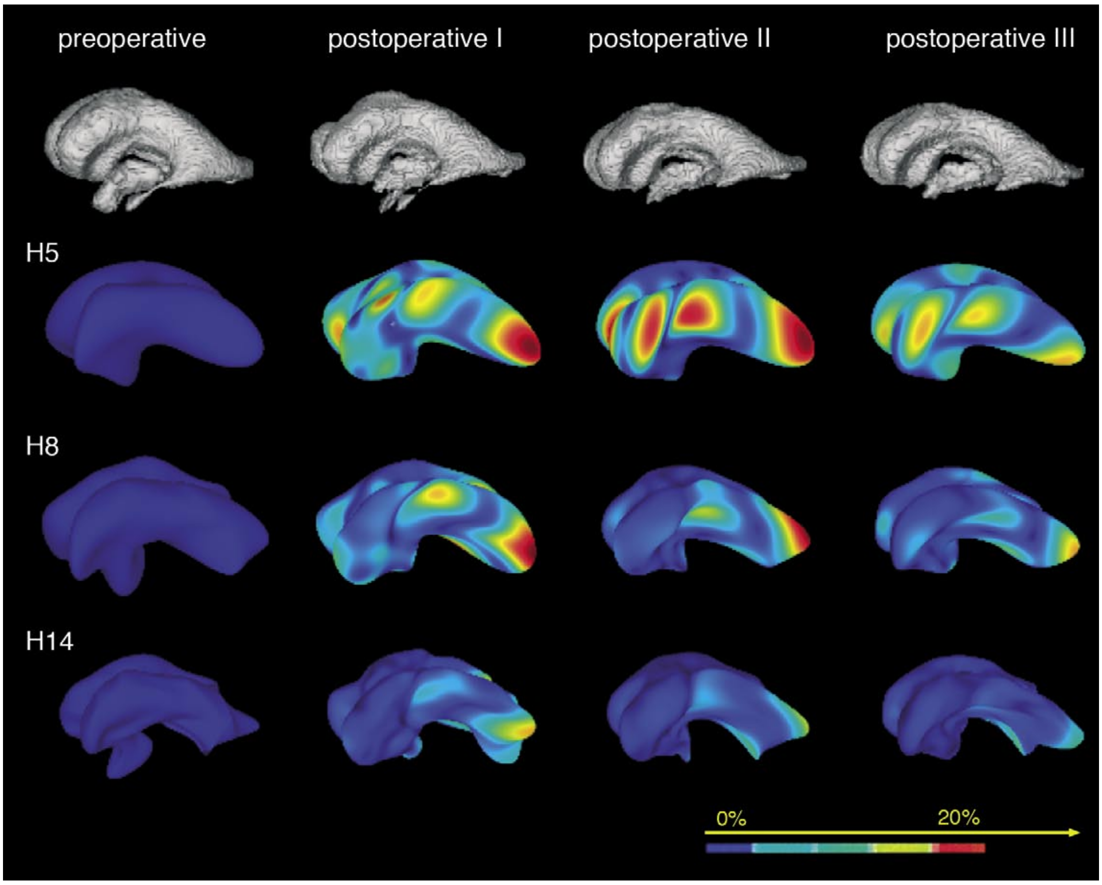

Figure 4.3 The 3 rows depict the models of the ventricular systems at harmony 5, 8, and 14 respectively. Color-coding reveals differences in variance to the respective preoperative ventricle. Postoperative adaptational processes are most pronounced in the early postoperative course, whereas later adaptations are discrete. In the more complex harmony steps the changes are less obvious than in the simpler ones.

4.1.3 The role of intact frontostriatal circuits in error processing

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The basal ganglia have been suggested to play a key role in performance monitoring and resulting behavioral adjustments. It is assumed that the integration of prefrontal and motor cortico-striato-thalamo-cortical circuits provides contextual information to the motor anterior cingulate cortex regions to enable its function in performance monitoring. So far, direct evidence is missing, however.
We addressed the involvement of frontostriatal circuits in performance monitoring by collecting event-related brain potentials (ERPs) and behavioral data in nine patients with focal basal ganglia lesions and seven patients with lateral prefrontal cortex lesions (Figure 4.4 A, B) while they performed a flanker task. In both patient groups, the amplitude of the error-related negativity was reduced, diminishing the difference to the ERPs on correct responses (Figure 4.5 A, B). Despite these electrophysiological abnormalities, the majority of patients was able to correct errors. Only in lateral prefrontal cortex patients whose lesions extended into the frontal white matter (Figure 4.4 C), disrupting the connections to the motor anterior cingulate cortex and the striatum, were error corrections severely impaired.
In sum, the fronto-striato-thalamo-cortical circuits seem necessary for the generation of the error-related negativity even when brain plasticity has resulted in behavioral compensation of the damage. Thus, error-related ERPs in patients provide a sensitive measure of the integrity of the performance monitoring network.

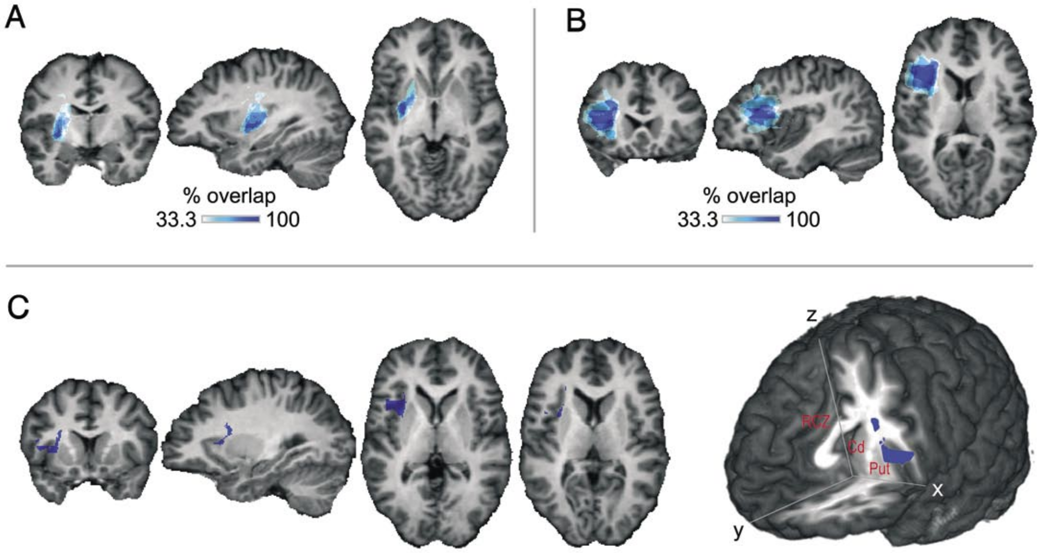

Figure 4.4 Lesion overlay plots. Lesions of each individual were segmented manually and overlaid on a healthy brain template after normalization to stereotactic space. (A) Lesion overlap of all basal ganglia patients. (B) Lesion overlap of all lateral prefrontal cortex patients. (C) Lesion part unique to the three lateral prefrontal cortex patients with impaired error correction. RCZ = rostral cingulate zone, Cd = caudate nucleus, Put = putamen.

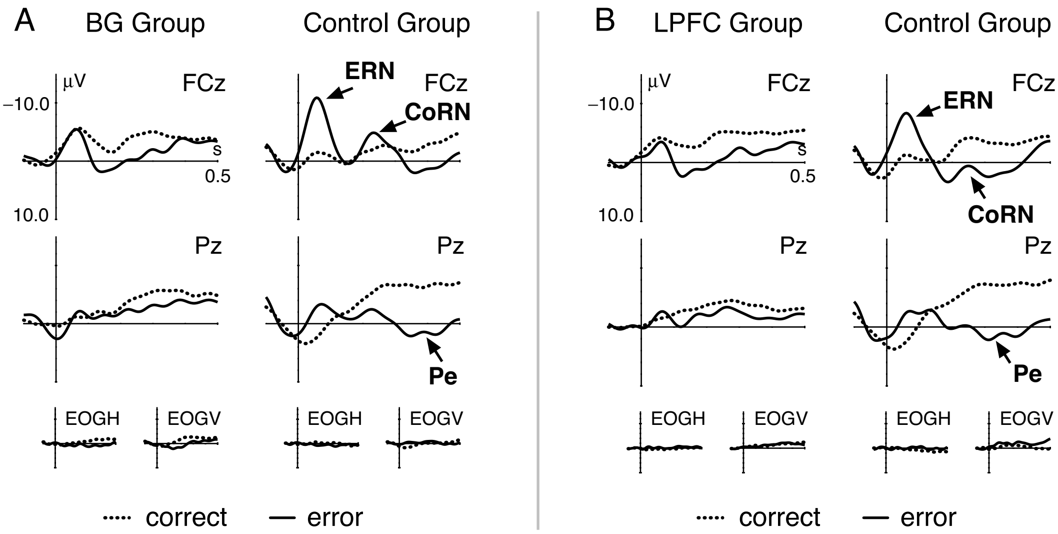

Figure 4.5 (A) Response-locked grand average ERPs at two midline electrodes for the basal ganglia patients and the according control group for correct (dashed) and incorrect (solid) responses on incompatible trials. (B) The same for patients with lateral frontal cortex lesions and their controls. BG = basal ganglia, LPFC = lateral prefrontal cortex, ERN = error-related negativity, CoRN = correction-related negativity, Pe = error positivity.

4.1.4 Emotional prosody recognition in BG-patients: Disgust recognition revisited

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One critical issue in studying emotion perception in patients is to understand which of the underlying mechanisms constituing an emotion are affected by a lesion. In recent years, the literature has suggested that the basal ganglia (BG), along with right hemispheric cortical structures, play an important role in the evaluation of emotional stimuli. In particular, there has been evidence that the BG modulate perception of disgust (facial and tonal) in Parkinson's and Huntington's disease patients (Pell & Leonard, 2003; Sprengelmeyer et al., 1996). However, while controversial, there is also evidence that the BG are involved in the recognition of facial-*fear*, but not in vocal-*fear* expressions (Kan et al., 2002). Furthermore, certain BG lesions also result in facial-*anger* recognition impairment (Calder et al., 2004). Latter evidence is supported by fMRI evidence on vocal-*anger* expressions (Kotz et al., 2003). In order to specify if BG lesions result in a selective or general emotional deficit, we tested the recognition of four vocal emotions (anger, fear, disgust, happiness and a neutral baseline) in BG lesion patients (n = 12; mean age = 46.69 years) and their age- and education-matched healthy controls in lexical and pseudo-sentences.

Results revealed that emotional prosody recognition was above chance level (20%), for both the BG-patient (48.16%) and healthy controls (75.25%). However, controls showed higher recognition rates than patients, *disgust* displaying the lowest recognition rate (62.91%). Results from BG patients revealed recognition rates below 50% for all emotional prosodies tested, but with extremely low recognition of *fearful* (40%) and *disgust* (34.58%) utterances. In particular, results revealed only slightly better recognition rates for vocal expressions of *disgust* than expected by chance. Additionally, results revealed differences between the lexical and non-lexical modality displaying a general emotional prosody recognition problem when no lexical content is present for BG patients.

Our paradigm allowed to test emotional prosodic vocalizations with and without lexical content. Results suggest that BG patients rely more on semantic information than on emotional prosodic information when listening to emotional stimuli. The data suggest that testing patients with BG lesions under 'pure' prosodic conditions reveals a categorization deficit for almost all emotional prosodic contours tested. This suggests that emotional prosodic recognition is influenced by lexical content even when categorizing emotional prosody. In sum, the current data serves as renewed evidence that the recognition of *disgust* is impaired in BG patients. Our results are in line with previous reports on selective deficits for disgust recognition, but point to the fact that the BG may be involved in emotional prosodic perception per se.

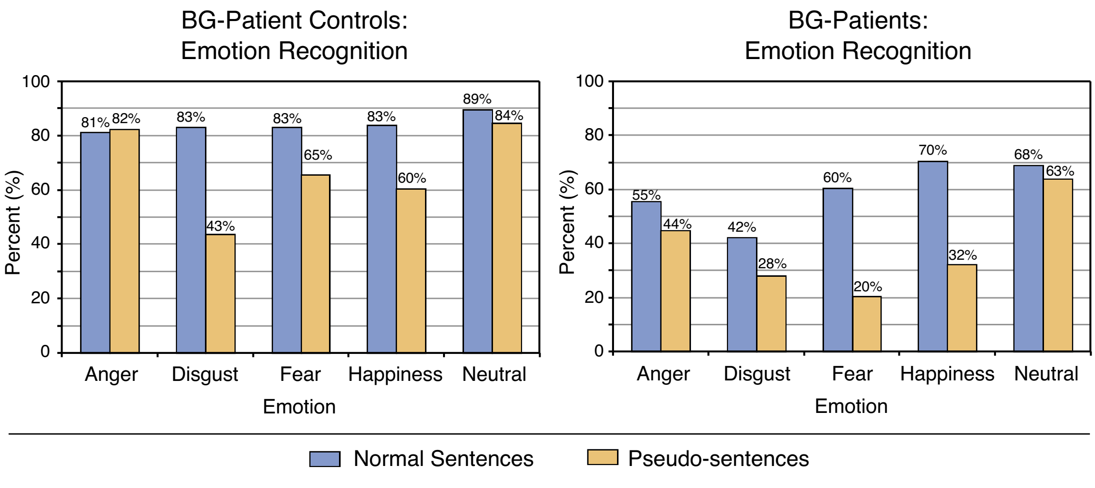

Figure 4.6

On the role of phonological short-term memory in sentence processing: ERP single case evidence on modality specific effects

4.1.5

Kotz, S.A.,[1, 2], von Cramon, D.Y.[1, 2] & Friederici, A.D.[1]

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Previous research argues that a variety of factors contribute to syntactic deficits in aphasia: Deficits of the mechanisms subserving syntactic processing in comprehension and production reduced short-term memory capacities or computational deficits affecting access or integration of syntactic information. Here, we explored a possible interaction between distinct language processes (both syntactic and semantic) and components of phonological short-term memory (pSTM) in a patient with a pSTM profile. Event-related brain potentials (ERPs) were recorded, while the patient and age-matched controls engaged in auditory and visual sentence correctness tasks. Stimulus onset asynchrony (SOA) was varied in the visual modality. Controls showed an early anterior negativity followed by a P600 for syntactic violations and an N400 for semantic violations in the auditory and the short visual SOA condition. In the long visual SOA condition, only a P600 and an N400 were observed. Across all tasks, the patient displayed a comparable early anterior negativity and N400 pattern to controls. However, the P600 was replaced by a centro-parietal negativity (500–800 ms) that was followed by a very late positivity (900–1300 ms) in the visual modality, indicating that late syntactic processes are sensitive to SOA manipulation. This result implies that the cortical regions lesioned in the patient may be part of a neural network that engages the pSTM system during "temporally variable" late syntactic processing in the visual modality. The combined results indicate that the pSTM system differentially impacts semantic and late syntactic processes.

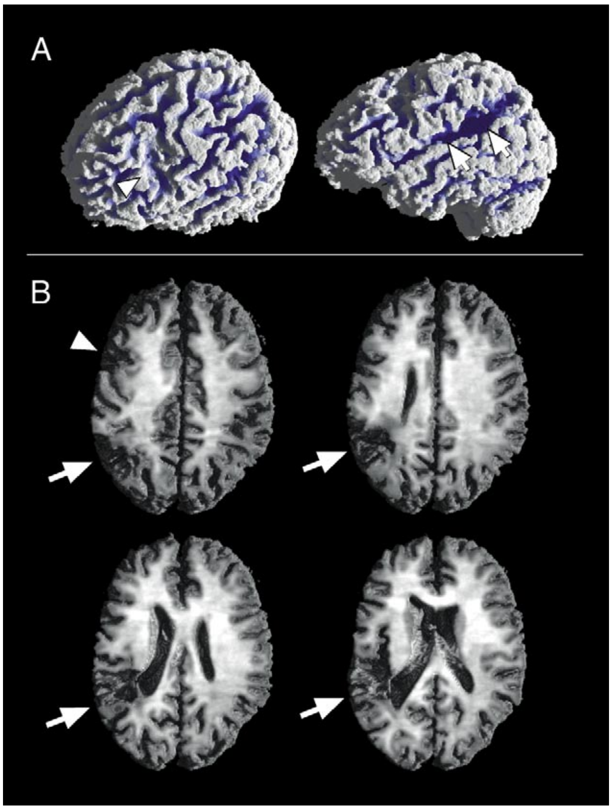

Figure 4.7 (A) lateral view; (B) axial slices
The patient had suffered a left-sided ischemic stroke within the supply area of the prerolandic artery (arrow head) and the posterior parietal artery (arrows) of the left middle cerebral artery.

Assessment of story comprehension deficits after brain damage

4.1.6

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Besides aphasic language deficits, brain injury often causes problems with text and discourse level language use. For these non-aphasic language deficits, few diagnostic instruments are available. In particular, control data of healthy, age- and education matched populations as well as comparison data for patients with different brain lesions are lacking.
In this study, a comprehension test previously developed for this purpose (Walther, 2000) was evaluated on a large number of participants. The test consists of two easily comprehensible stories about everyday events. To each story, 16 Yes/No-questions probed different aspects of the text comprehension process.

Inferencing abilities were tested in a comparison of questions about stated vs. implied information, and global structuring was probed using questions about main ideas and details, i.e., about information differing in salience. Fifty adult control participants and 109 consecutive patients at the Day Clinic of Cognitive Neurology were tested. The control participant's performance confirmed the expected interaction between explicitness and salience, with main ideas being easier than details, and implied main ideas more difficult than stated ones. The patient group performed only slightly worse overall (17% vs. 14% errors), and this difference was due to implied information only. Importantly, the performance on the four question types was systematically related to the brain damage. Patients with left-hemisphere damage (LBD) had particular difficulties with stated details, and patients with right-hemisphere damage (RBD) with implied details. For traumatic brain injury (TBI) patients, both types of questions were equally difficult. Correlations with neuropsychological test results confirmed that the questions indeed probed different cognitive functions. Errors on stated information were predicted by verbal long term memory, and errors on implied main ideas by tests of executive functions. To evaluate the diagnostic utility on a single case basis, cutoff scores were calculated from the control group's scores for each question type separately. Almost 40% of the LBD patients were above the cutoff for stated details, 42% or the RBD patients for implied main ideas, and 41% of the TBI patients for implied information pooled. These highly significant results show that the discourse comprehension measure is a useful clinical assessment instrument that provides specific information on inference and structuring processes during text comprehension.

4.1.7 Text comprehension in middle age: Is there anything wrong?

Ferstl, E.C.

In contrast to other cognitive processes, language comprehension has been shown to be relatively stable in healthy aging adults. There is even evidence for improvement of language comprehension skills, if they are based on situation model processing and the successful integration of general world knowledge. However, for many tasks useful for neuropsychological patient studies, control data from older participants is lacking. In the present study, we compared similarly aged groups of various educational levels on two different text comprehension tasks. In the first experiment, a coherence judgment task was used, in which the pragmatic connection between two successive sentences had to be evaluated (cf. Ferstl & von Cramon, 2001; Ferstl et al., 2002). In this task, which does not heavily depend on working memory and which can be solved using a situational representation, the 39 participants made equally few errors, independent of age (range 26–64 years). The second task used a word recognition paradigm. After reading a story, 60 participants (age range 20–69 years) were asked to decide whether words on a list had been mentioned in the text. The distractors included synonyms and related words, so that the discrimination was relatively difficult. Here, even the middle-aged participants made significantly

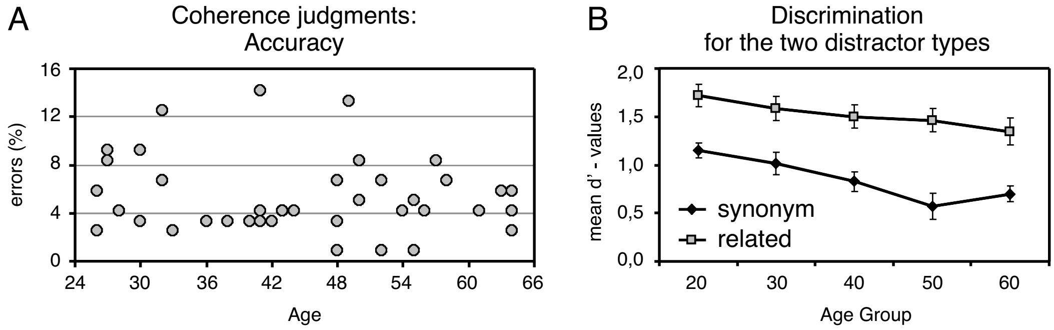

Figure 4.8 (A) Participants of all ages performed close to ceiling in the coherence judgment task. (B) The recognition of text words became more difficult with increasing age. The decline of discrimination performance with age was particularly evident for the synonym distractors.

more errors compared to the youngest group. This effect was particularly pronounced for the synonym distractors, because their correct rejection depends on an accurate representation of the verbatim form of the text, the so-called surface structure. These results confirm that processing on the surface level, but not on the situation model level, is subject to age-related decline. Most importantly, the performance decrements already appear during middle age. The present findings are important for the evaluation of text comprehension skills in neurological patient populations. Age effects have to be taken into account when choosing an appropriate methodology.

4.1.8 Spontaneous slow hemodynamic oscillations decline in cerebral microangiopathy

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It is well known that aging leads to a degeneration of the vascular system. Small-vessel disease or cerebral microangiopathy is a common finding in elderly people (Figure 4.9). This disease is related to a variety of vascular risk factors, namely arterial hypertension and diabetes, and may ultimately lead to subcortical ischemic vascular dementia. One may hypothesize that decrease of spontaneous oscillations in the cerebral microvasculature with aging (Schroeter et al., 2004) is accelerated by microangiopathy. To test this hypothesis, we measured spontaneous oscillations in the visual cortex during rest and visual activation (Schroeter et al., 2005). We applied optical imaging (functional near-infrared spectroscopy), because it is particularly sensitive to the microvasculature.

Visual stimulation led to comparable increases of oxyhemoglobin, total hemoglobin, and decreases of deoxyhemoglobin in all subjects. Peaks of normalized power spectral density were detected for spontaneous low (~0.1 Hz) and very low (~0.03 Hz) frequency oscillations with a higher amplitude for oxy- than deoxyhemoglobin (Figure 4.10). Spontaneous low frequency oscillations of oxyhemoglobin declined in microangiopathy during both rest and visual stimulation (Figure 4.10). Stimulation led to a smaller increase of very low frequency oscillations of deoxyhemoglobin in microangiopathy compared with controls, indicating a reduction in vascular reagibility. Interestingly, these changes were tightly related to neuropsychological deficits, namely executive dysfunction. Vascular alterations had to be attributed to the vascular risk factors arterial hypertension and diabetes, and could be reversed by medical treatment such as angiotensin-converting enzyme inhibitors/angiotensin II receptor blockers.

Reduction of spontaneous low frequency oscillations indicates a declining spontaneous activity in microvascular smooth muscle cells, in conjunction with an increased vessel stiffness in cerebral microangiopathy. Results suggest that spectral analysis is much more sensitive to changes in the microvasculature compared with time-line analysis of the functional hemodynamic response, and enables, therefore, an earlier detection of such alterations.

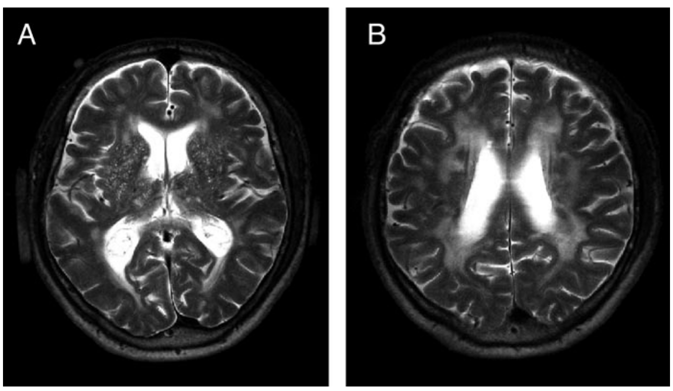

Figure 4.9 Structural changes in cerebral microangiopathy visualized with high-resolution magnetic-resonance tomography at 3 Tesla in T_2-weighted sequence. Characteristic abnormalities are (A), lacunar state of the basal ganglia and (B), periventricular white matter disease.

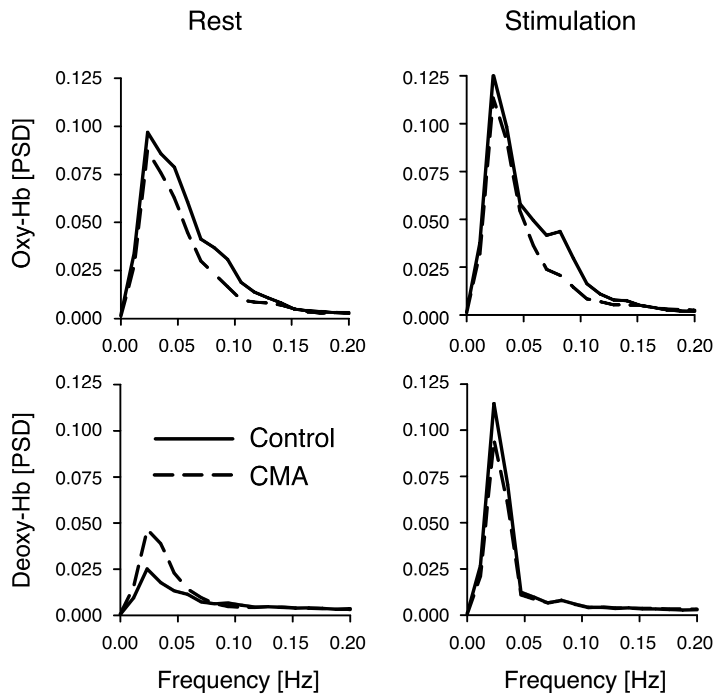

Figure 4.10 Normalized power spectral density (PSD) in comparison between patients with cerebral microangiopathy (CMA) and age-matched controls. Very low (VLFO) and low frequency oscillations (LFO). Hb = hemoglobin.

The working group "Functional Neuroanatomy of the Frontal Lobe" has been addressing neural correlates of higher cognitive functions and the specific contributions of areas in the human frontal lobes for more than five years. The group has been very successful, which is also reflected in the results gathered over the last two years. A major advantage of the group is the use and integration of a wide range of methods, including behavioral, functional magnetic resonance imaging (fMRI), electroencephalography (EEG), and near-infrared spectroscopy (NIRS) measures while focusing on a number of well-specified, mutually interconnected research topics. In addition to studies in healthy participants, patient studies have also been performed (reported in Section 4.1).

Two research lines within the working group focus on the implementation of flexible adjustments in goal-directed behavior in the human brain. Selecting, updating and preparing task sets allow successful task performance, even when it is necessary to switch between different tasks. Monitoring for deviations in the intended and expected action outcomes and for situations when the intended outcome is at risk, is a prerequisite to adjusting behavior to changes in the environment as well as to compensate for errors. There is a dynamic interplay between these two functions – performance monitoring and adjusting the task sets – forming the basis of cognitive control. The posterodorsal frontomedian cortex is consistently implicated in performance monitoring and signaling the need for adjustments, as revealed by a meta-analysis of fMRI studies (4.2.1). Simultaneous recording of fMRI and EEG revealed a trial-by-trial coupling of the error-related negativity (ERN; an event-related potential associated with errors), the fMRI signal within the rostral cingulate zone and subsequent behavioral adjustments (4.2.2). An EEG study tested the relationship of the ERN to immediate error corrections and error signaling responses (4.2.3). The implementation of cognitive adjustments recruits an area called the inferior frontal junction (IFJ). This region is thought to play a major role in updating task representations. The role of this region was further characterized in a metaanalysis including frontal activations from task-switching, set-shifting and stimulus-response-reversal studies (4.2.4). The implications of the IFJ functions for human behavior are discussed in 4.2.5. An EEG study made use of the high temporal resolution to investigate the interactions between the IFJ and posterior brain regions in task preparation (4.2.6). Moreover, an fMRI study addressed the roles of the pFMC, lateral prefrontal cortex, and parietal cortex in the voluntary selection of tasks (4.2.7). The development of IFJ involvement in dealing with interference and task set updating has been examined in a NIRS study in children and young adults (4.2.8).

More complex decision-making processes have been addressed in a further set of studies. A new line of research in our group focuses on behavior and decision making based on intuition. The neuroscience approaches for the investigation of intuition are outlined in 4.2.9. The implementation of multi-attribute decision making was studied with fMRI (4.2.10). A number of characteristic time courses of activity were found in the pFMC, lateral frontal and parietal cortex. Evaluative judgments of equally high abstraction were examined in an fMRI study that compared evaluative aesthetic judgments with descriptive symmetry judgments (4.2.11). Activity related to aesthetic judgments was found in the anterior frontomedian cortex (aFMC; rostral to the pFMC), lateral frontal, parietomedian, and temporal regions.

A prerequisite for humans to make decisions in their social context is the ability of language comprehension. In a series of fMRI studies, the functional neuroanatomy of text comprehension has been delineated (4.2.11). The following areas have been shown to play a major role in this function: the anterior temporal lobe, the aFMC, and parietomedian cortical areas. In emotional contexts, the ventral frontomedian cortex was seen to be involved as well. The development of text comprehension in healthy aging was addressed in a large behavioral study (4.2.12).

A further important focus of the group's work is put on the non-motor functions of the lateral and medial premotor cortex and their relationship to motor action. In this respect, neural correlates of anticipatory sequencing are of particular interest. An fMRI experiment investigated the role of attention to different properties of a sensory sequence, namely temporal duration and order of abstract stimuli. The data revealed that attention, but not mere exposure, to dynamic properties is necessary to engage the lateral premotor cortex (4.2.14). The correspondence of premotor correlates of motor action and perceptual attention was investigated in a further fMRI study (4.2.15). Brain activity elicited by the sensory serial prediction task was compared to the activity pattern found for motor imagery of arm, hand, and mouth movements. The results confirm the habitual pragmatic body map account of premotor cortex function.

4.2.1 The role of the posterior frontomedian cortex in performance monitoring

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Adaptive goal-directed behavior involves the monitoring of ongoing actions and performance outcomes, and subsequent adjustments of behavior and learning. A review of primate and human studies, along with a meta-analysis of the human functional neuroimaging literature, suggest that the detection of unfavorable outcomes, response errors, response conflict, and decision uncertainty elicits largely overlapping clusters of activation foci in an extensive part of the posterior frontomedian cortex (pFMC). A direct link is delineated between activity in this area and subsequent adjustments in performance. Emerging evidence points to functional interactions between the pFMC and the lateral prefrontal cortex, so that monitoring-related pFMC activity serves as a signal that engages regulatory processes in the LPFC to implement performance adjustments processes. Furthermore, the findings support the view that the RCZ signals the need for adjustments in order to optimize action outcome.

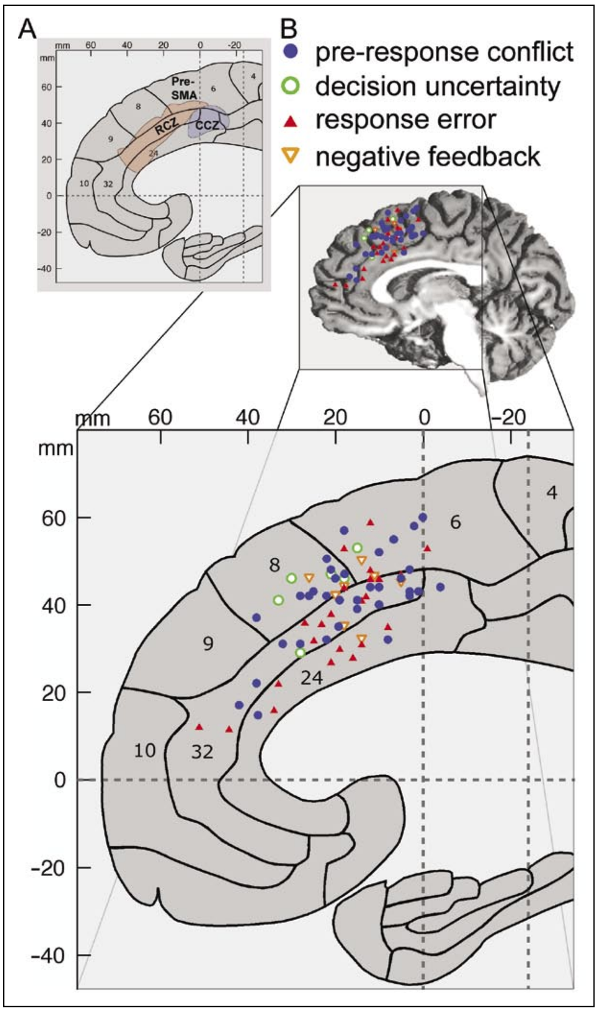

Figure 4.11 Areas in the pFMC involved in performance monitoring. (A) Schematic map of anatomical areas in the human pFMC. The area shaded in red encompasses the rostral cingulate zone (RCZ), and the area shaded in blue indicates the caudal cingulate zone (CCZ), homologues of the monkey's rostral and caudal cingulate motor areas, respectively. (B) Outcome of a meta-analysis of midline foci of activation reported in 38 fMRI studies published between 1997 and 2004 investigating brain activity associated with pre-response conflict, decision uncertainty, response errors, and negative feedback (20). In the upper part of the figure, the activation foci are superimposed on a sagittal slice of an anatomical MRI scan at x = 4. In the lower part, the activation foci are superimposed on the enlarged schematic area map. The majority of activations cluster in the pFMC, in a region where areas 8, 6, 32, and 24 border each other.

Trial-by-trial coupling of concurrent EEG and fMRI identifies the dynamics of performance monitoring

4.2.2

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Detecting errors and situations in which errors are likely to occur, is an essential prerequisite of goal-directed behavior. Current theories propose a performance monitoring system that continuously monitors the outcome of one's actions. Whenever the outcome of an action is worse than expected, for example after an error, the performance monitoring system signals the need for behavioral adjustments, thereby enabling compensatory mechanisms that allow remediation of the error and/or avoidance of similar errors in the future. Event-related potential (ERP) research has revealed the error-related negativity (ERN), a response-locked ERP associated with errors. Neuroimaging suggests an involvement of the rostral cingulate zone (RCZ) in performance monitoring. However, the relation of the ERP and neuroimaging correlates of performance monitoring is rather unclear, because little is yet known about the relation between scalp-recorded EEG signals and the blood oxygen level dependent (BOLD) response. To address this issue, we investigated the error-related negativity (ERN) using simultaneous 3 Tesla fMRI and 32 channel EEG recordings. Data were collected while participants performed a speeded flanker task. Following gradient and pulse artifact correction, single-subject EEGs were submitted to extended infomax independent component analysis (ICA). In all 13 participants, an independent component (IC) was identified, which was equivalent to the scalp-recorded ERN with respect to time course, topography and time-frequency characteristics (Figure 4.12A). Based on this IC, single-trial ERN amplitudes were determined (Figure 4.12B). As revealed in a parametric analysis of the fMRI data, the single-trial ERN amplitude predicted the BOLD signal in the RCZ (Figure 4.12C). Moreover, it was systematically related to behavior in the subsequent trial, thereby reflecting adjustments based on the performance monitoring signal (Figure 4.12D). In sum, the ERN and error-related activity in the RCZ reflect closely related performance monitoring processes. Furthermore, the findings support the view that the RCZ signals the need for adjustments in order to optimize action outcome. We conclude that our new approach addressing the dynamic coupling between EEG and fMRI opens new avenues for the study of timing and functional neuroanatomy of higher cognitive functions.

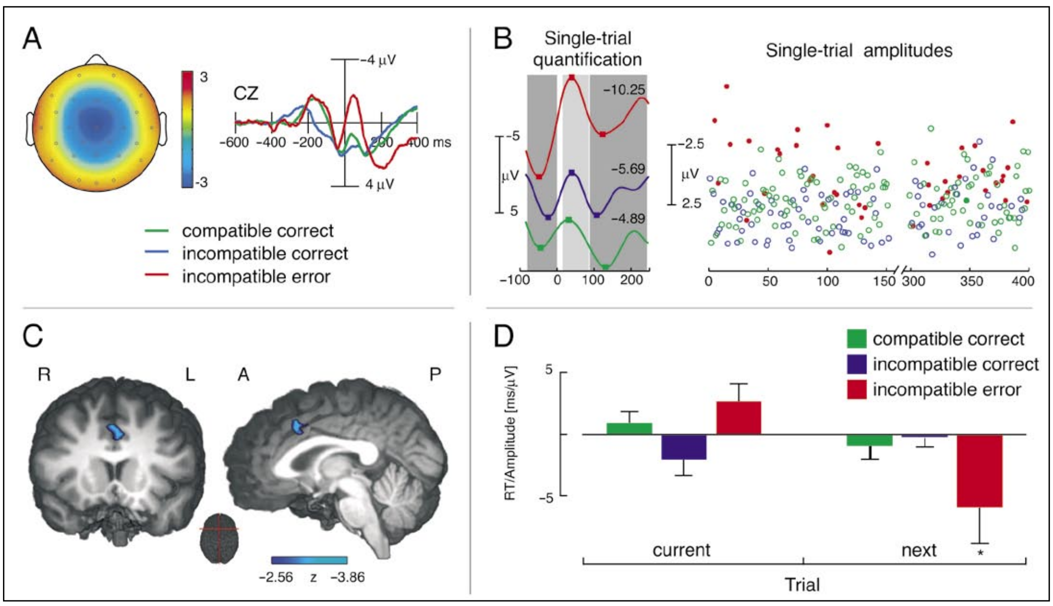

Figure 4.12 (A) Scalp topography and response-locked grand mean averages of independent component equivalent to ERN. (B) Single-trial amplitude quantification. (C) Result of parametric EEG-informed fMRI analysis. (D) Single-trial ERN amplitude predicts post-error slowing.

4.2.3 How does error correction differ from error signaling? An event-related potential study

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

It has been a question of debate whether immediate error corrections in speeded forced-choice reaction time tasks require an error detection signal from the performance monitoring system or whether they reflect delayed correct responses that are executed after the premature error like in a horserace. In contrast, signaling the error by pressing a response button that is unrelated to the primary task is based on error detection.

The present study investigated the similarities and differences between immediate error corrections and signaling responses by means of behavioral and event-related potential data. In a within-subject design, participants performed two sessions of the flanker task. In one session, errors had to be corrected by immediately pressing the correct response, in the other session, errors had to be signaled by pressing an error signaling button. Compared to the signaling session, in the correction session more errors and error corrections were made, reaction times were shorter, and the amplitude of the error-related negativity (ERN) was reduced (Figure 4.13). Whereas the error significance did not seem to differ across session, participants have most likely reduced the motor threshold in the correction session to enable efficient immediate corrections. This interpretation is supported by the lateralized readiness potentials showing stronger lateralization to the incorrect side (Figure 4.14) and is consistent with the response-conflict monitoring hypothesis of the ERN. We conclude that the error signaling procedure is a more direct and reliable way to behaviorally test the functional integrity of the performance monitoring system than the instruction to correct errors.

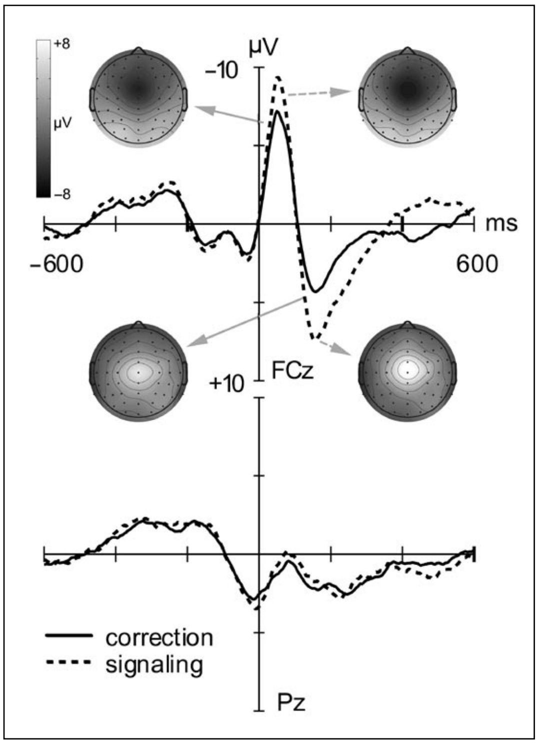

Figure 4.13 Response-locked grand mean average ERP waveforms for incompatible errors in the correction session (solid line) and the signaling session (dotted lines) at two midline electrodes. The insets show the scalp topographies for the ERN at 56 ms (upper plots) and the subsequent positivity at 156 ms (lower plots) for the correction session (left plots) and the signaling session (right plots). For the correction session, corrected errors are shown, for the signaling session signaled ones.

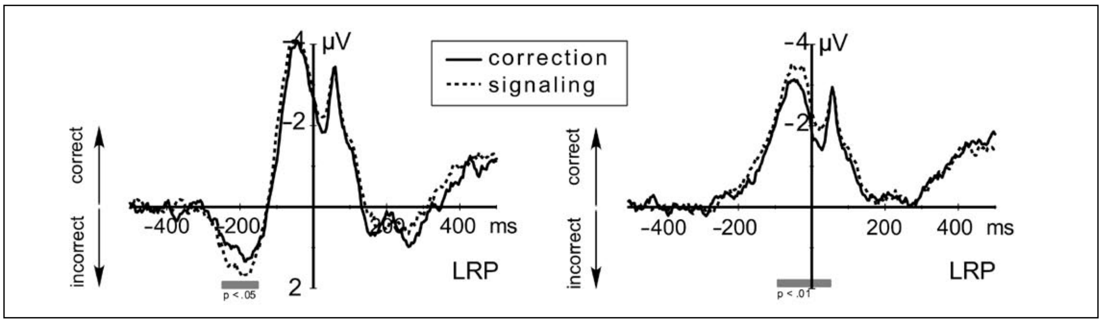

Figure 4.14 Response-locked grand mean LRP waveforms for incompatible correct trials (left panel) and compatible correct trials (right panel) in the correction session (solid line) and the signaling session (dotted lines). Time windows, in which the waveforms were significantly different, are indicated by a grey bar in the lower part of the panels.

Involvement of the inferior frontal junction in cognitive control: Meta-analyses of switching and Stroop studies

4.2.4

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In previous functional imaging studies, we have shown that the inferior frontal junction (IFJ) is involved intimately in cognitive control processes. Here, we investigated the consistency of this involvement by employing a meta-analytic approach. We conducted two quantitative meta-analyses of fMRI studies. One meta-analysis included frontal activations from task-switching, set-shifting, and S-R reversal studies, the other included frontal activations from color-word Stroop studies. Results showed highly significant clustering of activations in the IFJ in both analyses. The figure displays above-threshold voxels at the IFJ peak coordinates for (A) switching and (B) Stroop studies. These results provide strong evidence for the consistent involvement of the IFJ in both switching and Stroop paradigms. Furthermore, our results demonstrate how quantitative meta-analyses can be used to test hypotheses about the involvement of specific brain regions in cognitive control.

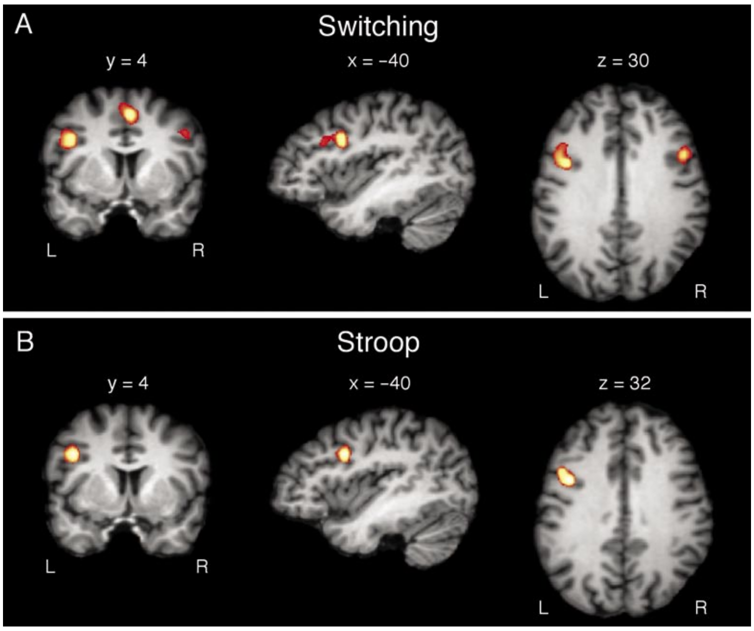

Figure 4.15

The role of the inferior-frontal junction area in cognitive control

4.2.5

Brass, M.[1], Derrfuss, J.[1,2], Forstmann, B.U.[1,3] & von Cramon, D.Y.[1]

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In our daily life we constantly alternate between different cognitive and motor operations with seemingly minimal effort. Cognitive psychology has assumed that this flexibility involves cognitive control processes. In the fronto-lateral cortex, such processes have been primarily related to mid-dorsolateral prefrontal cortex (mid-DLPFC). However, recent brain imaging studies (Brass & von Cramon, 2002; Brass & von Cramon, 2004; Derrfuss et al., 2004) and meta-analytic studies (Derrfuss et al., 2005) from our group suggest that a region located more posterior in the fronto-lateral cortex plays a pivotal role in cognitive control as well (Brass et al., 2005). This region has been termed inferior-frontal junction area and can be functionally and structurally distinguished from mid-DLPFC. As can be seen in Figure 4.16, a very

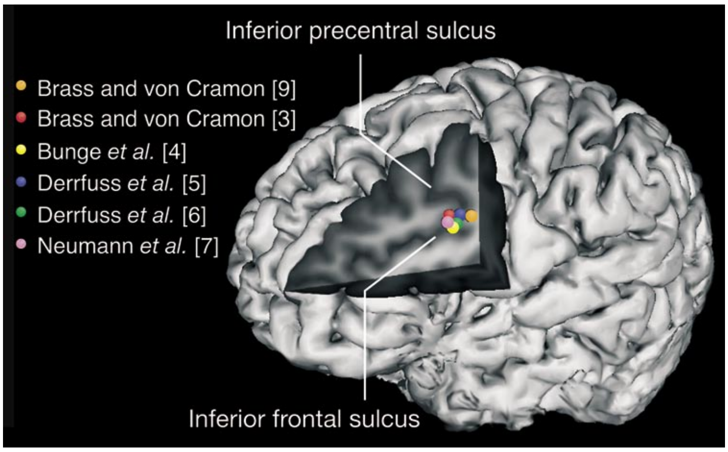

Figure 4.16

focused region has been found to be activated in a number of studies using different approaches. Furthermore, recent cytoarchitectonic work suggests that the IFJ cannot only be distinguished from adjacent areas on the basis of its functional neuroanatomy, but also on the basis of structural data (Amunts et al., 2004).

4.2.6 Who comes first? The role of the prefrontal and parietal cortex in cognitive control

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Cognitive control processes enable us to adjust our behavior to changing environmental demands. Although neuropsychological studies suggest that the critical cortical region for cognitive control is the prefrontal cortex, neuroimaging studies have emphasized the interplay of prefrontal and parietal cortices. This raises the fundamental question about the different contributions of prefrontal and parietal areas in cognitive control. It was assumed that the prefrontal cortex biases processing in posterior brain regions. This assumption leads to the hypothesis that neural activity in the prefrontal cortex should precede parietal activity in cognitive control. The present study tested this assumption by combining results from functional magnetic resonance imaging (fMRI) providing high spatial resolution and event-related potentials (ERPs) to gain high temporal resolution. We collected ERP data using a modified task-switching paradigm. In this paradigm, a situation where the same task was indicated by two different cues was compared with a situation where two cues indicated different tasks. Only the latter condition required updating of the task set. Task-set updating was associated with a midline negative ERP deflection peaking around 470 ms (Figure 4.17). We placed dipoles in regions activated in a previous fMRI study that used the same paradigm (left inferior frontal junction, right inferior frontal gyrus, right parietal cortex), and fitted their directions and magnitudes to the ERP effect. The frontal dipoles contributed to the ERP effect earlier than the parietal dipole (Figure 4.18), providing support for the view that the prefrontal cortex is involved in updating of general task representations and biases relevant stimulus-response associations in the parietal cortex.

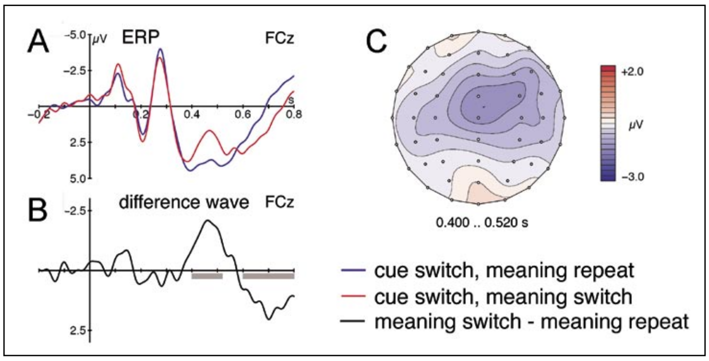

Figure 4.17 (A) Grand mean ERP waveforms for cue-target interval with (red) and without (blue) task set updating. (B) Difference wave of the two conditions. (C) Topographical scalp distribution of the ERP difference.

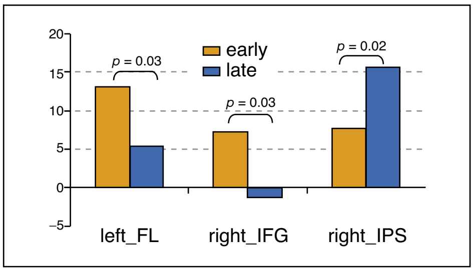

Figure 4.18 Dipole strength, averaged over subjects and time steps in early and late half of the negative ERP effect time window. *P* values refer to pairwise two-tailed *t*-tests.

Voluntary selection of task sets: An investigation with functional magnetic resonance imaging

4.2.7

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The prefrontal cortex (PFC) is thought to play an important role, especially for our ability to orchestrate thoughts and actions in accordance with internal goals. In experimental psychology, cognitive control has been investigated using the so-called task-switching paradigm. In this paradigm, participants have to selectively adapt their behavior to different situations and tasks. Most importantly, participants are always unequivocally told what to do and cannot deliberately decide, which task to perform. This leads to the question of whether the task-switching paradigm is suited to investigate active control processes.
Methods. The present fMRI study aimed at investigating processes which are relevant when participants (n = 22; 12 female) themselves can decide which task to perform. Four simple discrimination tasks were used. The number of tasks to choose from was varied between a non-choice (1 degree of freedom; DF) and two choice conditions (2 DF or 3 DF).
Results. The behavioral results revealed a difference for the choice conditions versus the non-choice condition (874 ms vs. 829 ms). No selection-specific difference between choice conditions was obtained (3 DF vs. 2 DF). The fMRI results corroborated these findings (Figure 4.19). The difference between choice conditions versus the non-choice condition revealed activations in the anterior midcingulate cortex (aMCC) and in the posterior parietal cortex (PPC).
Discussion. The findings indicate that distinct brain areas are involved in the free selection of abstract task set information in an all-or-none fashion. We propose that the PPC subserves the visual attentional selection of task sets. Finally, the aMCC is assumed to play a substantial role for the voluntary selection of the task set. This finding is in line with results providing evidence for the aMCC to be involved when we exercise our volition.

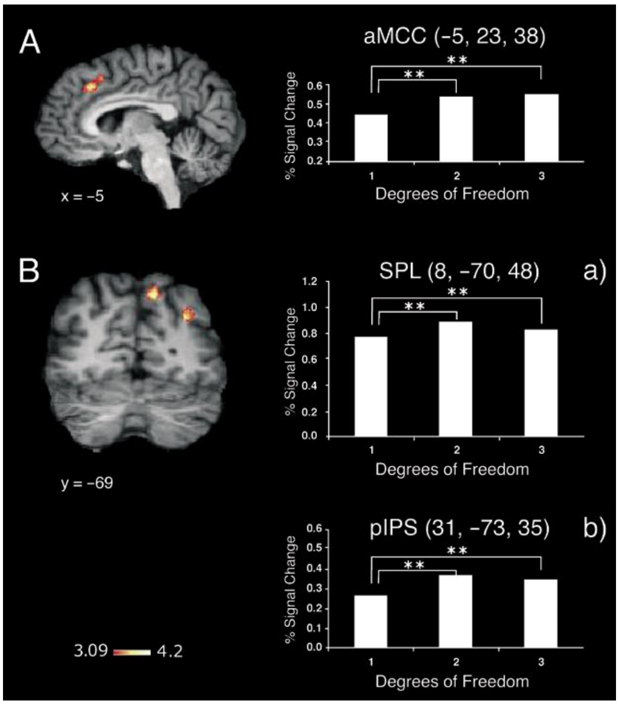

Figure 4.19 Main contrast of choice (Df 2 ∪ Df 3 > Df 1). (A) Sagittal plane showing activity in the left anterior midcingulate cortex (–5, 23, 38) and the corresponding percent signal change for Df 1–3; (B) Coronal plane showing activation in the right SPL (8, –70, 46) and the right pIPS (31, –73, 35); (B) a) The corresponding percent signal change for the SPL for the Df 1–3; (B) b) The corresponding percent signal change for the pIPS for the Df 1–3.

4.2.8 Prefrontal activation due to Stroop interference increases during development – An event-related fNIRS study

Schroeter, M.L., Zysset, S., Wahl, M. & von Cramon, D.Y.

The Stroop color-word task has been a classic measure of frontal lobe function. The aim of our study (Schroeter et al., 2004) was to investigate neural processes underlying cognitive development in the frontal lobe from childhood to young adulthood with functional near-infrared spectroscopy (fNIRS).

Oxyhemoglobin increased and deoxyhemoglobin decreased more during the incongruent compared with the neutral condition in the left lateral prefrontal cortex of children, and on both sides of the lateral prefrontal cortex in adults. In children, the hemodynamic response started roughly 3 s after trial onset, and peaked at ~8 s. In adults, the hemodynamic response occurred earlier. It started ~1 s and peaked at ~6 s after stimulus onset.

A correlation analysis between age, and the hemodynamic Stroop interference effect yielded a rising brain activation, and hence hemodynamic response in the dorsolateral prefrontal cortex with development (Figure 4.20). Regarding behavioral data, aging led to a decreasing interference effect of reaction time, which was correlated with increasing brain activation. Error rate did not change with development.

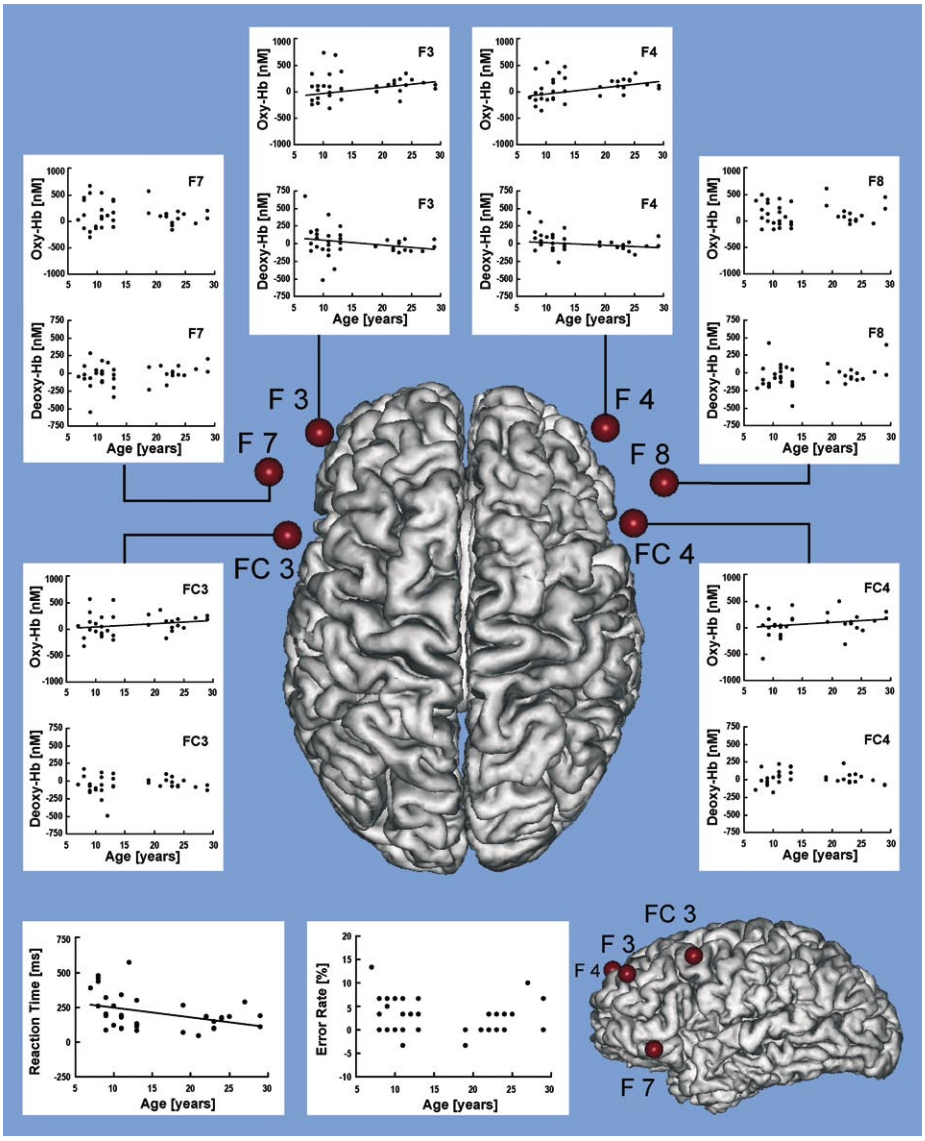

Figure 4.20 Impact of age on behavioral, and hemodynamic interference effect (incongruent minus neutral condition, respectively). Hb = hemoglobin. Regression lines are shown only, if the correlation analysis yielded significant results. Red spheres correspond with optode positions mapped onto an adult reference brain.

In summary, the interference effect of reaction time declined with aging in correspondence with previous behavioral studies indicating that young children have more difficulty than young adults in screening out interfering stimuli. Children (and adults) utilized the left lateral prefrontal cortex to cope with Stroop-related interference consistent with the verbal nature of the Stroop task. Activation in the dorsolateral prefrontal cortex increased during development, which is paralleled by a specifically decreasing interference effect of reaction time. Results agree with other neurodevelopmental studies of executive functions. Because performance matures in the tasks at different time periods (Go/NoGo ~12, stop 13–17, Stroop ~17–19 years of age, working memory into adulthood) conducting imaging studies with these paradigms opens a window to the neurodevelopment of executive functions. Results suggest that the developmental trajectory of cognitive processing needed for the Stroop task is characterized by increasing ability to recruit additional frontal neural resources.

4.2.9 Can neuroscience tell a story about intuition?

Volz, K.G. & von Cramon, D.Y.

According to the Oxford English dictionary, intuition is "the ability to understand or know something immediately, without conscious reasoning". Most people would agree that intuitive insights appear as ideas or feelings that subsequently guide our thought and behavior. However, the specific cognitive processes underlying intuitive decisions are not clear yet. One possibility of approaching this question is to incorporate neuroscientific results. Yet, until today, there has been a lack of imaging studies investigating the neural architecture of intuitive decisions, which is probably due to the rather blurry definition of this concept. One way out may be to consider the results of imaging studies investigating those cognitive processes underlying decisions that are reached without conscious reasoning, such as implicit memory, implicit learning, or feeling of knowing (FoK), so as to determine a potential common network.

The study on implicit learning has been dominated by a single paradigm, priming. Brain imaging data using the priming paradigm converge on the conclusion that modality-specific priming is mediated by an activation reduction in the corresponding modality-specific brain region (e.g., Bergerbest et al., 2004; Buckner et al., 1995; 1998; Squire et al., 1992).

The study on implicit learning has been dominated by two paradigms, the serial reaction time (SRT) task (Nissen & Bullemer, 1987) and the artificial grammar learning (AGL) task (Reber, 1967). A large body of research using the standard SRT or slightly modified versions observed activation within the striatum, a nuclear complex belonging to the basal ganglia, during implicit sequence learning (e.g., Aizenstein et al, 2004; Hazeltine et al., 1997; Rauch et al., 1998). However, following studies could show that striatal activation does not specifically reflect the unconscious component of the learning task as the striatum was observed to be comparably activated during explicit learning (e.g., Aizenstein et al., 2004; Willingham et al., 2002). Studies investigating implicit learning by means of the AGL are rather sparse and beyond inconsistent: When contrasting grammatical with non-grammatical items, Lieberman et al. (2004) observed significant activation within the basal ganglia, medial temporal lobe and inferior frontal cortex (IFG), whereas Skosnik et al. (2002) observed significant activation within superior occipital gyrus and fusiform gyrus. When comparing successfully with unsuccessfully discriminated items, significant activation was observed within superior occipital gyrus, angular gyrus, precuneus, and middle frontal gyrus (Skosnik et al., 2002).

Comparably inconsistent are the findings on the neural correlates of FoK. Generally, in these studies, subjects are asked to judge their FoK the correct answer when presented among alternatives for items where they failed to recall the answer. FoK-related activation was observed within the left IFG, dorsolateral and medial prefrontal gyrus, posterior parietal cortex, and ventromedial prefrontal cortex (Kikyo et al., 2002; Maril et al., 2003; Schnyer et al., 2005).

Together, the synopsis of imaging studies on decisions that are reached without conscious reasoning did not reveal a specific neural network. Hence, facing the current situation, it is suggested to either develop specific 'intuitive' paradigms, or to advance existing behavioral paradigms on intuitive decisions, so as to implement them in an fMRI environment. In our view, the paradigms used by Bowers et al. (1990) appear very promising (i.e., Waterloo Gestalt Closure Task and Dyads of Triads Task) and also AGL. Future research will show whether the concept of intuition is tenable, or whether it has to be defined subject to the specific situation.

4.2.10 The neural implementation of multi-attribute decision-making: A parametric fMRI study with human subjects

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Decision-making is not a unitary entity, but rather involves a series of interdependent processes. Decisions consist of a choice between two or more alternatives. Within the complex series of decisional processes, at least two levels can be differentiated: A first level of information integration (process level), and a second level of information interpretation (control level), leading to a subsequent motor response or cognitive process. In a single trial fMRI study, we implemented a simple decision-making task where subjects had to decide between two alternatives represented on five attributes. The similarity between the two alternatives was varied systematically in order to achieve a parametric variation of decisional effort. For easy trials, the two alternatives differed significantly in several attributes, whereas for difficult trials the two alternatives differed only in small details.

The fMRI results show a distributed neural network related to decisional effort. This network includes the left and right frontolateral cortex, the superior parietal lobe, the posterior medial frontal cortex, the anterior insula, as well as the caudate nucleus. Regions with early onset and steady increase in signal intensity are the presupplementary motor area (preSMA) and regions along the left intraparietal sulcus (IPS; see Figure 4.21). They are constantly working on integrating the attribute information and processing additional aspects of the two alternatives, and thus show a steadily increasing BOLD response. We argue that these regions subserve the process-level of decision-making. A second group of regions exhibits a delayed onset of the BOLD response. These regions include the left and right inferior frontal sulcus (IFS), the left insula as well as the anterior IFS. We suggest that these regions are related to the control-level of decision-making, i.e., a level which is conceived of as subserving the control of subprocesses. A third characteristic time course of the signal could be observed in the left inferior frontal junction area (IFJ). Here, the BOLD signal had an early onset, but saturated after 6 seconds. The IFJ is activated right from the beginning, but only for a short period of time after each presentation of an additional attribute. The present paradigm makes it possible to distinguish between the underlying cognitive processes based on the differences in the temporal dynamic of the BOLD signal.

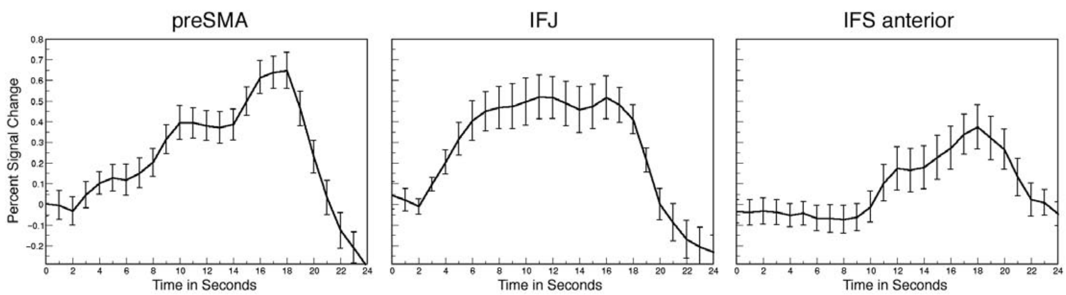

Figure 4.21 Group-averaged time courses for 3 specific regions of interest. The signal was averaged across the levels of similarity and the resting baseline was subtracted. The preSMA shows an example of an early onset and steady increase, the IFJ of an early onset and early saturation. The anterior IFS is an example of a delayed hemodynamic response.

Brain correlates of aesthetic judgment of beauty

4.2.11

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Functional MRI was used to investigate the neural correlates of aesthetic judgments of beauty. Participants performed evaluative aesthetic judgments (beautiful or not?) and descriptive symmetry judgments (symmetric or not?) on the same stimulus material. Symmetry was employed, because aesthetic judgments are known to be often guided by criteria of symmetry. Novel, abstract graphic patterns were presented to minimize influences of attitudes or memory-related processes, and to test effects of stimulus symmetry and complexity. Behavioral results confirmed the influence of stimulus symmetry and complexity on aesthetic judgments. Direct contrasts showed specific activations for aesthetic judgments in the frontomedian cortex (BA 9/10), bilateral prefrontal BA 45/47, and posterior cingulate, left temporal pole and the temporo-parietal junction. In contrast, symmetry judgments elicited specific activations in parietal and premotor areas subserving spatial processing. Interestingly, beautiful judgments enhanced BOLD signals not only in the frontomedian cortex, but also in the left intraparietal sulcus of the symmetry network. Moreover, stimulus complexity caused differential effects for each of the two judgments types. Findings indicate aesthetic judgments of beauty to rely on a network partially overlapping with that underlying evaluative judgments on social and moral cues, and substantiate the significance of symmetry and complexity for our judgment of beauty.

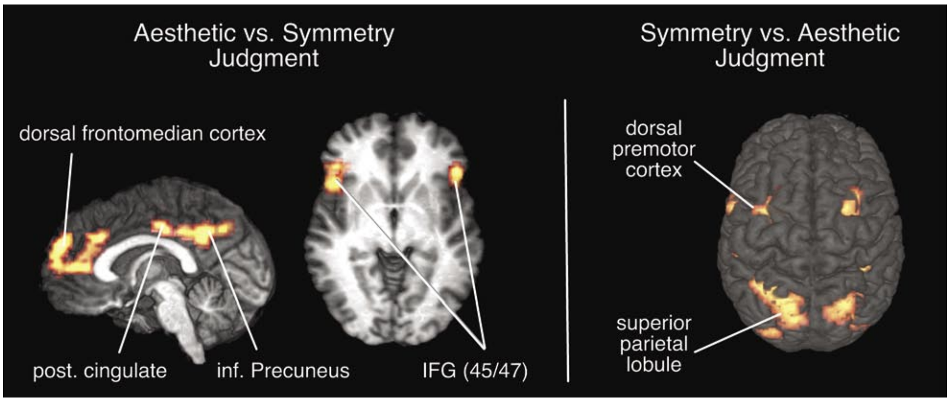

Figure 4.22 Group-averaged (n = 15) statistical maps of significantly activated areas for aesthetic judgments as opposed to symmetry judgments (left panel) and for symmetry as opposed to aesthetic judgments (right panel). Z-maps were thresholded at $z = 3.09$ ($p < 0.05$ corrected).

The functional neuroanatomy of text comprehension

4.2.12

Ferstl, E.C., Siebörger, F.T. & von Cramon, D.Y.

Language comprehension in context requires integration across sentence boundaries. A number of our own fMRI studies as well as reviews of the small, but growing literature on this topic have shown a network of brain regions including, but not restricted to the perisylvian language cortex to be consistently involved (Ferstl, in press a). An example for a typical result is displayed in Figure 4.23 (cf. Ferstl & von Cramon, 2005). Despite the claim of the right hemisphere being particularly important for text comprehension and pragmatic language interpretation, the network is clearly left dominant. The most important regions are the anterior temporal lobes (aTL) bilaterally, and the dorso-medial and parieto-medial cortices. When inspecting more specific subprocesses of text comprehension, a functional interpretation of the participating regions becomes feasible. In a study on situation model updating (Ferstl et al., 2005), the right anterior temporal region was sensitive to the consistency of information on a global text level. Thus, the aTL seems to be engaged during the on-line integration of words into the accumulating text representation.

When the target information concerned an emotional aspect, activation in the ventro-medial prefrontal cortex was seen. This finding, similarly replicated in a study on verbal humour (Siebörger et al., 2004), indicates that the situation model representation immediately triggers content-specific processes. When the target information concerned a chronological aspect, a network of fronto-parietal regions indicative of executive functions was found. Finally, the integration of emotional information into the situation model elicited activation in the dmPFC, once more replicating this area's importance for non-automatic inference processes during text comprehension (cf. Siebörger et al., 2003).

These and related results are a starting point for further investigating the properties of the extended language network. More fine-grained linguistic distinctions, such as anaphoric reference (Ferstl & Siebörger, in press), as well as their interaction with content variables can be studied. Neuroanatomical questions of interest include the overlap with the brain regions implicated for Theory-of-Mind processes (Ferstl, in press b), or, more generally, a domain-independent functional attribution of the participating regions. However, independent of the specific functional description, the convergence of results from studies using coherence judgment paradigms, situation model updating, the processing of verbal jokes, and task-induced coherence processes, establishes the dmPFC in particular as crucial for text comprehension across the sentence boundary. This result is important for neuropsychological theories of text comprehension and might aid in the diagnosis and treatment of brain injured patients with non-aphasic language deficits (Ferstl & von Cramon, 2005).

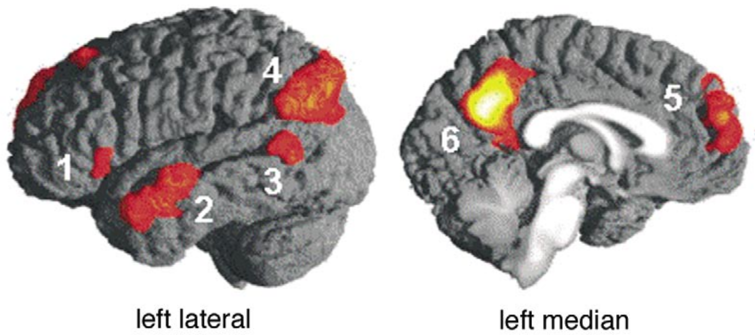

Figure 4.23 The extended language network illustrated using the results of an experiment on inference processes (Ferstl & von Cramon, 2002; 2005). The regions in the left hemisphere are the inferior frontal gyrus (1), the anterior temporal lobe (2), the posterior temporal sulcus (3), and the inferior parietal lobe (4). In the medial surface of the left hemisphere, the dorso-medial prefrontal (5) and the posterior cingulate cortex (6) are shown.

4.2.13 The role of attention to duration and order in abstract stimulus sequences

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

Experimental evidence suggests that the human lateral premotor cortex is involved in the processing of both pragmatic and dynamic properties of our environment. In contrast to pragmatic properties, which inhere in everyday artifacts, dynamic stimulus properties describe even abstract stimuli and refer either to their temporal duration (interval properties) or to their temporal order (ordinal properties). However, an open question remains regarding whether attention to dynamic properties is indeed a necessary prerequisite for premotor activation during processing of abstract stimuli. Alternatively, mere exposure to such properties could suffice, even if they were task-irrelevant. The present study used functional magnetic resonance imaging to address this question.

We presented sequences of abstract stimuli and instructed participants to perform three different forced-choice tasks on these stimuli, either on the basis of their duration, object-related, or spatial properties. Stimulus sequences followed either local transitions rules or were random, but these aspects were task-irrelevant. If attention to dynamic properties is not a necessary prerequisite for premotor involvement in the processing of abstract stimulus sequences, but mere exposure to them suffices, we expected performance in all three forced-choice tasks to elicit premotor activation during the presentation of ordered sequences, but not during the presentation of random sequences. If, alternatively, it is a necessary prerequisite, we expected only the forced-choice task based on stimulus duration to engage premotor areas, because duration is a dynamic property conveyed by each single stimulus. Data clearly confirmed the second hypothesis. We, therefore, conclude that attention, but not mere exposure, to dynamic properties suffices to engage human lateral premotor cortex in abstract stimulus processing.

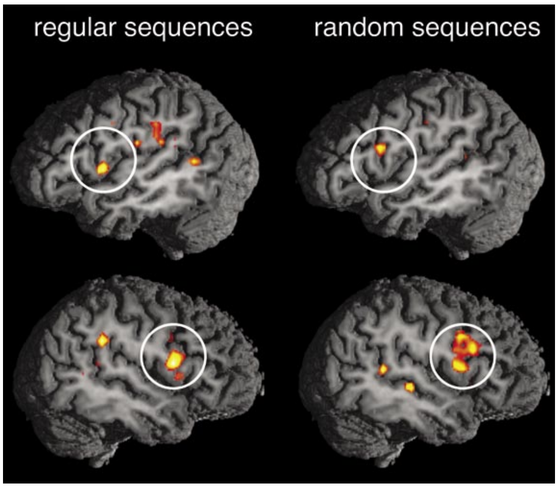

Figure 4.24 Group-averaged z-maps (n = 17, statistical threshold $z = 3.09$, $p < 0.05$ corrected) for the discrimination tasks based on duration as in contrast to those based on objects and positions. This effect did not depend on sequential regularity. Overall, premotor activation was not affected by exposure to regularity of stimulus sequences, but only by attention to duration.

4.2.14 Action-perception coupling in human lateral premotor cortex: fMRI evidence for a habitual pragmatic body map

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

Human and animal data support the view that the premotor cortex (PM) serves as a sensorimotor interface as this region is modulated by both body movement and mere attention to stimulus properties. Using functional magnetic resonance imaging (fMRI), the present study set out to test the correspondence of premotor correlates of motor action and perceptual attention following the habitual pragmatic body map account. This account holds that correspondence between action and attention is ruled by habituation such that, e.g., both spatial attention and a reaching action engage the same premotor subregion. Importantly, this is suggested to be true even for attending to stimuli not assigned a particular action or pragmatic meaning in everyday life. We employed attentional serial prediction tasks on spatial, object and rhythmic properties, which are known to engage PM. These properties would habitually call for premotor areas involved in reaching, grasping and articulation, respectively. Consequently, serial prediction tasks were compared to motor imagery of arm, hand and mouth movements. Behavioral data show that the participants were able to perform motor imagery. Both imagined and executed movement times recorded outside the scanner, reflect the different biomechanical constraints of the movements, with arm movements taking longest and mouth movements taking shortest (Figure 4.25, left panel). The fMRI results confirm the anatomical hypotheses derived from the habitual pragmatic body map account. As expected, prediction of positions specifically engaged the dorsal PM bilaterally, prediction of objects specifically engaged left superior ventral PM, and prediction of rhythms specifically engaged the inferior ventral PM bilaterally. Similarly, arm motor imagery specifically engaged the left dorsal PM, while hand motor imagery specifically engaged the left dorsal PM and the left superior ventral PM. The latter area was more strongly engaged during hand imagery as compared to arm motor imagery, but not as compared to mouth motor imagery. Mouth motor imagery specifically engaged the inferior ventral

PM, bilaterally. Premotor peaks of activation for all six tasks are depicted in Figure 4.25 (right panel). Moreover, the analysis of the maximal percent signal change extracted from these regions of interest revealed direct correspondence for mouth actions and rhythm attention (inferior ventral PM) and arm imagery and spatial attention (dorsal PM). Hand imagery activated both superior ventral PM and dorsal PM, thus suggesting a correspondence with both object and spatial attention.

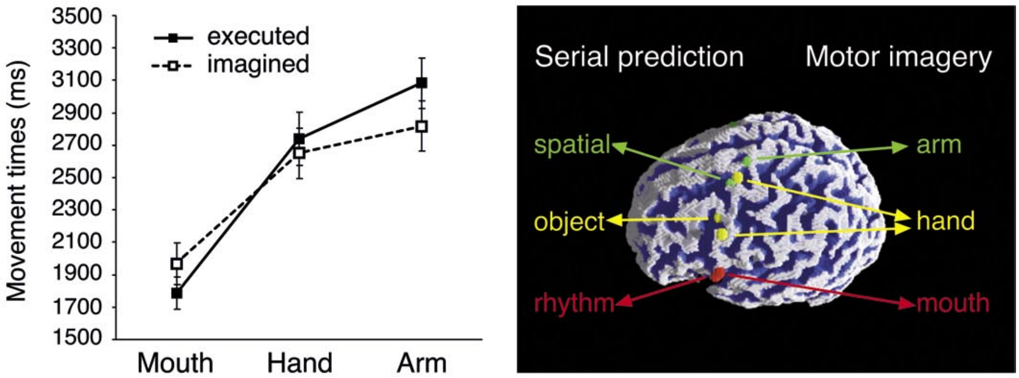

Figure 4.25 Left: Mean movement times for executed and imagined movements. Right: Peaks of property-specific activation in serial prediction and effector-specific activation in motor imagery tasks.

COGNITIVE PSYCHOPHYSIOLOGY OF ACTION 5.1

The Independent Junior Research Group "Cognitive Psychophysiology of Action" was active until the end of June 2005. In December 2004, the group leader, Edmund Wascher, obtained a full professorship at the Leibniz Research Centre for Working Environment and Human Factors in Dortmund, Germany. Despite the official break-up of the group in the middle of 2005, he continued to supervise ongoing Ph.D. projects.

The main goal of the group was to investigate the mechanisms involved in the transformation of (primarily spatial) information into action and their cortical correlates. Both behavioral and electrophysiological data were reported in a number of studies. The specific foci of the group were to (a), evaluate the properties of event-related components of the EEG (ERPs) in terms of their usability for the investigation of visuo-motor processing, and (b), to understand the mechanisms involved in the transformation of incoming information into action by studying the influence of irrelevant spatial information on behavior.

5.1.1 Event-related asymmetries of the EEG as indices for the investigation of spatial processing

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One purpose of cognitive science is to uncover the steps of information processing between input variables and observable behavior. With classical methods of experimental psychology, however, only the initial setting of the experiment (i.e., the manipulated variables) and the outcome (i.e., the overt behavior) are accessible. Cognitive psychophysiology extends this approach by introducing additional measures that are independent from overtly observable behavior. In particular, the potentially high temporal resolution of event-related potentials (ERPs) of the EEG, which markedly surpasses the resolution achieved by more recent imaging techniques, can provide important temporal information about the stream of information processing. Measures in cognitive psychophysiology that comply with these conditions should be: Attributable to a well-defined cognitive process, as well as predictive for behavior whenever that cognitive process is assumed to determine behavior in a particular task.

Wolber and Wascher (2005) have demonstrated that posterior event-related asymmetries of the EEG are reliable temporal markers for visuo-spatial processing. The extraction of the asymmetric portion of the EEG signal (by calculating contra-ipsi difference waves; see Figure 5.1) reveals a well-defined peak called posterior contralateral negativity (PCN). In three experiments, the variability of the PCN latency was closely related to behavior. In visual search, PCN latency varied in the same direction as response times with the number of distractors. These effects, however, were smaller than the effects observed in response times, indicating that the process underlying the PCN might have contributed to, but did not determine, the response time effects. In contrast, in attentional cueing tasks and a stimulus localization task where stimulus detection was the process of primary interest, PCN latency varied by the same amount as response times.

The method outlined above turned out to be very useful in evaluating cognitive constructs. In a follow-up study (Wascher, 2005), spatial S-R correspondence (Simon effect) was tested with the very same stimuli as depicted in Figure 1. The Simon effect is assumed to be the consequence of an automatic response activation evoked by the processing of the irrelevant stimulus location. Such activation has been reported to decline when responses become slower. Consequently, the Simon effect decays over time. However, it remains unclear when this activation starts and by what process it is initialized. Wascher (2005) showed that response activation is temporarily linked to the peak of the PCN. The Simon effect steadily decreased as a function of the time between PCN peak and the manual response, but was unrelated to the moment of stimulus onset.

Although posterior stimulus-evoked asymmetries (PCN) have been repeatedly described in connection with the allocation of attention, they are not consistent with a physiological view of attentional control. While the latter process is assumed to be performed by a fronto-parietal network, PCN is most probably generated in extrastriate visual areas. To achieve a deeper insight into the cognitive correlates of the control of visual attention, inhibition of return (IOR) was investigated with ERPs (Wascher & Tipper, 2004). IOR is defined as follows: Simple responses to non-informatively cued spatial stimuli can be delayed whenever a cue has been briefly presented at the location of the subsequent target. This phenomenon might be due to a mechanism that inhibits irrelevant information. However, with sustained cues, no inhibition is observed. It has been hypothesized that in the latter task inhibition is masked by an

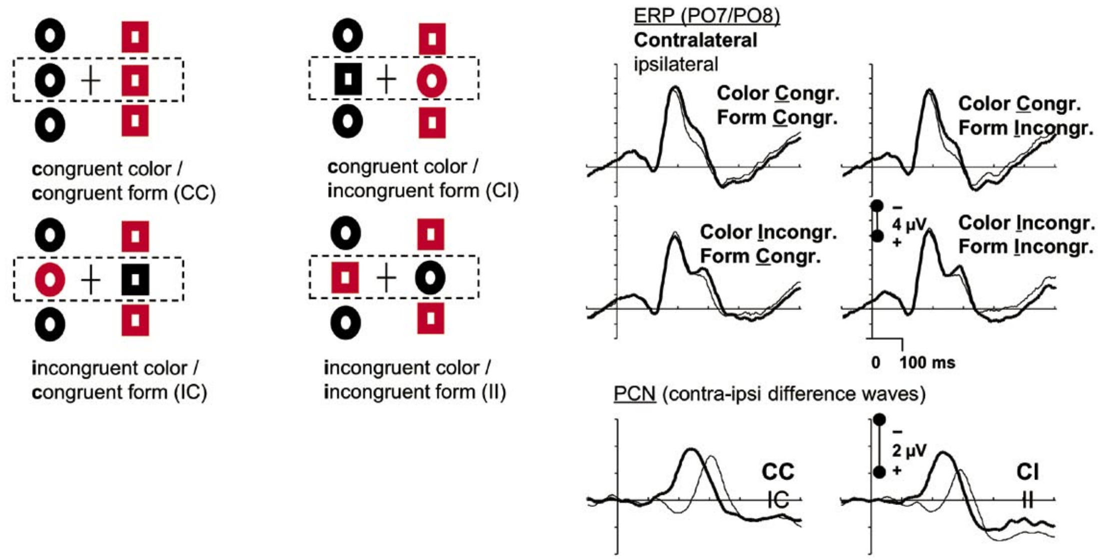

Figure 5.1 In the depicted task, subjects had to detect an element of a particular color in the middle line of a six-element stimulus array (left column). Whenever color was arranged congruently, stimulus detection was faster. Response time differences were comparable to the differences in peak latency of the PCN (right column, lower panel). From the regular ERP plot (upper panel), the temporal properties cannot be extracted.

excitation process. ERP measures supported the inhibition-excitation account: (A), P1 suppression, assumed to reflect inhibition, was observed for all targets presented at a cued location; (B), A later negative component (Nd250) increased with sustained cues, and hence might reflect the excitation process; (C), A negative component at right parietal electrode sites (Nd310) appeared only when IOR was observed. Thus, ERP measures seem to be able to distinguish between attentional control (Nd-components) and the expression of attention in visual areas (PCN), which is consistent with recent theories of visual spatial attention (Shipp, 2004). Further research on this topic is under way.

The method reported for calculating a PCN (contra-ipsi difference waves, also known as event-related asymmetries/ERLs of the EEG) has been extended for many years now to the measure of response activation. The corresponding component is the lateralized readiness potential. Even when investigating more complex representations of space, as may be necessary for accurate pointing, this component can be applied to gain more insight into underlying processes. A study by Bernd et al. (2005) addressed the question of whether horizontal pointing direction and the predictability of pointing direction modulated cortical asymmetries. To vary pointing direction predictability, targets were displayed either randomly at one of nine different positions on a screen ('random') or at the same horizontal position in five subsequent trials ('sequenced'), while vertical positions varied randomly. ERLs varied with pointing direction. This was true across changes in target eccentricity and pointing distance. Foci of the ERLs were in premotor and posterior parietal cortex, reflecting the critical involvement of these areas in the control of visually guided reaching. Direction predictability reduced the parietal ERL before pointing onset, probably reflecting a lesser effort in visuomotor transformation.

The distinct allocation of pointing movements to different locations in the parietal reach region and the possibility to investigate such movements with the EEG provided the basis for a study that tried to localize sources of EEG activity by repetitive application of an Independent Component Analysis (Große-Wentrup et al., 2005). This method appears to be a promising tool for complex information transmission in brain-computer interfaces.

5.1.2 Mechanisms involved in spatial visuo-motor integration

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Spatial stimulus-response correspondence (Simon effect; see *above*) is an often-used tool for investigating visuo-motor integration. The application of electrophysiological measures – and in particular the measurement of event-related EEG asymmetries – has been demonstrated to be very useful for the understanding of underlying mechanisms and their properties. As already mentioned above, PCN latency can help to track the assumed motor activation process over time (Wascher, 2005). Moreover, in a study that investigated attentional and intentional cueing in this task (Wascher & Wolber, 2004), PCN helped to clear up an inconsistency in the experimental literature. Advance information about the location of a stimulus (attentional cueing) does not affect the Simon effect, whereas advance information about the side of a response (intentional cueing) enhances the Simon effect. This dissociation was taken as evidence for the involvement of response selection in generating the effect. ERPs, however, indicated that the response-related mechanisms causing the Simon effect remain widely unaffected by advance information. Clear evidence for both response preparation and for attentional shifts in the cue-target interval was found. However, ERPs suggested that the increment of the Simon effect by intentional cueing might be due to perceptual factors rather than to an alteration of mechanisms involved in the generation of a regular Simon effect. This notion was subsequently evaluated by replacing the originally used visual cues by tactile ones (Buhlmann & Wascher, in press). In the latter study, the increase of the Simon effect with tactile intentional cues no longer occurred.

These findings have important implications for the discussion of which cognitive processes are affected by irrelevant spatial information. Following a line of argumentation that was initiated by Wascher et al. (2001), visuo-motor integration mechanisms were posited to rely on two separate sources: (A), a fast and transient visuo-motor activation that is initially observed with natural hand postures, and (B), a cognitive and long-lasting interference that may affect response selection, which, in the original study, became evident with crossed hands. The dissociation between the two assumed mechanisms was based on the calculation of effect functions. By segmenting the sorted response time distributions for corresponding and non-corresponding trials into 10 even bins, the size of the Simon effect can be explored as a function of the underlying response time.

When comparing Simon effects evoked by horizontal and vertical stimulus-response arrangements (Wiegand & Wascher, 2005), effect functions as well as LRP difference waves provided evidence for a fast, but transient influence of horizontal, and a slow, but stable influence of vertical spatial stimulus features on performance. Moreover, effect functions were additive for the two spatial dimensions (see Figure 5.2). These RT effect relations were also extended to situations in which performance was manipulated either by time pressure or by the addition of a secondary task. Thus, the data strongly indicate that there are two temporally dissociable mechanisms involved in generating the Simon effect for horizontal and vertical S-R relations.

These results, however, were at odds with data previously presented in the literature. Some studies reported decaying effect functions, indicating fast visuo-motor transformation for vertical stimulus-response arrangements as well. Thus, a series of experiments was performed to address the difference between studies that showed decaying effect functions for the vertical dimension and those that showed steadily increasing effects (Wiegand & Wascher, in press a, b). It turned out that decaying effect functions were only present for the vertical dimension when the S-R mapping was randomly assigned from trial to trial. Since such decaying effect functions were hitherto only observed when anatomical factors of

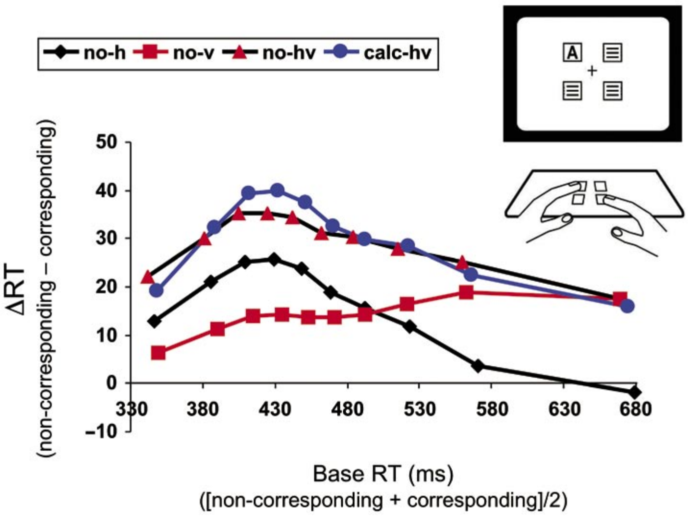

Figure 5.2 Effect functions observed for vertical and horizontal S-R correspondence. Stimuli (see upper right corner) could appear at one out of four positions. The response positions could correspond either horizontally, vertically, on both spatial dimensions or on neither dimension to the stimulus location. The effect for full correspondence (red triangles) was equal to the sum of vertical and horizontal correspondence effects (blue circles) across the entire response time distribution.

the response were the primary features of the response representations, Wiegand and Wascher (in press a; b) claimed that the variation in stimulus-response mapping forced subjects to continuously reconfigure their response system in such a way as to rely on anatomical representations. Additional experimental data supported this notion.

During the last two years, research activities in our group have progressed rapidly. We have further investigated music-syntactic processing in adults (5.2.1), and initiated new projects on music-syntactic processing in children (5.2.2) and patients. In particular, we expanded our research on music-semantic processing as well as on the investigation of emotion with music (5.2.3, 5.2.4). Another extensive project was launched to investigate the functional architecture of working memory for linguistic and musical information (5.2.5). The particular aim of this project is to investigate similarities and differences of working memory components engaged for the processing of language and music, also trying to elucidate possible effects of musical training on auditory working memory operations.
A considerable number of our studies were carried out as cooperative projects together with the Neuropsychology Department – these studies are concerned with the relation of language and music, and with the overlap of, as well as with the differences between neural resources underlying the processing of language and music (5.2.6, 5.2.2).
An important step forward was the initiation of projects on the investigation of action with music. Within a cooperative project together with the Psychology Department, we are now able to combine the expertise in both the action and the music domain to gain a better understanding of the processes underlying music production.
An important theoretical contribution of our group was the development of a model on the neural basis of music perception (Figure 5.3). One new aspect of our model is that, unlike any previous models, processing stages of music-syntactic and music-semantic information processing are integrated. Over the last years, our group has put considerable effort in investigating the neural correlates of music-syntactic and music-semantic processing, and although these aspects are most basic for the perception of music, they have been neglected in previous models. Another new aspect of our model is the conceptualization of effects of music perception on emotion, the autonomic nervous system and the immune system. Future research in this area will hopefully reveal better insights in the beneficial effects that music perception, and music production, potentially has on human health.

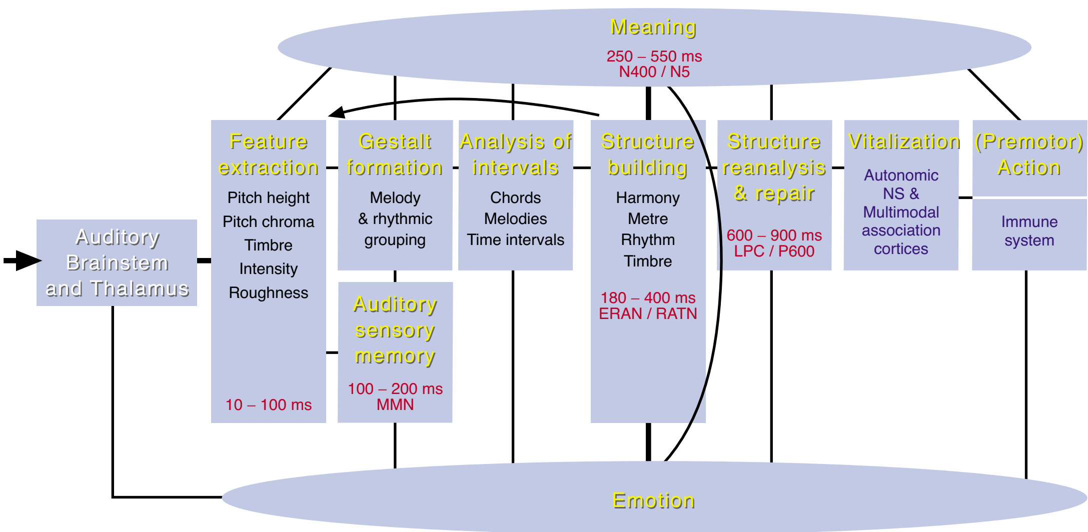

Figure 5.3

5.2.1 Processing of musical syntax – Tonic *versus* subdominant: An ERP study

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Bigand, Poulin and collaborators (2003) presented participants with eight-chord piano sequences, in which the last chord (target) was either a regular tonic chord or a less regular subdominant chord. Results showed that both musicians and non-musicians processed target chords faster, and more accurately, when target chords were regular tonic chords (compared to less regular subdominant chords). The neural mechanisms underlying these priming effects are still not well understood. Studies investigating the processing of harmonic structure with five-chord-sequences using ERPs found negative components elicited by irregular chords compared to regular chords (Koelsch & Friederici, 2003). In these studies, harmonically irregular chord functions elicited an early right-anterior negativity (ERAN), which is usually followed by an N5. However, other ERP studies also reported different results. In the study from Regnault and colleagues (2001), the last chord of eight-chord piano sequences was either a regular tonic chord or a less regular subdominant chord. The results showed that subdominant chords elicited a larger P300 than tonic chords. Thus, the results reported in previous ERP studies still lack convergence. The present experiment was designed as an attempt to understand this lack of convergence: The same type of irregularity (tonic *versus* subdominant) investigated by Regnault et al. (2001) was evaluated in an experimental design similar to the ones used by Koelsch and collaborators (e.g., Koelsch et al., 2000), in which the target chords were not task-relevant. With this design, the less regular subdominant chords were expected to elicit an ERAN followed by a larger N5 compared to the regular tonic chords, with no occurrence of a P300. Finally, the amplitudes of both ERAN and N5 were expected to be larger for musicians than non-musicians (Koelsch et al., 2002). Results showed, firstly, no P300 – contrary to Regnault et al. (2001), who investigated the same harmonic violations (tonic *versus* subdominant). Secondly, the less regular subdominant chords elicited a larger N5 than the regular tonic chords. This N5-effect was, however, only significant for musicians and is taken to reflect processes of harmonic integration (which are possibly reminiscent of the semantic integration processes reflected by the N400 originally observed in the language domain). Finally, no ERAN was observed, probably due to the fact that the harmonic irregularity investigated in the present study was very subtle: The subdominant chords are not frank irregularities, but only slightly less regular than tonic chords, and thus presumably not salient enough to elicit an ERAN.

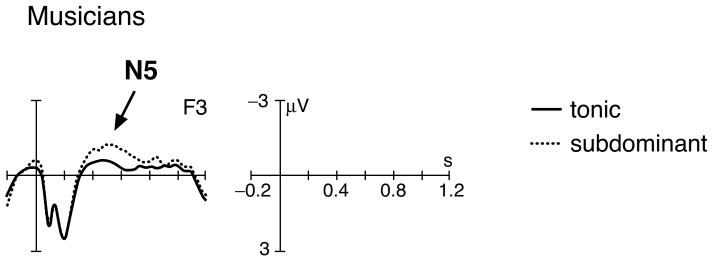

Figure 5.4

5.2.2 Musical training affects language-syntactic processing

Jentschke, S., Koelsch, S. & Friederici, A.D.

Language and music are human universals involving perceptually discrete elements that are organized in hierarchically structured sequences. The set of principles governing the combination of these structural elements into sequences may be denoted as syntax. There are two ERP components that reflect a violation of expectancies concerning syntactic regularities – the ERAN (early right anterior negativity) and the ELAN (early left anterior negativity). The ERAN is evoked by a violation of musical regularities, and the ELAN has been shown to reflect syntax processing in the language domain. The ERAN has been shown to be larger in adults with formal musical training (musicians), indicating that more specific representations of musical regularities lead to heightened musical expectancies. Moreover, there is evidence from adult data suggesting that both ERAN and ELAN are generated in overlapping brain regions. Therefore, we expected transfer effects between music and language due to shared processing resources, in particular. We investigated these issues in children, comparing children with and without musical training (11 years old) as well as children with or without language impairment (5 years old). Each child participated in two experiments, one music and one language experiment. In the music experiment, ERPs to chord sequences ending either on a regular (tonic) or an irregular chord (supertonic) were compared. In the language experiment, we used syntactically correct and incorrect sentences. In the 11-year-olds, an ERAN was elicited in both groups. The ERAN had a larger amplitude in musically trained children (see A in Figure 5.5), similar to effects of musical training on the ERAN amplitude which have previously been shown in adults. Importantly, the negativity elicited in response to a syntactic violation was also larger in the musically trained children (see B in Figure 5.5). Results show that neural mechanisms underlying syntactic processing are stronger, and develop earlier in children with musical training. Due to the overlap of neural resources engaged for music- and language-syntactic processing, it is conceivable that the superior development of the ELAN in children with musical training originates from the training of syntactic processes in the musical domain.

In the 5-year-olds, an ERAN was present in children with normal language development, but not in age-matched children with specific language impairment. That is, language impaired children also showed impairment in music-syntactic processing, again suggesting a close link between music- and language-syntactic processing. Results make it thoroughly conceivable that language impairment might be treated with music therapy.

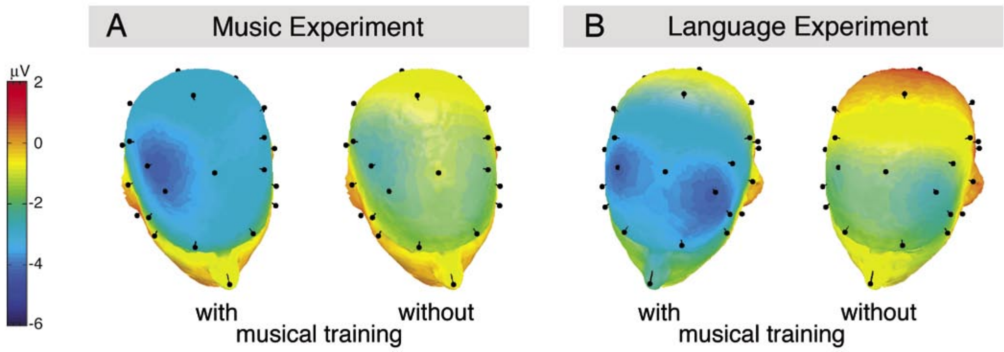

Figure 5.5

Emotional processing of harmonic expectancy violations

5.2.3

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The purpose of the present study was to investigate the effect of music-syntactic irregularities (which are perceived as expectancy violations) on emotions. Subjective response measures for tension and emotionality as well as electrodermal activity (EDA), heart rate (HR) and EEG were recorded from 12 musicians and 12 non-musicians to observe the effect of expectancy violations on subjective and physiological measures of emotions. Stimuli consisted of three matched versions of six Bach chorales, which differed only in terms of one chord. In the original composition, this chord was already mildly unexpected and we composed two further versions, in which this chord was harmonically more and less regular. That is,

the critical chord was harmonically either highly regular (and, thus, perceived as expected), or slightly irregular (mildly unexpected), or very irregular (very unexpected). The findings showed that tension, overall subjective emotionality and EDA increased with an increase in harmonic unexpectedness. Analysis of the event-related potentials (ERPs) revealed an early negativity for both the unexpected and the very unexpected harmonies taken to reflect the detection of the unexpected event. The early negativity in response to very unexpected chords was significantly larger in amplitude than the early negativity in response to merely unexpected harmonic events. The early negativities did not differ in amplitude between the two groups, but peaked earlier for musicians than for non-musicians. Both groups also showed a P3 component in response to the very unexpected harmonies, which was considerably larger for musicians and may reflect the processing of stylistic violations of Western classical music.
The present data have important implications: They show that irregular chord functions not only elicit brain responses related to music-syntactic processing, but also brain responses related to emotional processes. These responses were observed in musically trained as well as untrained listeners. In addition, our observations show early negativities in response to genuine compositions as these responses were elicited within chord sequences that were originally composed by Bach.

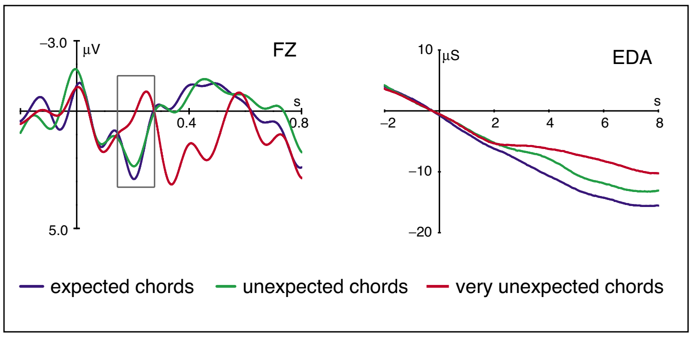

Figure 5.6 The left half shows the ERPs recorded at the FZ electrode in response to the three types of violations. The critical time window for the early negativities is marked by the box. The right half shows the skin responses, which demonstrate a clear increase in response to increasing harmonic unexpectedness.

5.2.4 Music and emotion: Electrophysiological correlates of the processing of pleasant and unpleasant music

Sammler, D., Grigutsch, M. & Koelsch, S.

The purpose of the present EEG study was to gain further insights into brain mechanisms underlying the processing of (un)pleasant, musically induced emotions by using the experimental paradigm of Koelsch and collaborators (2005). It was aimed at comparing (a) subjective ratings on the emotional valence experienced during (un)pleasant musical pieces, (b) heart rate changes while listening, and (c) neuroelectric oscillatory activity in order to identify neurophysiological correlates of emotional processing.
Eighteen non-musicians were presented with consonant musical excerpts and their electronically manipulated dissonant counterparts to induce pleasant or unpleasant emotions. Participants were asked to tap the metre with their right index finger while listening, and to rate their current emotional state on a six step scale after each musical piece. Silence periods served as baseline condition. For the quantitative characterization of EEG activity, power spectra were analyzed. Furthermore, heart rate was measured to investigate autonomic responses related to the experience of emotions during the musical stimuli.
We observed the classical triphasic pattern of heart rate response, and found this pattern to differ significantly between pleasant (consonant) and unpleasant (dissonant) musical pieces (Figure 5.7B). This difference was maintained throughout the musical piece and even increased towards the end of the excerpts (Figure 5.7A). This finding underlines that the applied paradigm provides a qualified tool to induce emotions in listeners while excluding effects of personal preference.
In the EEG data, pleasant musical pieces elicited an increase of Frontal midline (Fm) theta power compared to baseline (Figure 5.8). We surmise this effect to be generated in the anterior cingulated cortex (ACC), and assume that the activation of the ACC reflects a higher level of "emotional engagement" during the pleasant music: Emotional, autonomic, and attentional mechanisms are intimately linked in

the ACC, and the ACC appears to play a role for context-driven modulation of bodily arousal states, as well as for regulating cognitive and motor functions in relation to changes in emotional and motivational states. Importantly, the effect strength increased over the time of the presentation of a musical excerpt, leading to the idea that the temporal dynamics of emotion can be investigated by the use of spectral EEG analysis. In conclusion, the present findings emphasize the significance of heart rate changes as an index of individual emotional experience, and indicate that EEG is able to contribute to the understanding of human emotions.

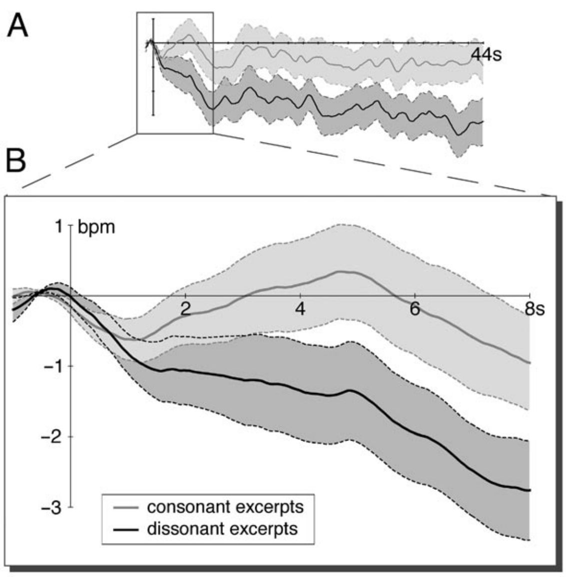

Figure 5.7 (A) Mean heart rate during the course of the musical pieces. HR decreased significantly more strongly during dissonant (unpleasant) compared to consonant (pleasant) pieces. Additionally, this deceleration intensified towards the end of the musical pieces. (B) The initial triphasic pattern of heart rate response differed significantly between consonant (pleasant) and dissonant (unpleasant) pieces (solid line: mean, dotted line/shadow: SEM).

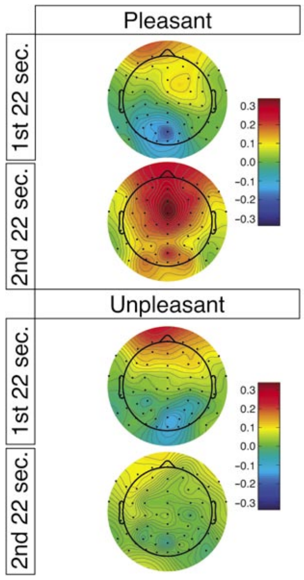

Figure 5.8 Relative theta power (compared to baseline) during the 1st and the 2nd half of pleasant and unpleasant musical pieces. Frontal midline theta power increases mainly towards the end of pleasant musical pieces, presumably reflecting a higher level of "emotional engagement".

5.2.5 Neural components of working memory in non-musicians and musicians – An fMRI study

Schulze, K., Zysset, S. & Koelsch, S.

Considering the differences and similarities in the processing of language and music, we designed a functional magnetic resonance imaging (fMRI) experiment to compare their organization and underlying neural networks of working memory (WM) using tonal and verbal stimuli. In addition, based on anatomical and functional differences between musicians and non-musicians, we were interested in the influence of musical expertise on the neural organization of WM.

Non-musicians and musicians listened to sequences of five auditory stimuli. Each stimulus consisted of a spoken syllable and a simultaneously presented sine wave tone. Subsequently, participants had to rehearse subvocally either the syllables (verbal condition) or the sine wave tones (tonal condition). Then, subjects had to indicate whether a probe syllable or probe tone had already been presented during the sequence. To compare a strategy-based with a non-strategic maintenance of tonal information in musicians, two types of tonal sequences were designed based on musicological rules: "key" sequences (all tones belong to one tonal key, and three of the tones belong to a triad) and "non-key" sequences (tones do not belong to one key).

Verbal and tonal WM in non-musicians. Non-musicians showed a superior performance for verbal compared to tonal stimuli. Our preliminary fMRI results show a remarkable overlap between the neural networks underlying WM for tonal and verbal stimuli. However, some areas were also specifically engaged, and/or more involved in verbal or tonal WM processes. For example, verbal rehearsal engaged Broca's area and the premotor cortex more strongly, whereas the left angular gyrus was more strongly involved during tonal rehearsal.

Tonal WM in musicians and non-musicians. Musicians performed significantly better than non-musicians. Additionally, musicians showed stronger activation of the left ventrolateral premotor cortex and the left inferior parietal lobe during the rehearsal of the tonal stimuli. This might either be an effect of different strategies, and/or the effect of use-dependent brain plasticity.

Key and non-key sequences in musicians. Only musicians showed a superior performance for key sequences compared to non-key sequences. In the fMRI data, this was reflected in a stronger activation of the right mid-dorsolateral prefrontal cortex during the rehearsal of key sequences, an area implicated in manipulating information during WM tasks.

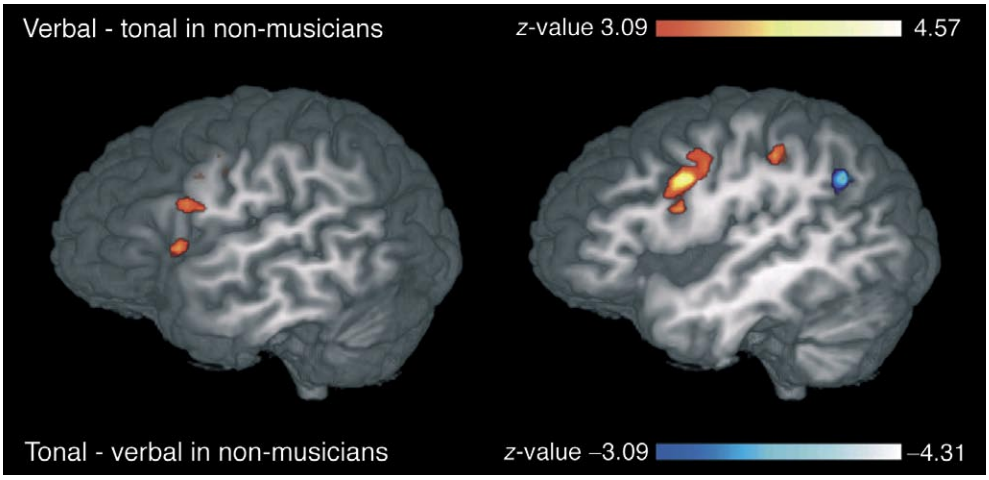

Figure 5.9 Comparison between verbal and tonal rehearsal in non-musicians.

5.2.6 Effects of selective attention on neurophysiological correlates of music and speech processing

Maidhof, C. & Koelsch, S.

Previous electroencephalographic (EEG) studies suggest a pre-attentive, automatic processing of syntactical information in music and language. These studies tested the effects of attention in experiments in which the processing of the syntactic structure was task-irrelevant or in which attention was directed to visual stimuli (e.g., participants played a video game, read a book, or watched a silenced movie).

The present study investigated effects of selective attention on two syntax-related event-related potential (ERP) components (ELAN and ERAN). Two auditory stimuli (speech and music) were presented simultaneously and participants were asked to strongly focus their attention either on music or speech. During the processing of music, music-syntactically irregular chord functions are known to elicit an early right anterior negativity (ERAN). During the processing of language, word-category violations (i.e., syntactically irregular words) elicit an early left anterior negativity (ELAN).

Results showed, firstly, that an ERAN was elicited even when participants focused attention strongly on simultaneously presented speech (and thus ignored the music). Secondly, the ELAN was elicited even when speech was ignored (i.e., even while participants focused their attention on the musical information). Thus, both ERAN and ELAN were elicited under strong ignore conditions showing that the neural processes underlying the generation of the two syntax-related components possess a remarkably high degree of automaticity.

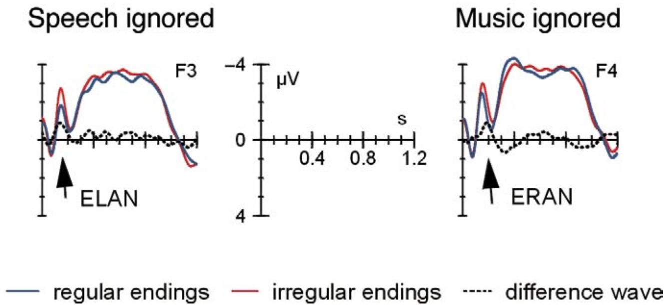

Figure 5.10 The left part shows the ERP's recorded at the F3 electrode when participants focused attention on the musical information and thus ignored speech. The right part shows the ERPs recorded at F4 electrode when music was ignored. The blue line represents the response after regular sentences or chord sequences, the red line after irregular sentences or chord sequences, and the black line depicts the difference waves. Even under ignore conditions, the violation of musical or linguistical syntax elicited the syntax-related component (ERAN and ELAN).

The Junior Research Group "Neurotypology" was established in June 2005 with the principal research aim of investigating and modeling cross-linguistic unity and diversity in the human ability to comprehend language. In essence, this endeavor is motivated by the apparently diverging conclusions of two linguistic subdisciplines that have hitherto been viewed as orthogonal to one another: linguistic typology and psycho-/neurolinguistics. While research in the former domain has revealed a striking amount of variability between the characteristics of the languages of the world (of which there are more than 6000), the latter has traditionally relied on the assumption that the cognitive and neural mechanisms supporting language processing are largely similar from language to language.

It is the aim of the neurotypological research program to examine how the insights on human language gleaned from these two very different perspectives can be reconciled with one another. To this end, we have adopted the working hypothesis that comprehension strategies may indeed differ considerably between individual languages and, moreover, that such differences may not always be straightforwardly predictable from surface characteristics of the languages in question. However, a second important assumption is that neurocognitive processing signatures – as revealed, for example, by ERPs or fMRI – may be used to classify cross-linguistic similarities or differences in how comprehension proceeds. In terms of such neurocognitive signatures, completely unrelated languages may show a higher similarity to one another than closely related languages. A comprehension-based "typology" of this kind can, therefore, provide fundamentally new insights into the unifying and diverging characteristics of languages and, thus, into the precise properties that uniquely characterize *human* language.

Ongoing research within the Neurotypology framework is based on the idea that language comprehension draws upon a set of basic – and, therefore, universal – mechanisms. These are, however, subject to substantial language-particular specialization that depends crucially upon the properties of the particular language in question. This hypothesis is currently being pursued in several domains, including the interaction between linguistic prominence hierarchies and language-specific linearization requirements (5.3.1) and mechanisms of incremental argument interpretation in typologically different languages (5.3.2). In addition, in order to examine more closely how electrophysiological patterns map onto functional interpretations, we are studying problematic cases of this mapping in grammatical function reanalyzes in German and pursuing alternative means of analysis for EEG data on language comprehension (5.3.3). Finally, a major focus also lies on the development of an adequate cross-linguistic model of language comprehension (Bornkessel & Schlesewsky, in press).

5.3.1 Broca's region and the linearization of prominence hierarchies

Bornkessel, I.D.[1], Grewe, T.[2], Zysset, S.[1], Wiese, R.[2], Friederici, A.D.[1], von Cramon, D.Y.[1] & Schlesewsky, M.[2]

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A great deal of research on the functional neuroanatomy of language comprehension has focused on Broca's region (comprising the pars opercularis and triangularis of the left inferior frontal gyrus, IFG). Within this tradition, it is commonly assumed that this cortical region plays a crucial role in the comprehension of ("non-canonical") sentences, in which the object precedes the subject, though interpretations differ as to the precise nature of the processes involved.

By contrast, recent results from German suggest that non-canonicity may not be the key to explaining pars opercularis activation. Thus, object-initial orders do not elicit increased activation in this region when the object-initial order is rendered unmarked by some other linguistic property (as in [1] or [2]).

[1] *Gestern wurde erzählt, dass dem Jungen die Lehrer auffallen.*
yesterday was told that [the boy]$_{DAT}$ [the teachers]$_{NOM}$ are-striking-to
'Yesterday, someone said that the boy finds the teachers striking.'

[2] *Dann hat ihm der Lehrer den Spaten gegeben.*
then has him$_{DAT}$ [the teacher]$_{NOM}$ [the spade]$_{ACC}$ given
'Then the teacher gave him the spade.'

In [1], the (nominative) subject of the clause is not the participant primarily responsible for the event in question, since it is a property of the boy whether he finds the teachers striking or not, rather than a state of affairs that the teachers can volitionally influence. Thus, the object-initial order allows for an independent preference to be upheld, namely that "Actors" should precede "Undergoers". Similarly, the object-initial order in [2] is licensed by the rule that pronouns should precede non-pronominal nominals independently of grammatical functions. In both cases, object-initial orders do not engender increased pars opercularis activation in comparison to subject-initial controls (Bornkessel et al., 2005, for 1; Grewe et al., 2005, for 2, see also Figure 5.3). A series of further experiments revealed a number of additional influences on pars opercularis activation, including *animacy* and *definiteness/specificity*. It is, therefore, apparent that the activation of the pars opercularis during sentence comprehension reflects the interaction between a variety of linguistic information types, rather than depending solely on the relative ordering between subject and object.

On the basis of findings such as these, we have recently formulated the "linearization hypothesis" of pars opercularis function (LH; Bornkessel et al., 2005; Grewe et al., in press). The LH assumes that languages must provide a *linearization* of a variety of different hierarchically structured information types on account of the inherently sequential nature of speech. While these hierarchies are typically grounded in general conceptual prominence of some description (e.g., Actors vs. Undergoers, old vs. new information etc.), languages differ with respect to how they have conventionalized the applicability of such information and, thereby, as to which distinctions determine word order. Therefore, the information types shown to correlate with differences in pars opercularis activation correspond very closely to the cross-linguistic prominence hierarchies that are a central explanatory concept in language-typological research (e.g., Comrie, 1989). The pars opercularis, therefore, appears to play a crucial role in decoding abstract representations (i.e., hierarchical dependencies in the sense described above) from underlying patterns in the linguistic input (i.e., the linear order).

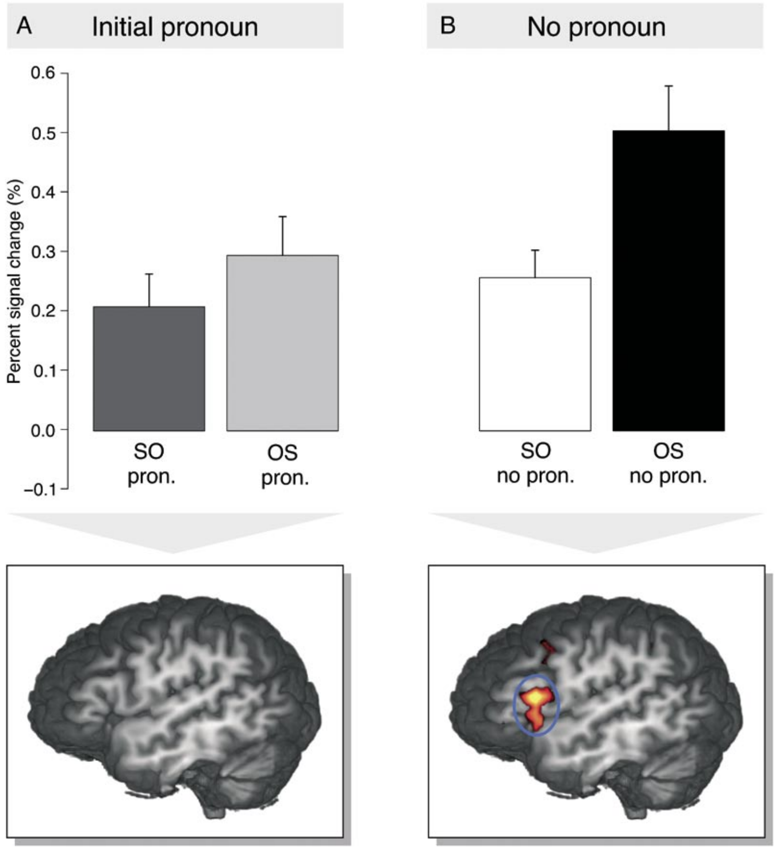

Figure 5.11 Averaged activation (n = 16) for object- vs. subject-initial sentences with pronouns (panel A) and without pronouns (panel B). The bar graphs show the percent signal change within the pars opercularis for each individual condition, with error bars indicating the standard error of the mean. The data are from Grewe et al. (2005).

5.3.2 Real time argument interpretation in typologically different languages

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Successful sentence comprehension presupposes the efficient and accurate analysis/interpretation of sentential arguments (or event participants). In collaboration with the University of Marburg, the Junior Research Group Neurotypology is examining argument interpretation processes in typologically different languages in order to determine how these processes are shaped by the particular properties of the individual languages in question. Two main issues are being pursued in this regard, namely the properties determining the thematic interpretation of arguments and the processing of word order variations.

Thematic interpretation of arguments. With respect to the question of how arguments are assigned a thematic interpretation online, previous studies have revealed word order and case morphology as important factors that are subject to cross-linguistic variation (Schlesewsky & Bornkessel, 2004). Thus, while German, for example, relies primarily upon case marking (as evidenced by an N400 effect for conflicts in Actor assignments), English predominantly draws upon word order in this regard (correlating with a left-anterior negativity, LAN). As a test case, we have recently examined the processing of Icelandic, a language which has both a rich case marking system and rigid word order. Our results show that Icelandic patterns with German rather than English, thus indicating that case overrides word order in this language. We attribute this choice of processing strategy to the existence of dative subjects in Icelandic, which render case interpretively relevant. In addition to the role of case marking and word order, we are currently examining the influence of further properties such as the availability of argument drop (Chinese, Hindi, Japanese, Turkish) and ergative alignment (Hindi) and the interaction of such factors with semantic information such as animacy.

Processing of word order variations. As word order phenomena have long played a central role in linguistic typology, they appear particularly well-suited to the research aims of the Neurotypology group. In addition, previous experimental investigations in German have revealed a specific electrophysiological correlate of word order variations, namely a fronto-central negativity with a slight focus to the left ("scrambling negativity"; e.g., Rösler et al., 1998; Bornkessel et al., 2002; Schlesewsky et al., 2003). In a recent study, we were able to show that, in the auditory modality, the onset latency of this component decreases to approximately 100 ms after the onset of the critical case information and that it is associated with a slightly broader topographical distribution (see Figure 5.12).

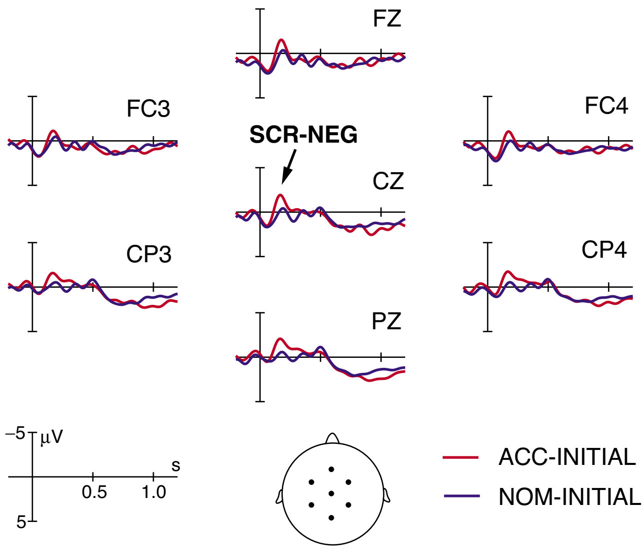

Figure 5.12 Grand average ERPs (n = 24) from the onset of the determiner of NP1 for scrambled (ACC-initial) vs. non-scrambled (NOM-initial) sentences in German with auditory presentation.

Within the extended Argument Dependency Model (eADM; Bornkessel & Schlesewsky, in press), the scrambling negativity is interpreted as resulting from an incompatibility between an intransitive phrase structure and the case marking of the initial (object) argument. This gives rise to the cross-linguistic prediction that, in languages allowing subject arguments to be dropped, the scrambling negativity should only be observable under circumstances in which subject-drop is highly unlikely. This hypothesis was tested in Japanese, a language allowing extensive argument drop, by comparing object- and subject-initial word orders in conjunction with a prosodic manipulation that either permitted subject drop or rendered it highly unlikely. While, under the latter circumstances, we observed a scrambling negativity very similar to that shown in Figure 5.12 for German, no such effect was apparent when subject drop was possible. These findings thus provide converging support for the interpretation of the scrambling negativity advanced above and, in addition, illustrate very nicely how language-specific properties may impact upon processing behavior.

A second study on word order variations was conducted in Mandarin Chinese, an SVO language that permits SOV orders in the so-called *bá-construction* (S bá O V). As this construction is only possible with a certain class of verbs, we compared clause-final verbs not compatible with the *bá-construction* with verbs permitting this construction. The ERP effect observed in this comparison was clearly distinguishable from the N400 elicited by a plausibility violation condition and is highly similar in terms of latency and topography to the scrambling negativity described above. As the word order variation examined here is quite different in nature to scrambling, this finding raises the intriguing possibility that the scrambling negativity may, in fact, index more general aspects of linear ordering in language (see also section 5.3.1).

Mapping problems in the functional interpretation of ERP components

5.3.3

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While it is well-known that the mapping between ERP components and particular cognitive subdomains/processes is not one-to-one (e.g., Roehm et al., 2004), the electrophysiological correlates of reanalysis processes in German pose a particularly difficult challenge to the functional interpretation of standard language-related components such as the N400 and P600. Thus, it has been demonstrated that the dispreferred resolution of a grammatical function ambiguity towards an object-initial reading gives rise to a P600 when the object bears accusative case, but to an N400 when the object is assigned dative case (Bornkessel et al., 2004). Originally, this striking dissociation was interpreted in terms of different reanalysis operations for the two types of structures: As dative-nominative is a possible unmarked word order (e.g., with particular types of verbs), no structural reanalysis is required in these constructions, while reanalysis towards an accusative-nominative order always requires a revision of the phrase marker.

However, further studies have revealed a much more complex data pattern. Thus, when the disambiguation of verb class (accusative or dative) occurs before word order disambiguation (as in [1]), disambiguation towards a dative-nominative word order engenders a biphasic N400-P600 pattern, whereas disambiguation towards an accusative-nominative order elicits only a P600 (see Figure 5.13)

[1] *a. ... dass Richard Künstlerinnen gesehen/gedankt haben, …*
... that $\text{Richard}_{\text{AMB.SG}}$ $\text{artists}_{\text{AMB.PL}}$ seen(ACC)/thanked(DAT) have_{PL} …

We interpret this dependence on the relative availability of the disambiguating information as evidence for a reliance on *good-enough* representations during sentence comprehension (e.g., Ferreira et al., 2002). When the verb class information is available in parallel with the information effecting the word order disambiguation, the processing system may draw upon the knowledge that dative-nominative is a possible underived word order even when this word order is not compatible with the particular type of dative verb in the sentence currently being processed. Thus, only an N400 is observable under these circumstances. By contrast, when the verb class information is available before the word order disambiguation, such a "good-enough" solution is not possible. Here, the additional P600 reflects the processing of a more marked structure. An interpretation along these lines is supported by the finding that reanalyzes with verbs associated with an unmarked dative-initial word order (i.e., dative object-experiencer verbs) engender only an N400 component even when verb class is disambiguated before word order. These results, therefore, also indicate that, in contrast to the P600, the N400 effect does not result from the application of good-enough representations.

As there is additional evidence that the component pattern correlating with reanalysis effects may be modulated by the modality of presentation (Leuckefeld, 2005) and possibly by task requirements, we are presently examining ERP correlates of subject-object reanalyzes in ecologically valid stimuli in order to estimate the influence of these factors. Finally, as an alternative approach to the same questions, underlying similarities and differences between ERP components that may not be evident from a surface perspective are being examined by means of frequency-based analyzes (Roehm et al., in press).

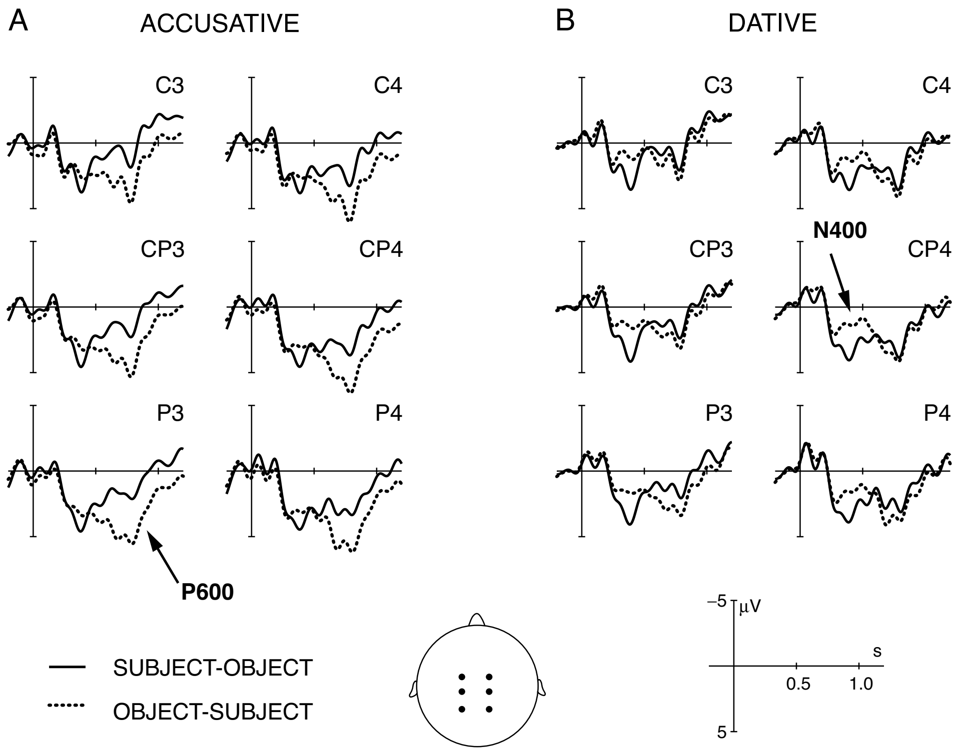

Figure 5.13 Grand average ERPs (n = 20) at the position of the disambiguating auxiliary (see example 1) for sentences disambiguated towards object- vs. subject-initial readings. This comparison is shown for sentences with accusative verbs in panel A and for sentences with dative verbs in panel B.

INFANT COGNITION AND ACTION 6.1

The research group "Infant Cognition and Action" is investigating the early development of the cognitive mechanisms of action perception and action control. The main aims of the unit are threefold, (1), to analyze the cognitive aspects of infant action control and how they develop, (2), to study the development of the infant understanding of actions performed by other persons, and (3), to investigate how these two aspects of action control are related to each other in early development. The theoretical approach to our research is based on is the *common-coding* theory. The application of the notion of a common representational domain for perception and action to infant research leads to two main assumptions.

First, we assume that even young infants have an abstract representation of actions. This representation is used by both the perceptual system to perceive and interpret actions of other persons as goal-directed and by the motor system to perform goal-directed actions. Starting from this assumption, various conclusions can be drawn concerning the relation between the two aspects of action control we are interested in, namely active performance and the interpretation of other persons' actions. The most interesting conclusion concerns the direction of influence. In the literature, there is disagreement with regard to the question of whether understanding oneself as an agent precedes the understanding of others as agents or vice versa. From the perspective of a common representational domain for own and other people's actions, all kinds of influences are feasible, even that both aspects of action control develop independently (Aschersleben, in press). Therefore, a part of our projects studies the interplay between action perception and action production.

The second main assumption that can be derived from the application of the common-coding theory to early ontogeny concerns the format of action representations. Similar to adults, it is assumed that it is a distal one, that is, actions are represented in terms of their anticipated effects in the environment. As a consequence, action effects should play an important role in infant action perception as well as in infant action production. To prove this assumption valid, in a number of projects, we demonstrated an influence of action-generated effects on how infants control their own actions and, moreover, on how infants interpret actions that are performed by other persons.

6.1.1 Actions performed by a human agent

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To study infants' perception of goal-directedness in other persons' actions, we applied the habituation/familiarization paradigm. Woodward (1998; 1999) demonstrated that 6-month-old infants pay more attention to changes in the goal objects of grasping actions than to changes in the motion path. She interpreted this finding in terms of an early sensitivity to action goals. Nevertheless, when infants were presented with a non-purposeful action – a hand falling backwards onto one of two objects – there were no signs of the distinctive looking pattern described above, neither at the age of 6 months nor at 9 months. Woodward suggested that infants' understanding of actions as goal-directed is restricted to familiarity. However, we were able to extend Woodward's argumentation about familiarity. By using her paradigm, we tested the hypothesis that a salient action effect is an important feature for young infants to interpret actions as goal-directed (Hofer, 2005). We argue that infants are probably quite familiar with the grasping motion and its consequences, namely object manipulation. In contrast, when infants watch a new action, they probably need a salient action effect to be able to interpret this action as goal-directed. Consequently, we modified Woodward's back-of-hand condition by adding an effect: The hand was not only lowered onto the object, but then pushed the object towards the rear end of the stage (Figure 6.1, left part). As predicted, 6-month-olds recovered attention after habituation more strongly when the target object was changed than when the motion path was altered. Thus, the results support the notion that action effects play an important role for infants' interpretation of actions as goal-directed.

Figure 6.1 Infants in a familiarization/habituation paradigm facing the live stage (left) and the computer screen (right).

6.1.2 Video versus live presentation of goal-directed actions

Hofer, T.,
Klein, A. &
Aschersleben, G.

It has been shown that 6-month-old infants can perceive the goal of an action performed by a human actor (Woodward, 1998; Hofer, 2005). However, in these studies, actions were always presented live on a stage. In a follow up, we asked whether 6-month-old infants would interpret an action as goal-directed when it is shown on television instead of being shown live (Hofer, 2005; see Figure 6.1, right part). This would provide evidence that young infants are able to perceive and interpret information from television. As it is known from imitation studies, infants' performance is impaired when the modeled action is presented on video instead of live. However, these studies do not address the question of whether these problems result from infants having problems to perceive and interpret these actions or from memory problems or problems in transferring the knowledge into own actions.

In our study, 6-month-old infants were tested using the same back-of-hand action as described earlier. One group of infants saw the video presentation, the other group received the same action displays matched for all important features, but live on stage. Results revealed that 6-month-olds in the video group interpreted the human action as shown on television as goal-directed. The same result pattern was found for the live group, thus replicating earlier studies. Most importantly, the comparison across both groups revealed practically no difference in the overall looking pattern between the two groups. Thus, these findings show that infants as young as 6 months of age can interpret televised actions in meaningful ways. However, in an imitation study with 12-months-olds comparing live vs. video presentation of goal-directed actions we observed slightly weaker imitation scores with the televised model. In sum, this indicates that infants do not have any problems perceiving and interpreting information presented on television, but there seem to be some problems in action reproduction.

6.1.3 Actions performed by a mechanical device

Hofer, T.[1], *Hauf, P.*[1,2], *Jovanovic, B.*[3] & *Aschersleben, G.*[1]

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In the literature, there is disagreement about the question of whether infants in their first year of life are able to understand the goal-directedness of non-human actors. Support for the constructivist view assuming that infants acquire an understanding of actions as goal-directed through experience with actions of exclusively *human* agents comes from studies using the Woodward paradigm described above. Here, the hand was replaced by a mechanical claw and no goal attribution took place in 6-month-olds. Similarly, we observed no goal attribution in 6- and 9-month-olds when the action was followed by a salient action effect (object displacement; Figure 6.2; Hofer, 2005). This indicates that young infants' action interpretation distinguishes a human from a non-human agent. Moreover, it supports the constructivist view suggesting that infants' attribution of goal-directedness is preferentially applied to human agents.

Figure 6.2 A mechanical claw grasping one object and carrying it to the back of the stage.

However, our studies also revealed that at 12 months of age infants seemed to interpret the action performed by a mechanical claw as goal-directed. At this age, infants begin to employ tools during their daily activities in a goal-directed manner. Consequently, we derived the alternative interpretation that the 12-month-olds did not interpret the mechanical claw as a non-human agent, but as a tool. To test this hypothesis, before the habituation paradigm took place, 9-month-olds received an information phase in which they were informed about the fact that the claw was operated by a human. Under these conditions, 9-month-old infants were indeed able to interpret the action performed with the assistance of a claw as goal-directed (Hofer et al., 2005). On the basis of these findings, we claim that 9- to 12-month-old infants recognize the claw as a tool, operated by a human agent, and therefore, attribute the goal to the human. This implies that infants understand that the claw is used as a means to an end. By the end of their first year of life, infants seem to be able to integrate their knowledge about means-end problems and tool use and understand that human actions are performed in a goal-directed manner.

6.1.4 Influence of mother's interactional style on infants early action interpretation

Hofer, T., Hohenberger, A. & Aschersleben, G.

Various studies have shown that the style of mother-infant interaction has an influence on later cognitive development (Aschersleben et al., 2005). To demonstrate such a link already in early cognitive development, we investigated the impact of the quality of mother-child interaction on infants' action understanding abilities (Hofer, 2005). Using a televised familiarization paradigm as described previously, 6-month-old infants were tested to see whether they would interpret the back-of-hand movement as a goal-directed action. To measure the maternal interactional style, all infants and their mothers were videotaped in a 5-minute free play situation. The interaction behavior was analyzed based on the coding system CARE-Index, which allowed the classification of mothers on a tri-dimensional scale, with sensitive as the positive point and controlling and unresponsive as the two negative points. Using cluster analyses strategy, we grouped mothers into three clusters of maternal interaction styles, namely sensitive, unresponsive and moderately controlling. When dividing infants into the three groups, accordingly, we found that, although – as a group 6-month-old infants interpreted the unfamiliar human action as goal-directed – this did not hold for two of the three subgroups (Figure 6.3). Only infants of mothers with a moderately controlling interaction style were already able to interpret the human action as goal-directed. Neither infants of sensitive mothers nor of unresponsive mothers encoded the action display as goal-directed. These results suggest that the ability to interpret an action as goal-directed is more enhanced in 6-month-old infants of controlling mothers. Taken together, these findings indicate that a mother's interaction style is indeed related to infants' early action interpretation.

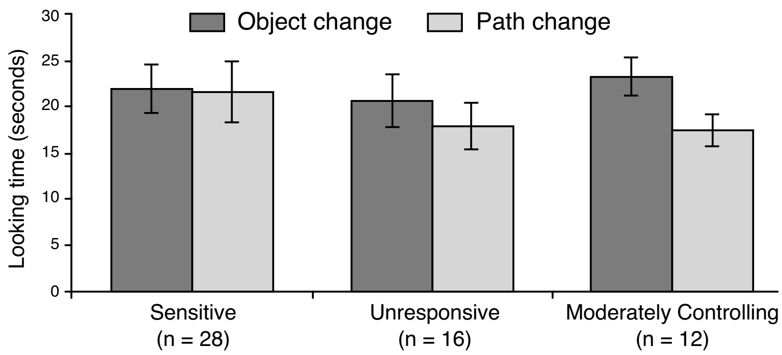

Figure 6.3 Mean total looking time for each test event and each group of infants (clustered according to their mothers' interactional style).

6.1.5 The role of action effects in action production

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To demonstrate the important role of action effects not only in infant action perception but also in infant action control we applied the imitation paradigm. Twelve- and 18-month-old infants watched a three-step-action sequence, in which one action step was followed by a salient action effect. In three experimental groups, either none, the second, or the third action step elicited an acoustical action effect. In a subsequent test phase, both age groups produced the action step that elicited an action effect not only more often, but also with lower latency and in most cases at first. Thus, the results support the notion that infants control their actions by anticipating desired action effects (Hauf et al., 2004).
To extend these findings to even younger infants, we had to use a simpler experimental setup, a two-button box which required infants only to press a button instead of remembering a complex three-step action

sequence. Depending on the experimental condition, the action resulted in an action effect (illumination and sound) or not. Nine- and 11-month-olds, but not 7-month-olds, performed the target action that caused the salient action effects with lower latency and in most of the cases as the first action (Figure 6.4). These results demonstrate that, already in their first year of life, infants use the anticipation of action effects to control their own actions. This interpretation was supported by another study with 9-month-olds. Here, infants observed an adult demonstrating either the same action performed with two different objects or two different actions performed with one object. However, only one specific combination led to an interesting acoustical effect. In all conditions, infants preferred to reach for the object that was presented in combination with an effect. Moreover, they imitated the action that did produce an effect. In sum, our results support the assumption that 9-month-olds already relate certain actions to certain effects and that they draw on this knowledge to control their behavior.

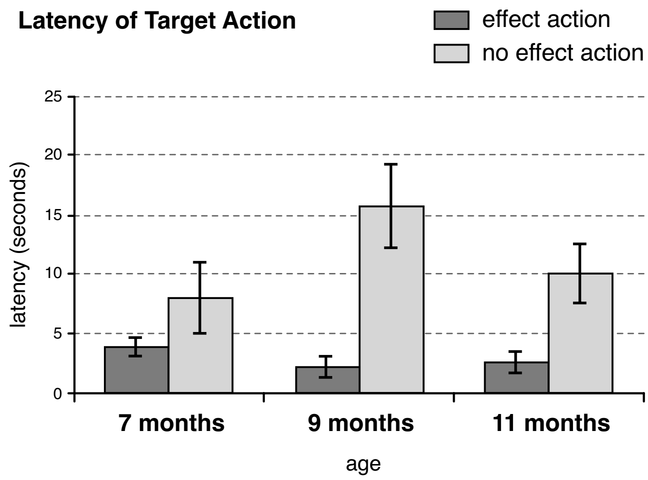

Figure 6.4 Latency of first occurrence of the target actions in the three age groups.

The interplay of action perception and action production

6.1.6

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Human beings act within and also interact with their social environment from the beginning. Accordingly, infants' behavior is shaped by observing others and agentive experience shapes their interest in others (Prinz et al., 2005). In that way, the idea of the functional equivalence of self-performed actions and perceived actions performed by others is useful for action understanding not only in adults, but also in infants (Hauf & Prinz, 2005). The underlying question is whether infants come to understand other person's actions *after and because* they understand their own actions – or whether exactly the reverse is true, and they understand their own actions *after and because* they understood others. To answer this question, we investigated the interplay of both aspects of action control. We developed a completely new paradigm combining imitation with preferential looking technique. (1) In the *other-condition* infants first watched a short video clip, which showed two adults playing with a toy. Afterwards, the infant was allowed to play with the toy shown on the video and a novel toy. (2) In the *self-condition,* the infant first played with one toy and then saw two video clips simultaneously. In both movies, two adults played with either the same or a novel toy (Figure 6.5). In both conditions, 7-month-old infants showed no significant preference for one of the toys indicating that the perception of other person's actions had no influence on the infant's own active action performance or vice versa. However, the 9- and 11-month-olds preferred to watch the same-toy video indicating an influence of action production on action perception at this age.

Figure 6.5 Infant watching two video clips simultaneously, in which two adults either played with the toy the infant had played with before or with a novel toy.

The research unit "Sensorimotor Coordination" is investigating governing principles in the formation and the coordination of neural central commands in human movements. We are developing a combination of precise measurements of kinematic, dynamical and neurophysiological variables with sophisticated modeling of the human biomechanical periphery. One of the goals of our group is to understand the emergence of controllable degrees of freedom from the interplay of perception and action neural systems.

Laboratory Equipment. The Sensorimotor Coordination laboratory is equipped with different experimental systems, allowing a wide range of studies in human movement control. The Optotrak 3020 system is a highly accurate 3D motion and position measurement system, based on infra-red (IR) sensing. The Optotrak is currently being used to record the movement of rigid parts of the body in 6D (three positional and three rotational degrees of freedom/DOF) like the jaw and head. For soft tissue structures like the lips, in which the number of DOF is not clearly defined, we do recordings with a relatively high number of IR markers. This allows a good kinematic description of the orofacial movements.

For the haptic interface, the laboratory is equipped with two Phantom robots. These are robots with 3 DOF that can exert feedback controlled force fields in real time, allowing the simulation of diverse virtual conditions needed by our experiments. The two current applications of the robots in the laboratory are (1), the measurement of mechanical impedances of the jaw and the finger/wrist systems, and (2), the simulation of virtual situations for measuring the subjects interaction forces while controlling visually guided movements. Two Nano-19 force/torque transducers (from ATI Inc.) are attached to the tip of each robot. They measure the reaction forces exerted by the subjects in perturbation or virtual reality experiments done with the Phantoms.

Electromiographic (EMG) measurements are made with Amplifier System from Grass Telefactor Inc. We have currently two quad amplifiers, with which we can do simultaneous measurement of the activity of up to eight muscles. A variety of electrodes is used in the experiments, most of them being surface electrodes whose electrical characteristics adapted to the different muscles involved in the experiments. We collect data for the orofacial systems (jaw, tongue and larynx) using both, surface and needle EMG. In the future, the system will be extended with two extra quad amplifiers and recordings of the muscles involved in the control of wrist/finger movements will be possible.

6.2.1 Mechanical impedance of the jaw

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This project is carried out in collaboration with Prof. David Ostry, Department of Psychology, McGill University, Montreal, QC, Canada, and is funded in part by the National Institutes of Health grant 5R01DC004669-02.

This project aims at studying the control of human orofacial movement that focus on the jaw. The goal is to understand the ways in which neural signals interact with orofacial mechanics to determine movement outcomes in speech. The experimental approach is novel in the context of orofacial research – The use of a servo-controlled robotic manipulator to deliver precise mechanical perturbations in 3D to the jaw. By determining the extent to which subjects adapt to various loading conditions and the generalization that occurs to novel loads and tasks, we document the properties of the mechanical periphery that the nervous system specifically compensates for in the production of orofacial movement. We are currently investigating the differences in the stiffness of the jaw during speech and non-speech tasks. Thirty subjects were asked to pronounce the sentence "*See sassy again*" and also to produce opening/closing movements of the jaw, which matched the speech sequence "*sas*" both, in duration and amplitude. Perturbations were applied with a Phantom robot during the opening/closing movements and reaction forces were measured with a force transducer (see Figure 6.7). Using a mechanical model of the jaw, we could infer the globalstiffness at the level of the condile. We could show significant differences in the stiffness level, suggesting that speakers are capable of tuning the impedance of the peripheral system according to the task.

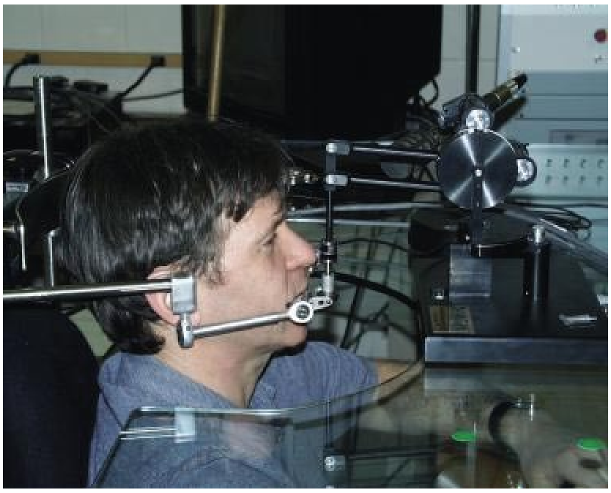

Figure 6.7 Experimental setup for the jaw perturbation experiment.

6.2.2 Optimal trajectories in constrained movements

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This project was partly carried out in collaboration with the Riken Institute, Japan, and the Faculty of Engineering, Nagoya University, Japan

Opening a door, turning a steering wheel, rotating a coffee mill are typical examples of human movements constrained by the external environment. The constraints decrease the mobility of the human arm and lead to a redundancy in the distribution of interaction forces between the arm joints. Due to this redundancy, there is an infinite numbers of ways to form the arm trajectory. The specific question that we are addressing is: *How does the central nervous system resolve this excess of degrees of free-*

dom problem? To investigate this problem, trajectories of the human arm in a crank rotation task were observed. Formation of point-to-point constrained rotation movements are explained using a criterion minimizing hand contact force change and actuating force change over time. The experiments show a close matching between the prediction and the subjects' data (Ohta et al., 2004), indicating that smoothness principles are important in the formation of constrained movements. A new experiment is being conducted to verify whether this principle of trajectory formation can be extended to bimanual manipulation in constrained environments. Our first results suggest that subjects optimize the forces exerted by each hand in an independent way (see Figure 6.8).

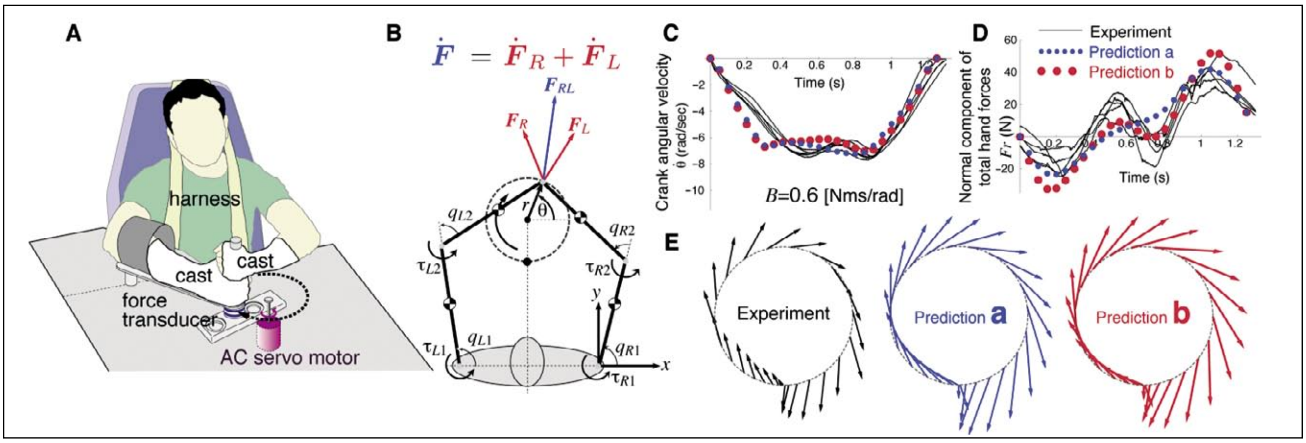

Figure 6.8 Dual-arm crank rotation experiment.

Self/other effects in lip-reading

6.2.3

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Interactions between perception and action at different levels of the cognitive system have been shown in many empirical studies. However, questions still remain regarding the way humans can take advantage of their own motor schemas in order to recognize movements related to those schemas. Previous studies conducted in our Institute involving character drawing and dart throwing have shown interesting self/other effects. The main result is that subjects are better at recognition and prediction tasks when they observe their own actions. We extend these studies to a similar self- and other-recognition task of lip movements with better controlled experiments. Recording of lip movements for selected speech tokens (the non-sense words "*aba*", "*awa*", and "*aua*", which involve labial movements) is done with the Optotrak system. A recognition test is then performed later by the same subjects, in which the Optotrak markers are shown on the computer screen (see Figure 6.9). Subjects show a systematically higher rate of recognition when they observe their own productions instead of that of the others (see Figure 6.10)

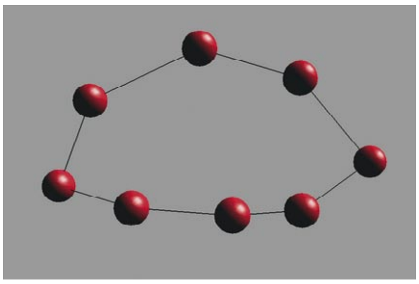

Figure 6.9 Appearance of the Optotrak markers attached to the contour of the lips in the recognition experiment.

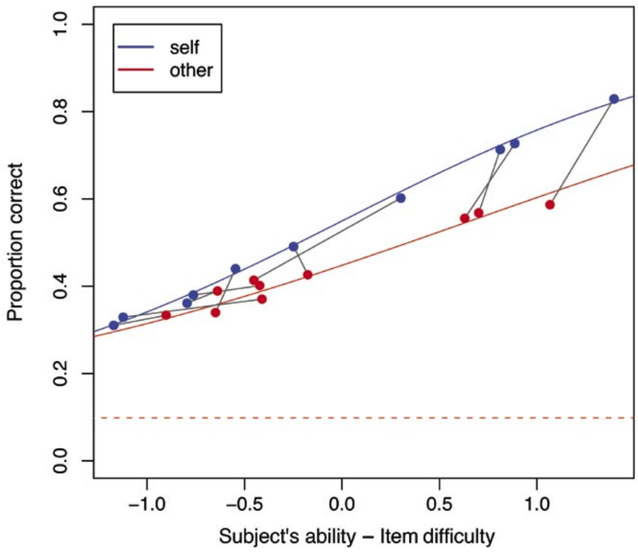

Figure 6.10 Results of the self/other experiment on lip readings. An Item Response Theory (IRT) model has been fitted to the data. The fitted logistic curves for each condition (red: own production, blue: production of the others) are shown. The horizontal axis represents the difference between subject's ability and item difficulty. The vertical axis is the rate of correct recognition.

6.2.4 Strength-dexterity tradeoffs in finger movements

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This project is financed through an Alexander von Humboldt Fellowship awarded to Francisco Valero-Cuevas.

The Strength-Dexterity Test quantifies the ability to dynamically regulate the magnitude and direction of fingertip force vectors. This test is based on the principle of buckling of slender compression springs beyond a critical load. We define "Strength" as the dynamical ability to regulate the *magnitude* of fingertip force vector to produce the necessary spring compression force (determined by the spring stiffness given by the material properties, number of coils and diameter of the wire). "Dexterity" is the dynamical ability to regulate the *direction* of that fingertip force vector to prevent the buckling of the spring (determined by the aspect ratio of the spring). Arbitrary combinations of Strength and Dexterity are achieved by manipulating the spring design parameters. How far a person can compress and hold the spring beyond its buckling load quantifies the ability of their fingertips to dynamically regulate the magnitude and direction of fingertip force vectors to stabilize the spring. We are conducting new tests in conjunction of stiffness measurements of the thumb during the task. Perturbations are delivered by the Phantom robots and forces are measured by the ATI force transducers (see Figure 6.11).

Figure 6.11 Photograph of our current Strength-Dexterity test for one digit.

Nunner-Winkler, G., Meyer-Nikele, M. & Wohlrab, D.

The study to be reported focused on civic virtues, which are taken to be a functional prerequisite for the maintenance of constitutional democracies. Two dimensions are involved: The cognitive dimension referring to the content of attitudes and norms, and the motivational dimension referring to the willingness to abide by these norms.

In this study, 203 (96 female, 107 male) 16-year-old east and west German students of the highest and lowest educational track participated. A mix of methods was used, which included open-ended interview questions, narrative stimuli, standardized scales, and an experiment. For analyses, we transformed the qualitative data into quantitative data by developing a coding manual, by constructing indices and devising rating procedures. The following constructs were assessed: strength of moral motivation/attitudes towards as well as experiences with violence/particularism and hostility towards foreigners/justice orientations/tolerance and democratic values/belief in moral relativism, determinism as well as in the homo oeconomicus model of man. Some findings will be reported in more detail (cf. Nunner-Winkler et al., 2006).

Moral motivation and gender stereotypes. Strength of moral motivation was measured by a rating procedure based on participants' responses to moral conflicts (7 point scale, interrater reliability $r_s = 0.81$). The ratings could convincingly be validated by two self-reports and an experiment. On all three measures, participants rated as higher in moral motivation significantly differed from those rated as lower: They attributed higher self-relevance to moral as compared to non-moral values. They expected to experience remorse and regret rather than delight or indifference after having transgressed a moral rule in order to satisfy personal interests. In a simplified version of a one-shot prisoner dilemma game, they more often responded with a cooperative move to an unknown partner's cooperative move.
Girls were significantly higher in moral motivation than boys (girls $M = 3.83$, $SD = 1.46$ vs. boys $M = 4.67$, $SD = 1.50$, $t\ (199) = 4.00$, $p = 0.00$ two-tailed).
This finding is explained in terms of collectively shared stereotypes and individual differences in gender identification: In agreement with findings of representative polls in Germany, 80% of the participants believe that men and women differ by nature. The content of these assumed differences was explored by open-ended questions. Features considered typical for men were mostly negative (49% vs. positive: 2%). Features seen as typical for women were mostly positive (42% vs. negative: 20%). All attributes favorable to morality (e.g., considerate) were ascribed to women (12% vs. men: 0%). In contrast, attributes detrimental to morality (e.g., ruthless) were hardly ever ascribed to women (4%), yet very often to men (37%).
For assessing gender identification, we asked participants to check on a 5-point scale how much different a person they would be, if of the opposite sex.
Gender identification and moral motivation correlated in boys, yet not in girls (boys $r_s = 0.18$, $p = 0.07$ vs. girls $r_s = -0.08$, $p = 0.42$). A closer inspection of data showed that the relationship is especially strong among highly gender identified boys (gender identification scale value 5): 58% of them, in contrast to only 26% of boys with low gender identification, are low in moral motivation (scale values 6+7) (see Figure 6.12).

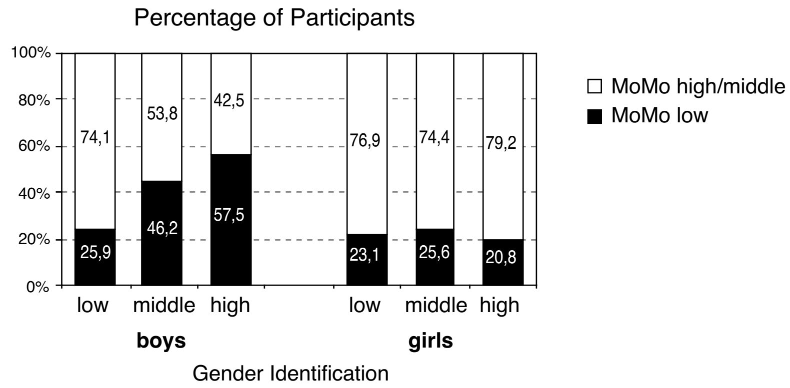

Figure 6.12 Gender identification and strength of moral motivation.
Boys: χ^2 (2 FG, n = 106) = 6.51, $p = 0.04$, girls: χ^2 (2 FG, n = 93) = 0.20, $p = 0.91$

In other studies, no gender differences are found till the end of childhood in moral understanding. Thus, the present correlational finding allows a causal interpretation: Gender identification in boys results in a decrease in moral motivation. Boys who define themselves in terms of a (gender) role identity may, in case of conflict, give priority to male role expectations (including morally adverse ones) over universal moral rules and/or use them to rationalize the pursuit of personal interests. In girls, gender identification does not produce an increase in moral motivation: Female features mostly describe social competencies, which may, but do not need to be used in a moral way.
Usually (assumed) gender differences in moral understanding are accounted for in terms of differences in genetic make-up or in early socialization experiences. The present study explains the differences found in strength of moral motivation in terms of socially defined sex roles (cf. Nunner-Winkler et al., in press).

Violence. In agreement with everyday understanding, which our participants share, violence was defined as intentional physical harm. About one half of the participants explicitly objected to the use of violence. In agreement with the literature, a significant correlation was found between the experience of physical abuse or neglect in the family and frequency of acts of violence (Dornes, 2004; Wetzels, 1997) . Schools differed widely in rate of violence. A regression analysis showed that pacifistic school milieu (defined in terms of quota of students disapproving of violence) predicted rates of violent acts better than sex or quality of family experiences: In pacifistic schools, even students with negative family experiences commit only few violent acts, whereas in non-pacifistic schools, even students with positive family experiences commit several and those with negative family experiences many violent acts. (see Figure 6.13; cf. Nunner-Winkler et al., 2005).

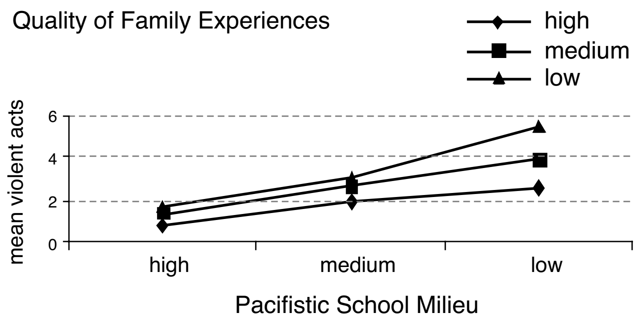

Figure 6.13 Violent acts and quality of family experiences and pacifistic school milieu.
Quality of family experiences positive: F (2,107) = 5.70, $p = 0.00$, medium: F (1,52) = 4.29, $p = 0.02$, negative: F (2,24) = 5.27, $p = 0.01$

Ethnocentrism. The concept ethnocentrism comprises favoritism to in-group members (particularism) and devaluation of out-group members (hostility towards foreigners). Usually, these two attitudes are interpreted as end-poles of one dimension. However, neither one is a (logically or psychologically) necessary implication of the other. We assessed both dimensions independently. For several reasons we assumed universalism/antiparticularism to be higher in west than in east Germany: Functional differentiation was higher, in consequence of the 68-debates nationalism was explicitly rejected and in east Germany, there were traces of a barter economy. Indeed, among the East German participants, we more often found particularistic orientations. However, the level of hostility towards foreigners was not higher. Overall, particularism is correlated with hostility towards foreigners, yet this correlation is stronger in the more antiparticularistic west German milieu. In other words, in the west particularistic attitudes indicate hostility towards foreigners much better than in the east (see Figure 6.14).

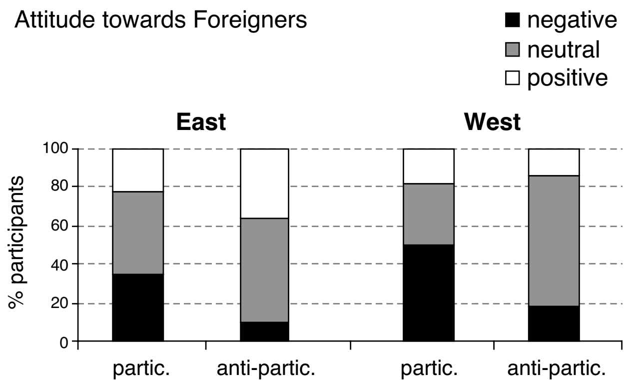

Figure 6.14 Attitudes towards foreigners and (anti)particularism.
East: χ^2 (2 FG, n = 104) = 9.55, $p = 0.01$; West: χ^2 (2 FG, n = 99) = 13.28, $p = 0.00$

This finding has two implications: Theoretically, the antiparticularistic west German position may fail to acknowledge that particularistic obligations (e.g., special duties towards one's fellow compatriots) are justifiable on universalistic terms. Methodologically, the frequently reported finding of a higher hostility towards foreigners in east Germany might be an artefact, given that studies often use items that express in-group favoritism and interpret them as indicating hostility towards foreigners.

Across the other attitudes assessed, there were only few differences between the sexes and between regions. Boys and girls alike acquire attitudes mostly by implicit learning mechanisms (e.g., reconstructing rules underlying interaction experiences, social institutions, the shared language game), and for the younger east German generation, enculturation takes place in a democratic society.

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Since 1992, the **G**enetically **O**riented **L**ifespan Study of Differential **D**evelopment (GOLD) in Munich has been continuing a longitudinal study started with 90 mono- and dizygotic pairs of twins in 1937. During wave 5 (1995–1999), the original sample – in the meantime numerically reduced to 20 pairs – was enlarged with 171 new pairs of same and older age (63–85 years of age). After a period of 4.5 years, a follow-up (wave 6 from 2000–2003) completed the study with 148 pairs of twins. The mean age in the retest group increased from 70.8 to 75.3 years (varying now from 68 to 88.5 years of age).

The research interest of the project is mainly focused on individual differences: Do individual differences remain stable beyond childhood in adult and old people? To what extent are inherited and environmental conditions responsible for the observed stability of individual differences?

These global research questions required a multitude of tasks, tests, questionnaires and interviews covering developmental domains such as cognitive processes and intellectual abilities, motivation and emotion, personality, social relations and moral understanding. Results with the focus on single developmental domains mainly of wave 5 have already been published (Geppert & Halisch, 2001; 2002; Geppert et al., 2004; Geppert & Spinath, 2004). The former collaborators of the GOLD study are preparing a book for 2006 to give a comprehensive overview of the study.

Besides looking into developmental change and stability in the very old, the heredity analyses, i.e., the estimation of genetic and environmental influences, became refined. Coming off univariate heredity estimations multivariate analyses (based on structural equation modeling methods) resulted in the detection of high genetic overlap of genetic variance between personality traits and more specific characteristics such as motives, control beliefs, and coping processes. A Cholesky decomposition for multivariate twin data allowed to isolate the separate and the shared variance contributions of genetic and environmental influences. Genetic influence on individual differences appeared to be more global. The influence of environment, on the other hand, proved to be more construct-specific.

The Cholesky model not only enables the isolation of variance contributions of different constructs measured simultaneously, but also the analysis of developmental processes in a repeated measurement design. Developmental change in the trait extraversion from wave 5 to 6 will serve as an example. Extraversion decreased from wave 5 to 6 (Figure 6.15) in particular in the older group of our sample. The path diagram (squared path coefficients to get the variance) at the top of Figure 6.16 (Model 1) describes a latent ACE model not only with direct paths to the construct extraversion measured during wave 5 (W5), but also cross-paths to the construct extraversion measured during wave 6 (W6). The ACE factors (additive genetic influence, common shared environmental and individual non-shared environmental influence) of construct W5 are assigned the first priority to explain W5 and as much of W6. Then, the ACE factors of construct W6 explain what is left of W6. Model 2 in Figure 6.16 is a transformation of the bivariate Cholesky model to a common/specific factors model. The squared paths of this model depict not only the strong common variance contributions of the twice measured construct extraversion (overlap: 56% genetic and 35% non-shared environmental influence), but also a separate genetic variance contribution (18%) specific to the second measurement of extraversion. Thus, a change in genetic influence on individual differences in extraversion can be assumed. Becoming more introverted in old age might result from specific genetic effects such as now activated age genes. But this might be a rather speculative assumption.

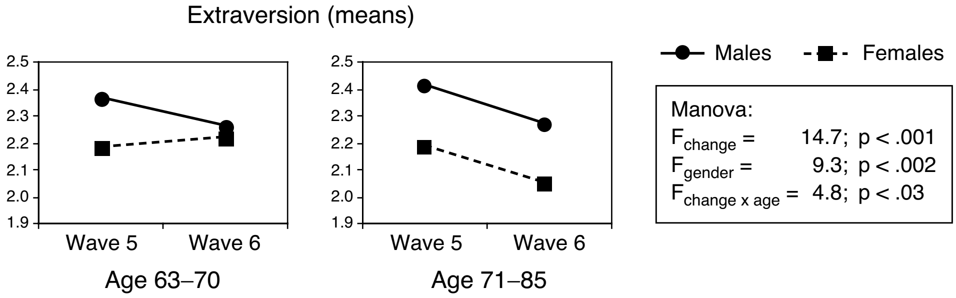

Figure 6.15 Developmental change in extraversion from wave 5 to 6, depending on gender and age.

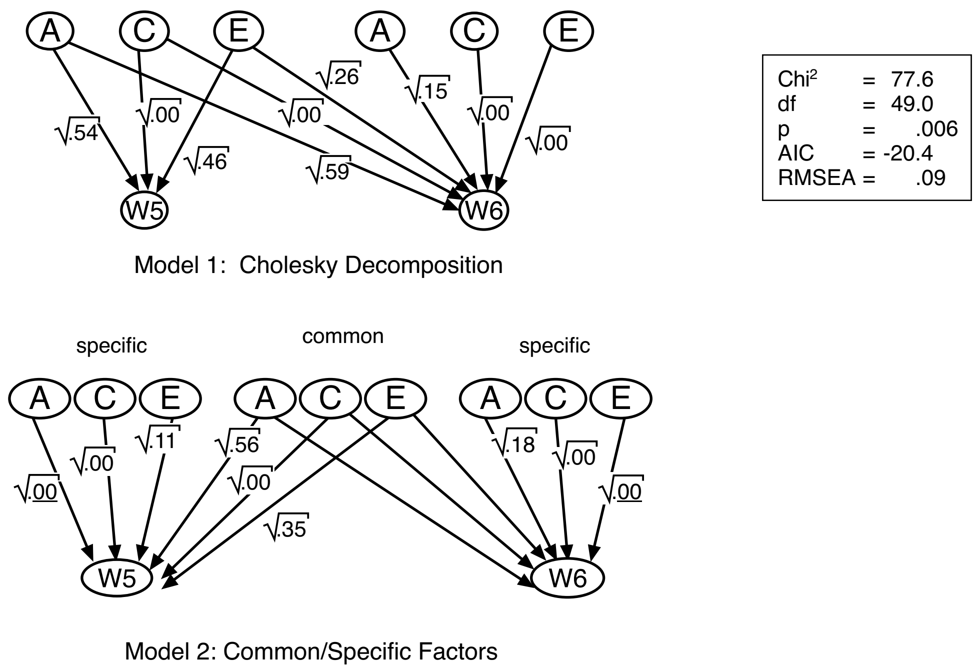

Figure 6.16 Bivariate Cholesky decomposition of genetic and environmental variance allowing the isolation of separate and shared variance contributions to the repeated measurements of the construct extraversion (wave 5 vd. wave 6).

NUCLEAR MAGNETIC RESONANCE 7.1

The years 2004/2005 may be characterized as a time of consolidation. Within only 10 months, three graduate students left the group after earning a Ph.D. and accepting post-doctoral positions at prestigious national and international MRI centers. Both MRI systems underwent significant modifications: The home-made 'MPIL' environment, which had served the Institute for more than eight years providing high-quality imaging sequences for the Bruker MedSpec 30/100 system, was gradually retired, and a major effort of programming and refinement was invested to upgrade the scanner to ParaVision 3.01. On the Siemens Magnetom Trio, a second RF channel was installed to permit non-proton NMR experiments in the near future.

Perfusion imaging by continuous arterial spin labeling (CASL) continued to be an area of fruitful research (7.1.1). Constant progress led to the first quantitative functional study with a cognitive paradigm and permitted the detection of subtle increases of the local cerebral blood flow (CBF) by only 20%. Such methodological improvements were also backed up from the hardware end. A double-loop labeling coil was designed to overcome previous limitations of tagging only the blood delivered to one hemisphere at a time (7.1.2). Further encouraging results were obtained with a novel helmet coil concept based on stripline technology, which drastically reduces the stray field outside the coil volume, yielding much better coverage in two-coil CASL experiments (7.1.3). As another option of generating contrast in fMRI, the sensitivity of intermolecular double-quantum coherences to local hemodynamic changes was explored with a hypercapnia paradigm that does not affect oxidative metabolism (7.1.4). Besides such developments of strategies to study cortical activation, different methods for parametric imaging of the resting brain and quantitative spectroscopy were integrated to investigate age-related changes in the cerebral white matter (7.1.5). All projects greatly benefited from fruitful collaborations with colleagues from within and outside the Institute. Another encouraging result of a joint venture initiated by colleagues at the University of Leipzig and performed with the Physikalisch-Technische Bundesanstalt (PTB) was the Innovation Prize of the Federal Minister of Education and Research (BMBF) for the proposal of a novel coil design.

At the time of writing this, there is also a glimpse of the near future as construction of a new NMR bay has just begun, which will eventually host a 7 T scanner.

7.1.1 Quantification of blood-flow changes during cognitive task activation

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

Expected improvements in the localization of activation due to the capillary/tissue origin of the perfusion contrast and in the quantification of functional signal changes are attracting arguments for multi-slice perfusion-based functional magnetic resonance imaging (p-fMRI). Previously, the method was demonstrated by mapping cerebral blood-flow (CBF) changes in subjects performing a motor paradigm (Annual Report 2002, Section 2.8.6). Aim of the present work was to detect more subtle functional CBF changes in different areas of the human brain related to an established cognitive paradigm (color-word Stroop task). Perfusion contrast was created by continuous arterial spin labeling (CASL) of the blood in the left common carotid artery, which was applied for all repetitions of the functional run in a quasi-continuous fashion. The acquisition of the control images necessary for quantification was performed in a short separate scan. In addition to p-fMRI, functional control measurements without the application of the labeling RF were performed under otherwise identical conditions, using the identical paradigm. This was referred to as no-label (nl)-fMRI. Finally, BOLD contrast was detected for comparison using conventional gradient-recalled echo (GE) echo planar imaging (EPI).

Positive activations in BOLD imaging appeared as negative signal changes in p-fMRI corresponding to an enhanced transport of inverted water spins into the region of interest, i.e., increased CBF, cf. Figure 7.1. P-fMRI was capable of reproducing most of the GE-BOLD-fMRI activations, such as in the pre-supplementary motor area and the primary motor cortex. A difference between the localization of activation of p-fMRI and BOLD-fMRI was observed in the inferior frontal sulcus (Figure 7.1; middle column). However, in the intraparietal sulcus and the frontal eye field, strong GE-BOLD activations were not detectable with p-fMRI.

After removal of residual BOLD contributions by subtracting the group-averaged nl-fMRI time series, quantification of CBF changes during cognitive task activation on a multi-subject basis yielded CBF increases of the order of 20–30%. In future, imaging sequences with even shorter echo times or stronger flow weighting should further decrease the perturbing influence of remaining BOLD signals, which is the main limitation of the current method. This might render the acquisition of nl-fMRI maps dispensable.

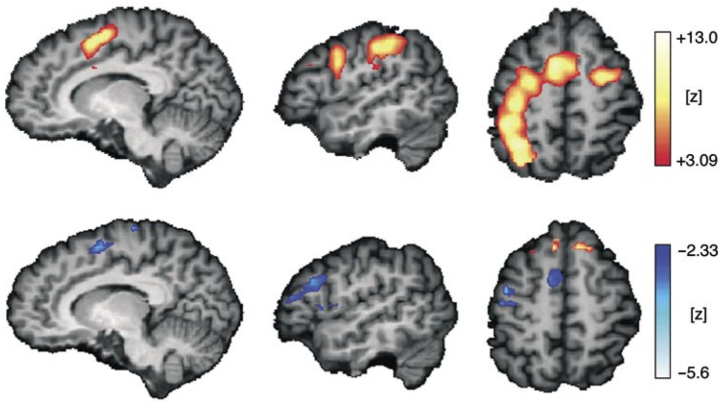

Figure 7.1 Activation maps obtained with GE-BOLD-fMRI (top) and p-fMRI (bottom) for the Stroop task contrasted against baseline. The maps represent the average over all subjects and are mapped onto an individual brain. GE-BOLD and p-fMRI maps are thresholded at $z = 3.09$ ($p < 0.001$) and $z = 2.33$ ($p < 0.005$), respectively. Views at x = –11 (left), x = –49 (middle), and z = 50 (right) are shown.

7.1.2 An optimized labeling coil for whole-brain perfusion studies

Hetzer, S., Mildner, T., Driesel, W. & Möller, H.E.

Continuous arterial spin labeling (CASL) for human brain perfusion imaging can be achieved by the use of a local surface coil to label the arterial blood at the neck (Annual Report 2001, Section 2.9.2). A limitation of the previous setup was that perfusion contrast could only be created in either the left or the right hemisphere of the brain. The goal of this project was the construction of a labeling coil that allows the creation of perfusion contrast in the whole brain.
As the efficiency of CASL crucially depends on the strength of the RF field (B_1), the blood velocity, and the strength of the magnetic field gradient along the arteries, computer simulations of the B_1 field distribution in the human neck were performed using various labeling coil designs. Considering previous numerical results (Annual Report 2003, Section 2.7.4) and optimizing the geometrical coil parameters, a perpendicular pair of circular surface coils (6 cm diameter each) was found to produce a sufficiently strong B_1 field, even at the position of the vertebral arteries. The corresponding B_1 field distribution is depicted in Figure 7.2A.
In a next step, the simulated B_1 field was verified by phantom experiments using a prototype labeling coil. In order to assure the patient safety and as a prerequisite for obtaining CE certification, calibration of the input power for the simulation of the local specific absorption rate (SAR) was performed. These simulations confirmed that the legal SAR limit of 10 W/kg was not exceeded at the maximum possible input power of 1.5 W for the labeling channel. Furthermore, a critical coupling between the helmet coil for perfusion imaging and the labeling coil was excluded by phantom experiments.
Figure 7.2B shows a whole-brain perfusion map obtained with the new CE certified double-loop labeling coil. It illustrates that both hemispheres are labeled to the same degree, including perfusion territories of the vertebral arteries. Thus, the double-loop labeling coil facilitates human whole-brain perfusion studies for diagnostic or functional purposes.

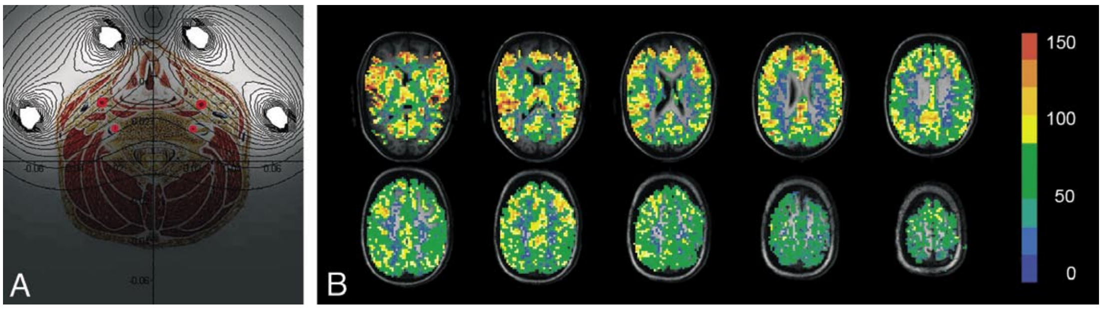

Figure 7.2 (A) Simulated B_1 field distribution of the optimized labeling coil in an axial slice of the human neck. The positions of the arteries are marked with red dots. (B) A whole-brain perfusion map obtained by arterial spin labeling. The colors correspond to cerebral blood flow values in ml/100g/min.

7.1.3 New helmet coil concept using strip lines

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

A new helmet coil without a circular base was developed using strip-line (SL) technology. It is characterized by a moderate gradient of the radiofrequency field B_1 along the *z*-axis and a very low straight field outside its circumscribed volume.
The new coil consists of thin strip conductors over a ground plane, separated by a low-loss dielectric material (Figure 7.3). For the first prototype, a 5 mm thick polypropylene substrate was used. To suppress eddy currents, the metal substrate on both sides was made from self-adhesive Cu foil (10 μm thick). At the end near the neck, the SLs are terminated by a short. Standing waves are created along the line with a maximum of current at the termination point. The most important advantage of a resonator is the "quasi"-transverse orientation of the electromagnetic field. A shunt capacitor at the input is used for tuning to 125.4 MHz. A series capacitor matches the impedance at the tuning capacitor to the imped-

ance of the semi-rigid cable (50 Ω). To reduce cable waves, a custom-made quarter-wavelength balun was used to fit the unbalanced coaxial cable to the balanced load of the coil. In addition to the balun we used a parallel resonance circuit for further suppression of standing waves on the outer jacket of the semi-rigid cable. A high degree of isolation (better than 16 dB) between the two channels is obtained with this symmetric arrangement of the helmet coil.
To optimize the design, finite element calculations of the distribution of the B_1 field were performed with a commercial program package (HFSS 9, Ansoft) and analyzed with respect to the efficiency and the occurrence of unwanted hot spots. The corresponding vector field in axial slices demonstrated a high degree of homogeneity and circular polarization in the region of interest. Experimental verification at 3 T (Bruker Medspec 30/100) in healthy human volunteers verified that the new coil permits investigations of the entire brain with good tissue contrast. The modified design enables the use of a passively decoupled labeling coil at the common carotid artery without exceeding the safety-relevant critical coupling between the helmet and the labeling coil. Dual-coil whole-brain perfusion studies become feasible with this setup.

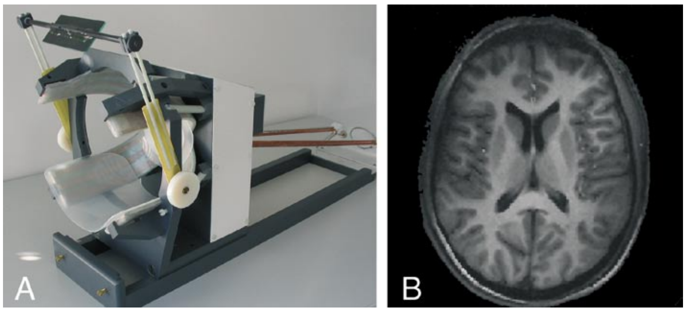

Figure 7.3 (A) Design of the new dome-like helmet coil (23 cm inner diameter; 18 cm height) and (B) Axial T_1-weighted MDEFT image (T_R 1.3 s, T_E 9.2 ms, acquisition matrix 256 × 252).

7.1.4 Effect of hypercapnia on the iDQC response

Schäfer, A.[1], Zysset, S.[1], Heinke, W.[2] & Möller, H.E.[1]

[1] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig · Munich, Germany
[2] Department of Anesthesiology and Intensive Care Therapy, University of Leipzig, Germany

It is well known that the fMRI baseline signal of human gray matter increases linearly with expired carbon dioxide (CO_2) from hypocapnic to hypercapnic levels. Hypercapnia produces a global increase in cerebral blood volume (CBV) and flow (CBF). By contrast, no changes in the cerebral metabolic rate of oxygen consumption (CMR_{O2}) are expected for moderate hypercapnia, which thus provides a means for manipulating cerebral hemodynamics without affecting oxidative metabolism. In search for novel contrast mechanisms, intermolecular double-quantum coherences (iDQC) have previously been used for susceptibility-sensitive functional magnetic resonance imaging (fMRI), and it was hypothesized that this contrast is fundamentally different from the conventional blood-oxygen level dependent (BOLD) effect. As the origin of iDQC signal changes is not well understood, the hypercapnia paradigm was used with iDQC imaging and compared to conventional BOLD-based fMRI.
Figure 7.4 shows the correlation map of a single subject obtained with SE-BOLD and iDQC ($z > 3.09$). Both methods yield strong positive correlations with end-tidal CO_2 ($ETco_2$). Activated voxels were well localized in gray matter. The time courses of activated voxels and the general pattern of activation were similar for both methods. Fewer activated voxels were obtained with iDQC than with SE-BOLD despite similar maximum *z*-scores. Qualitatively, the iDQC images seemed more susceptible to signal loss in areas with strong field variations, which might explain the absence of functional contrast in frontal brain areas. The percentage signal change averaged over all subjects was approximately 20% and 3% in case of iDQC and SE-BOLD, respectively. This seems to underline the increased sensitivity of double quantum coherences to local susceptibility changes. The iDQC contrast recorded at a correlation distance of 100

μm might also be more weighted towards veins, whereas the SE-BOLD contrast is weighted towards the capillaries.

The results indicate that iDQC-based fMRI is sensitive to pure hemodynamic changes in the absence of changes in CMR_{O2}, which is qualitatively similar to conventional BOLD fMRI. Additionally, the high level of signal change during hypercapnia and the global nature of the response should provide good conditions for further optimizing sequence parameters in iDQC imaging.

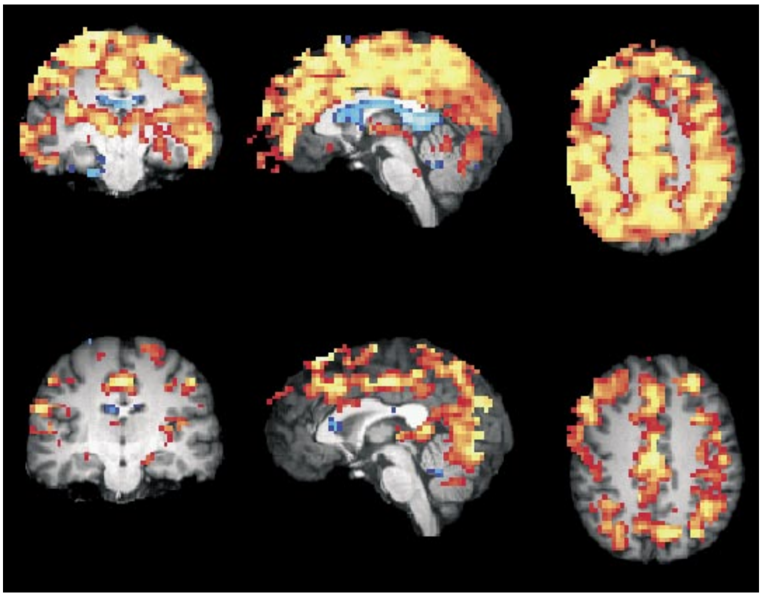

Figure 7.4 Correlation maps corresponding to changes in $ETco_2$ recorded in a single subject (top: SE-BOLD; bottom: iDQC). Hypercapnia was induced by inhalation of a gas mixture with 5% CO_2. The mixture was inhaled for 1 minute after 1 minute of breathing regular air (total time 11 min).

7.1.5 Investigation of white-matter aging by quantitative MRI and MRS

Wetzel, T., Tittgemeyer, M., Anwander, A. & Möller, H.E.

Cerebral white matter (WM) undergoes a variety of degenerative changes with normal aging. At least in certain brain regions and during certain segments of adult age span, such changes seem to be more prominent than cortical changes. Parametric MRI methods provide quantitative markers to study such changes. The magnetization-transfer ratio (MTR) is a sensitive identifier of underlying structural changes in the brain. Besides the MTR, diffusion-tensor imaging (DTI) and proton magnetic resonance spectroscopy (MRS) were used to elucidate age-related WM changes and their microstructural correlate. In this study, 22 neurologically healthy volunteers, 12 young (29 ± 3 y), 10 elderly (62 ± 5 y), were examined with the following protocol:

MT-weighted MRI: Spoiled gradient-echo sequence (α 30°, TR 750 ms, TE 10 ms, 0.9 × 0.9 × 3.0 mm^3) with and without pulsed off-resonance saturation of the bound water.

Diffusion-weighted MRI: Spin-echo EPI (TR 8100 ms, TE 120 ms, 44 axial slices, 1.7 × 1.7 × 3.0 mm^3, 2 acq.; b-factors 0 and 1000 s/mm^2, 24 directions) to calculate mean water diffusivity (trace) and fractional anisotropy (FA).

3D T_1-weighted MRI: MPRAGE for fully automated segmentation of gray and white matter (GM, WM), and CSF.

2D T_2-weighted MRI: RARE to obtain lesions after segmentation and to co-register the EPI images.

Imaging data analysis: WM histograms of the MTR, trace and FA maps were compared among groups (microangiopathic lesions in the elderly subjects were excluded).

MRS: PRESS spectra (TR 5 s, TE 30 ms, 128 acq.) of a 3-mL voxel in the fronto-parietal WM; absolute metabolite concentrations estimated using LCModel.

The histogram analysis demonstrated significant age-related changes in MTR and DTI data as shown in Figure 7.5 for the group-averaged histograms of the ADC data. For the elderly volunteers, a lower mean value and peak height of the MTR, an increased mean value and lower peak height of the ADC and an increased peak height of the FA histogram were found. Peak widths were not significantly different among groups in all measures. However, there is considerable inter-individual variation in the histograms. For MRS, significant metabolic differences among both groups included reduced *N*-acetylaspartate (NAA) and increased *Myo*-inositol (Ins) and, as a trend below significance, increased total choline (tCh) in the elderly volunteers.

The different MTR, ADC, and FA values in the two age groups suggest microscopic WM changes consistent with an increasing distance between myelinated fibers with advancing age. These results are consistent with earlier studies demonstrating the vulnerability of WM. MTRs have already been shown to be essential in the study of specific disorders of aging. Our results indicate that parameters derived from DTI provide additional important information to improve our understanding of the gross WM microstructural changes in the aging brain. This picture derived from MRI is finally supported by MRS: Decreased NAA indicates age-related axonal damage, while increased Ins (and tentatively tCh) might point to subtle cell membrane breakdown or gliosis.

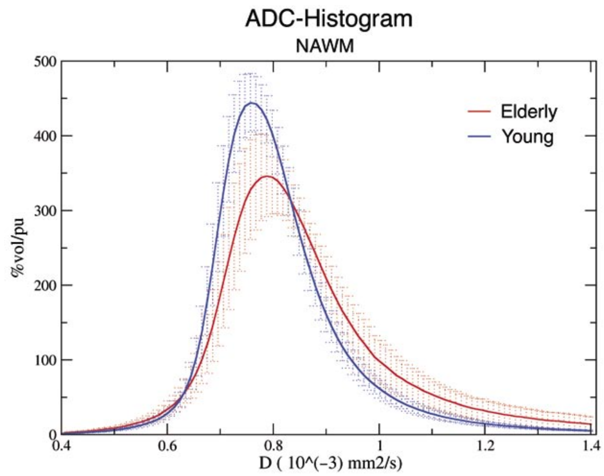

Figure 7.5 Group-averaged apparent diffusion coefficient data for young and elderly volunteers.

The working group "Mathematical Methods in fMRI" focuses on the development of new methods for the post-processing 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. A new version of Lipsia was released in September 2005.

Over the course of the past few years, the Lipsia group has developed a whole range of new methods and software, many of which have already evolved beyond the experimental stage and have become standard tools of data analysis in our Institute. Examples of this are Bayesian methods for second-level fMRI data analyses, tools for meta-analyses of fMRI data, spectral methods for investigating the temporal dynamics of the BOLD response, and various segmentation tools for morphometric studies.

An exciting new aspect of our research in the past two years was the meta-analysis of fMRI data. Meta-analysis has become a major topic, because of the rapidly growing number of functional neuroimaging studies and the availability of data in publicly accessible databases. To date, the enormous potential of available data has not nearly been explored in full. In a recent project, we have developed a new method for the meta-analysis of performed functional imaging experiments. The method is based on the concept of "replicator dynamics" and activation likelihood estimation (ALE). "Replicator dynamics" is a concept that originated in theorectical biology and was previously introduced by us into the analysis of fMRI raw data. We have adapted this method for the specific needs of meta-analysis. Already, our new method has been used in several studies that were conducted in our institute during the past year.

Other investigations by our team are aimed at investigating the relationships between fMRI time courses in different voxels of the same dataset. We found that spectral measures provide a better characterization of the interconnection of BOLD signals than previously used similarity measures. In contrast to correlation analysis, spectral analysis takes the temporal variability of the BOLD response into account and, moreover, provides measures for the temporal dynamics of BOLD. Using these measures, we have discovered a strong correlation between BOLD signal strength and latency that is consistent across fMRI data sets of different subjects and different lengths of stimulation.

Finally, we have continued our research into understanding human cortical folding. In a recent study, we investigated the variability of "sulcal basins" in the frontal cortex. "Sulcal basins" are compartments of the cerebral sulci. It is a concept that we had previously introduced and that allows us to reference cortical locations in a way that is anatomically more meaningful than stereotactic coordinates.

7.2.1 Lipsia – Leipzig image processing and statistical inference algorithms

Lohmann, G.[1], Müller, K.[1], Neumann, J.[1], Bohn, S.[2], Rudert, T.[1] & von Cramon, D.Y.[1]

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[2] Innovation Center Computer Assisted Surgery (ICCAS), University of Leipzig, Germany

Lipsia is a software package for the analysis of functional MRI data, which provides tools for pre-processing, registration, statistical evaluation, segmentation, and visualization. The new Lipsia release 1.2 contains major software developments. The software for statistical evaluation was completely re-written and now supports the approach of both pre-coloring and pre-whitening. Several second-level analysis tools were added for the evaluation of group studies. Lipsia 1.2 also contains new tools for analyzing averaged fMRI time courses. Basic properties such as time-to-peak and dispersion can be computed and visualized for all voxels of the brain. The results of fMRI data evaluation can be visualized using an interactive 3D-rendering within a new graphical user interface.

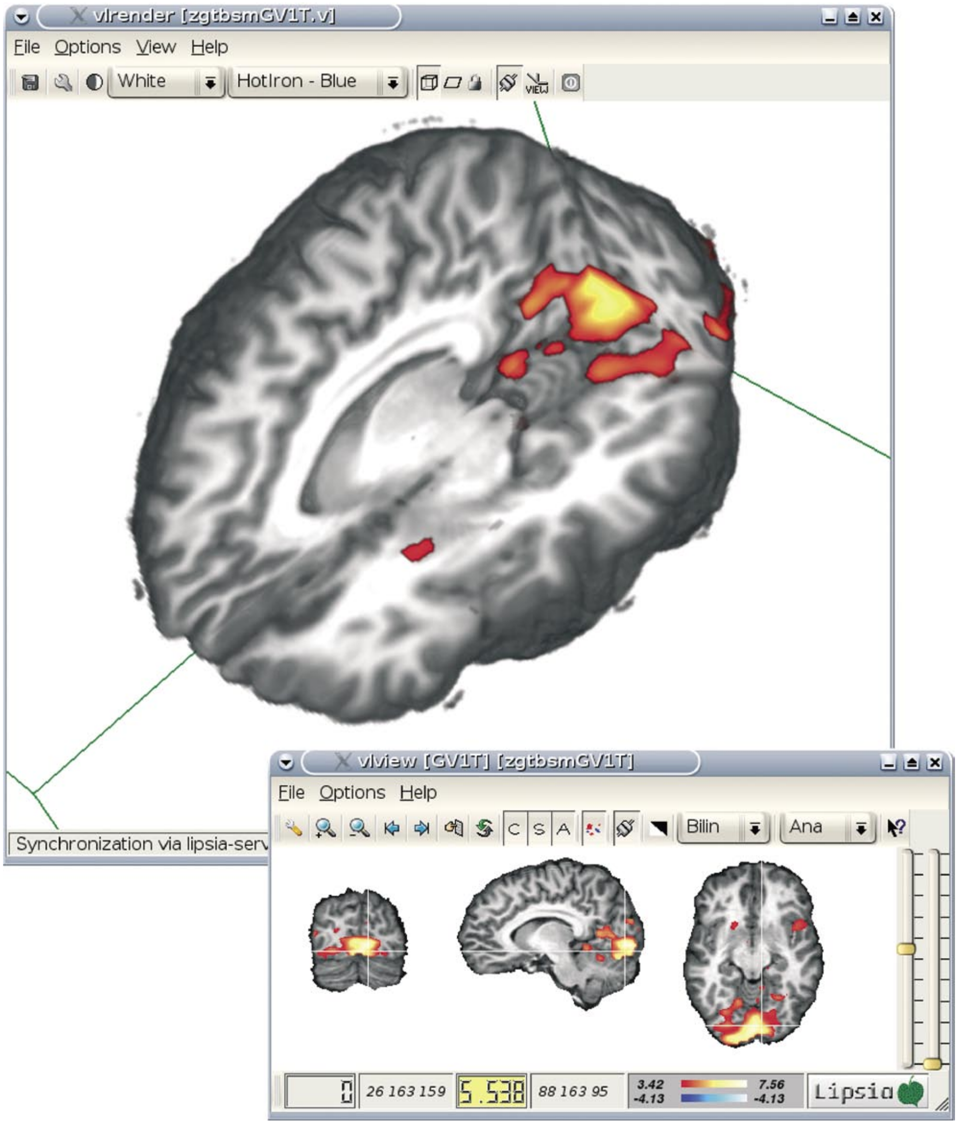

Figure 7.6 The creation of 3D-renderings can be completely controlled within a graphical user interface in real-time. Anatomical and functional maps can be rendered in a single step. Clipping objects like planes or boxes can be placed freely to resect parts of the volume and show the structures inside the brain. The rendering software can be linked to another visualization tool, which shows coronal, sagittal, and axial slices. Just by navigating through these orthogonal slices, the clipping object of the rendering software follows the current cursor position as long as both programs are connected.

Using replicator dynamics for the meta-analysis of functional neuroimaging data

7.2.2

Neumann, J., Lohmann, G., Derrfuss, J. & von Cramon, D.Y.

Functional neuroimaging provides a powerful tool for the detection of task-related neural activity in the human brain. The increasing availability of experimental results in publicly accessible databases combined with sophisticated spatial normalization and registration methods and a standardized coordinate system have opened up the possibility to compare and integrate results from a large number of independent studies with meta-analytic techniques.

We have developed a new method for the meta-analysis of functional imaging experiments. Our method is based on the assumption that cortical areas, which play an integral role in solving a particular task, will be found jointly activated in the majority of experiments addressing this task. We, therefore, use the co-occurrence of activation foci as input to a replicator process, from which, following the principle of natural selection, a so-called dominant network of the most often co-occurring activation foci emerges. The activation foci are derived from lists of activation coordinates using activation likelihood estimation prior to the replicator process.

Our method is efficient, easy to implement and can be applied to experiments employing different hardware configurations and imaging modalities. It thus enables the comparison and integration of results from studies carried out in different laboratories. The results of an analysis of 15 experiments addressing different forms of the Stroop interference are shown in Figure 7.7. Data were extracted automatically from the publicly accessible BrainMap database.

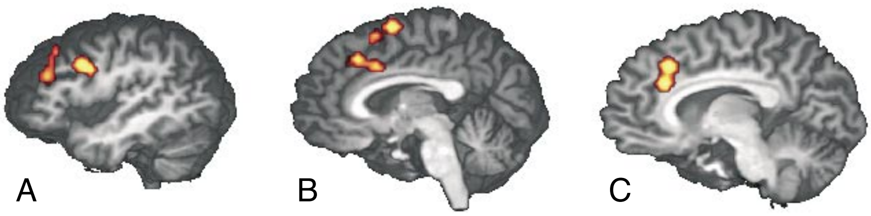

Figure 7.7 Five cortical areas selected as members of the dominant network for the Stroop paradigm. They include the IFJ, IFS extending into middle frontal gyrus, preSMA, and ACC of both hemispheres extending into BA 8. (A) and (B) show the left lateral cortex at x = –44 and x = –3, respectively, (C) shows the right lateral cortex at x = 7.

The correlation between BOLD signal strength and latency

7.2.3

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

Within the last decade, BOLD-based functional magnetic resonance imaging has become the most widely used noninvasive method for investigating the functional system of the human brain. However, the BOLD response is a very complex signal produced by a number of interacting processes. The investigation of the BOLD response itself can further our understanding of the functional contribution of the BOLD signal. Looking for characteristic properties of the BOLD signal, we revealed a strong correlation between BOLD signal strength and latency. To determine the BOLD signal latency, we used the phase shift of the spectral analysis method as well as time-to-peak calculated from trial-averaged time courses. For both latency measures, we observed a high correlation between BOLD signal strength and latency. Moreover, we have shown that this correlation is independent of the length of visual stimulation. Thus, the correlation between BOLD signal strength and latency seems to be an inherent property of the BOLD response that is independent of the length of stimulation and can be observed using different methods of determining signal latency.

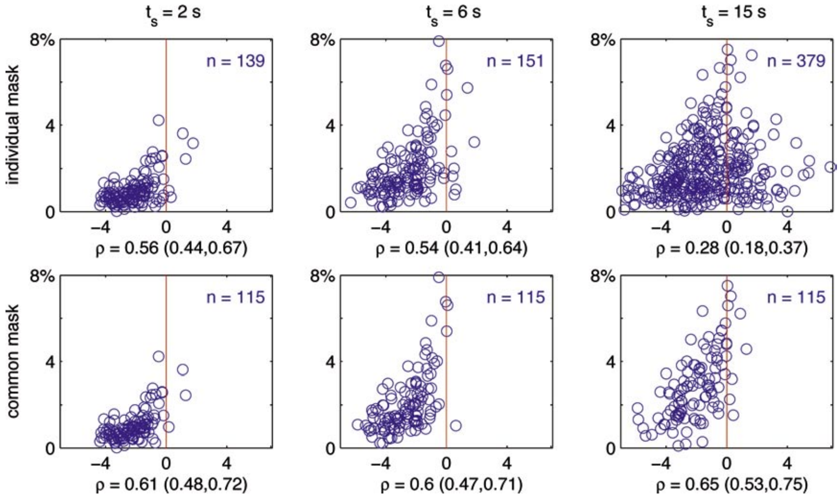

Figure 7.8 Dot plots showing the dependence between BOLD signal strength and phase shift for an individual subject. In the first row, all voxels showing significant activation in the individual runs were included in the analysis. With increasing stimulation length, the number of activated voxels increases and the correlation between signal strength and phase shift decreases. The second row shows only voxels activated in all 3 runs. For these voxels, the correlation between signal strength and phase shift is around 0.6 independent of the length of visual stimulation. Confidence intervals are provided for an error probability of 0.05.

7.2.4 Magnetic resonance imaging of the human frontal cortex reveals differential anterior-posterior variability of sulcal basins

Huttner, H.B.[1], Lohmann, G.[2] & von Cramon, D.Y.[2]

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[2] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig · Munich, Germany

In this project, we analyzed MRI data of 100 healthy human brains. Our aim was to establish a neuroanatomical map of the most frequently occurring 'sulcal basins' of the human frontal cortex. Sulcal basins are defined to be concavities in the white matter surface that constitute components of entire sulci. The sulcal basins were found to fall into two groups, one containing on average eight anterior basins in the prefrontal and premotor region, and the other containing four posterior basins in the motor region of the frontal lobe (Figure 7.9A). We determined their volume, depth and inter-individual variability (Figure 7.9B). We found that, compared to posterior basins, anterior basins are characterized by lower volume and depth. Furthermore, they showed greater inter-individual variability in volume, depth and occurrence. Our results indicate the existence of a mechanism for cortical folding, which shows a greater flexibility in the phylogenetically younger, anterior prefrontal areas.

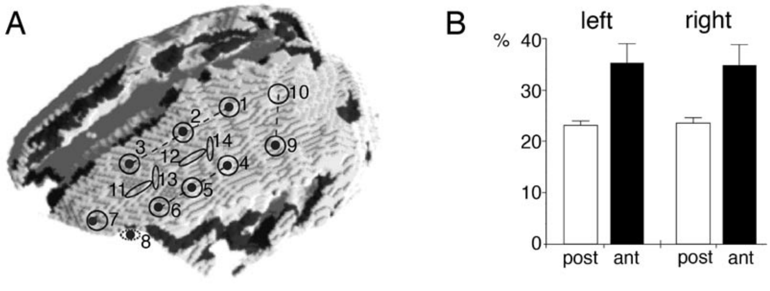

Figure 7.9 (A) The fundus regions of the various sulcal basins are shown schematically on a lissencephalic brain from a top left view. Each basin constitutes either a segment of a sulcus or a complete sulcus. (B) For each of the 100 human individuals, the percent deviation in the volume of a given basin from the mean volume for this basin in all 100 cases was determined. The mean of this deviation for the 100 individuals was calculated and is referred to as variability in volume of each basin. The mean variability of the anterior versus posterior basins of the left and right hemisphere is shown.

During the last two years, members of our group have conducted studies within different fields of cognitive neuroscience and methodology.

Processing Meaning. Correct and semantically incorrect sentences were presented auditorily during magnetoencephalographic recordings (7.3.1). Distributed source modeling of the evoked N400m effect indicated specific regions for processing of semantic anomalies and a temporal lead for the processing of correct sentences. In another study, a strong coupling of θ-phase and γ-amplitude during the earlier phase of stimulus processing was found for visual processing of meaningful and non-meaningful pictures (7.3.2). Partial directed coherence analysis (PDC) was applied to data of two further EEG studies. Semantical context was varied by auditory presentation of words and pseudo-words (7.3.3) or visual presentation of recognizable and non-recognizable pictures (7.3.4). Beta-Band coherences within the time range of the N400 effect were found to be sensitive to more intensive semantical memory search.

Music. The Closure Positive Shift (CPS) component is a neural correlate for phrase boundary perception in music. In both EEG and MEG studies, the influence of musical expertise and systematic variation of local acoustic cues at the phrase boundary on the CPS(m) were studied (7.3.5). In a further EEG study (7.3.6), the N2b component varied between groups of Western and Chinese musicians as a function of the musical style (Western or Chinese). The CPS response was found to be indicative for a general phrase processing independently of musical styles and cultural background.

Counting. Enumerating the number of items in a set is a basic mathematical skill. The time course of EEG activation was measured in a task involving both enumeration and discrimination (7.3.7). Discrimination mainly affected the earlier ERP, whereas enumeration varied later responses (beyond 200 ms).

Modeling. The influence of structural and electrical anisotropy in both the skull and the white matter conductivity on the EEG and MEG source reconstruction was thoroughly investigated and field distributions, isopotential surfaces, volume correct as well as statistical error measures were visualized (7.3.8).

Anatomical Connectivity. Methods to parcellate Broca's area based on diffusion tensor imaging (DTI) MR data were developed (7.3.9). Connectivity signatures extracted from probabilistic tractography were analyzed by an automatic clustering method to identify cortical regions, here putatively BA 44, BA 45, and the deep frontal operculum. This technique provides, for the first time, a means to investigate the anatomical subdivision of Broca's area in the individual living subject.

Rehabilitation. The effect of repeated execution of extension and flexion movement of the wrist on the sensorimotor cortex activation was studied (7.3.10) by means of MEG. The sensorimotor training increased the dipole magnitude reflecting the activity of efferent neurons, whereas the magnitude of propriospective afferent neuronal activity was not affected.

7.3.1 Localizing the distributed language network responsible for the N400 measured by MEG during auditory sentence processing

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We studied auditory sentence comprehension using magnetoencephalography, while subjects had to judge the correctness of sentences. The localization and the time course of brain electrical activity during processing of correct and semantically incorrect sentences were estimated by computing a brain surface current density within a cortical layer for both conditions. Finally, a region of interest (ROI) analysis was conducted to determine the time course of specific locations. Regions were determined as local maxima of current density elicited by the semantically incorrect condition at latency 500 ms.

The magnetic N400 effect was present in six different ROIs. Significance was tested for different ROIs and time windows separately, and is visualized by gray bars in Figure 7.10. Semantic anomalies caused an exclusive involvement of the left inferior frontal gyrus (BA 47) and left Broca's region (BA 44/45). The anterior parts of the superior (BA 22) and inferior (BA 20/21) temporal gyri bilaterally were activated by both conditions. The activation for the correct condition, however, peaked earlier in both left temporal regions (approx. 32 ms). In general, activation due to semantic violations was more pronounced, started later and lasted longer as compared to correct sentences.

The findings reveal a clear left hemispheric dominance during language processing first by the mere number of regions showing a condition effect (four in the left vs. two in the right hemisphere), and second by the observed specificity of the left frontal ROIs (left Broca and left inferior frontal) to semantic violations.

The temporal advantage observed for the correct condition in the left temporal regions supports the notion that the established context primes the final word. Semantically incorrect words, which do not fit into the primed context, result in longer integration times probably due to longer search in memory.

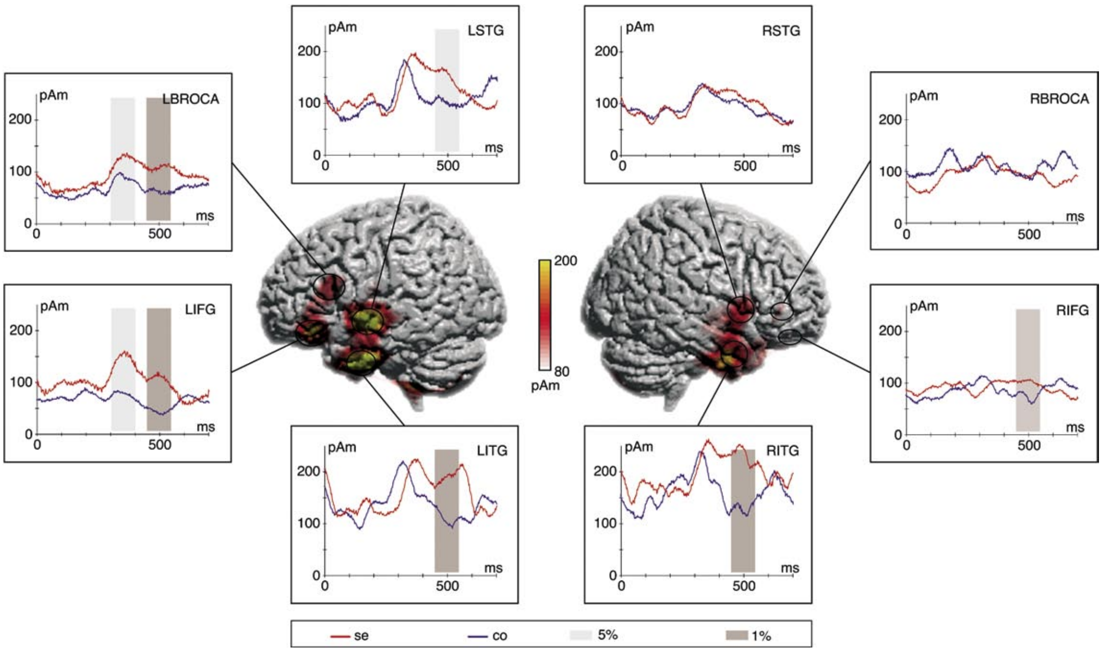

Figure 7.10 Views onto the left and right hemispheres displaying the mean current distribution of the semantically incorrect condition at a latency of 350 ms. The mean time courses for each of the specified regions of interest (ROI) and the two experimental conditions are displayed in boxes: red – semantically incorrect, blue – correct. The ROIs are visualized by black outlines.

Evidence for gamma-amplitude to theta-phase coupling in human EEG — 7.3.2

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Demiralp, T.[1,2], Bayraktaroglu, Z.[1], Lenz, D.[2], Junge, S.[2], Busch, N.A.[2], Maess, B.[3], Ergen, M.[1] & Herrmann, C.S.[2]

Human subjects typically keep about seven items (plus or minus two) in short-term memory (STM). A theoretical neuronal model has been proposed to explain this phenomenon with physiological parameters of brain oscillations in the gamma and theta frequency range, i.e., roughly 30–80 and 4–8 Hz, respectively. In that model, STM capacity equals the number of gamma cycles (e.g., 25 ms for 40 Hz) which fit into one theta cycle (e.g., 166 ms for 6 Hz). The model is based on two assumptions: (1) Theta activity should modulate gamma activity and (2), the theta/gamma ratio should correlate with human STM capacity. The first assumption is supported by electrophysiological data showing that the amplitude of gamma oscillations is modulated by the phase of theta activity. However, so far, this has only been demonstrated for intracranial recordings. We analyzed human event-related EEG oscillations recorded in a memory experiment, in which 13 subjects perceived known and unknown visual stimuli (see Figure 7.11).

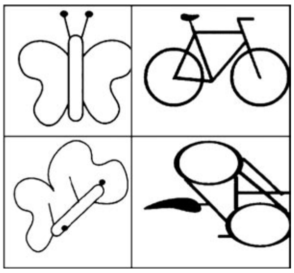

Figure 7.11 Four examples of the stimuli used in our experiment. Top: For a butterfly (left) and a bicycle (right) subjects already have representations in their long-term-memory. Bottom: For the distorted versions of these objects, no such memory representations exist. Objects in the left column were supposed to be judged as round objects, while those in the right column were supposed to be judged as edgy.

Subjects had to judge whether the presented objects were round or edgy and to press a button accordingly. The paradigm revealed event-related oscillations in the gamma range, which depended significantly on the phase of simultaneous theta activity during the first 300 ms after stimulus onset (see Figure 7.12). Note, there was no significant enhancement of gamma amplitudes during the later time window 500–800ms.

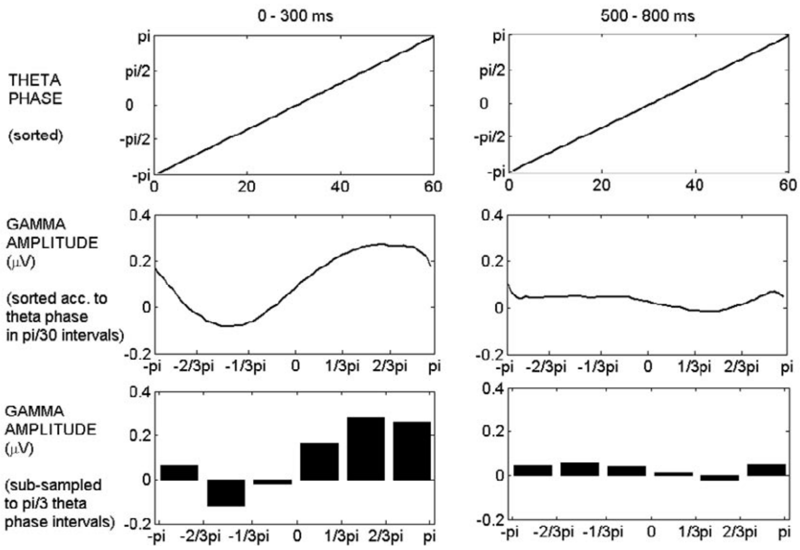

Figure 7.12 Grand average of the sorted mean theta phases within $\pi/30$ intervals (upper row). Grand average of the gamma amplitudes (middle row) and sub-sampled gamma amplitudes (lower row) sorted according to the theta phase. The left column shows the results obtained for the early (0–300 ms) and the right column for the late time window (500–800 ms). For the early time window (0–300 ms), the gamma amplitudes were significantly larger during positive theta phases compared with those occurring during negative theta phases (F (5,60) = 8.28; $p <$ 0.002) with a maximum at $2/3\ \pi$ and a minimum at $-2/3\ \pi$.

Our data seem to support the notion that gamma activity is modulated by the theta phase (Lakatos et al., 2005). However, our results do not exactly resemble the ones of that study, which is based on the measurement of current source densities in the auditory cortex of macaques with implanted multi-contact electrodes. While Lakatos et al. (2005) correlated the gamma amplitude and theta phase of spontaneous oscillations, we observed such correlations in event-related oscillations. In addition, the correlation was only evident during the first 300 ms after stimulation but not during the later time interval. This difference might be due to the spatial extent of the signals measured with both techniques. The spontaneous gamma-theta coupling observed in the local circuits with intracranial measurements might not be observable in the scalp recordings, because of the superimposition of a wide range of theta and, to a lesser extent, gamma oscillations from neighboring structures due to spatial smearing in surface recordings. However, as more specific and local generators would be responsible for the event-related activity, the event-related gamma and theta oscillations might stem from a more local and more specific network, in which they interact with each other.

Our data are the first scalp-recorded human EEG recordings revealing a relationship between the gamma amplitude and the phase of theta oscillations, supporting the first assumption of the abovementioned theory. Interestingly, the involved frequencies revealed a 7:1 ratio. However, this ratio does not necessarily determine human STM capacity.

7.3.3 Semantic memory retrieval: Cortical couplings in object recognition in the N400 window

Supp, G.G.[1,2,3], Schlögl, A.[2], Fiebach, C.J.[4], Gunter, T.C.[1], Vigliocco, G.[5], Pfurtscheller, G.[2] & Petsche, H.[6]

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[2] *Institute of Human-Computer Interfaces, Technical University of Graz, Austria*
[3] *Department of Neurobiology and Animal Behavior, Institute of Zoology, Karl Franzens University, Graz, Austria*
[4] *D'Esposito Neuroimaging Laboratory, Department of Psychology and Helen Wills Neuroscience Institute, University of California, Berkeley, CA*
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To characterize the regional changes in neuronal couplings and information-transfer related to semantic aspects of object recognition in humans, we used partial-directed EEG-coherence analysis (PDC). PDC seems to be advantageous over other coupling measures (such as classical coherence or phase locking statistics), since it informs us whether and how two positions under study are effectively connected, rather than merely describing mutual synchronicity. Common disturbing influences or sources (recorded at any third position) are not taken into account, so that due to this "partial" coherence approach solely direct dependencies between two positions are characterized (Baccala & Sameshima, 2001; Kaminski et al., 1997). The attribute "partial" in partial-directed coherence refers to the fact that common sources are partitioned or separated and so they do not enter the determination of PDC values. The PDC values are "directed" insofar as the obtained relationships are characterized by their direction of information transfer.

In the current study, we examined the differences of processing recognizable and unrecognizable pictures as reflected by changes in cortical networks within the time window of a determined event-related potential (ERP) component, namely the N400. Fourteen participants performed an image recognition task while sequentially confronted with pictures of recognizable and unrecognizable objects. The images of the unrecognizable objects were designed in such a manner that they physically matched the meaningful images in every possible way (e.g., complexity, part-structure, size) except for familiarity – see Kanwisher et al. (1997). That is, meaningless objects do not match any particular known object and, therefore, lack any specific reference.

Differences of PDC in the beta-band (13–30 Hz) between both conditions were represented topographically as patterns of electrical couplings, possibly indicating changing degrees of functional cooperation between brain areas.

Our PDC results obtained the following coupling patterns: Viewing meaningful, recognizable pictorial objects results in differential coupling increases in the beta frequency that involve the left anterior temporal and parietal position, forming a functional network with frontal positions during the N400 time window. This left temporo-parietal network provides enhanced information-input to bilateral frontal positions, which may reflect cortical coupling patterns underlying successful semantic memory retrieval in response to meaningful pictorial objects. This proposal is in line with the general conjecture to regard the N400 time window as an interval for semantic processing. Finally, the greater number of coherence increases for meaningless object processing suggests enhanced recruitment of more distributed left and right areas during unsuccessful memory search (Supp et al., 2005).

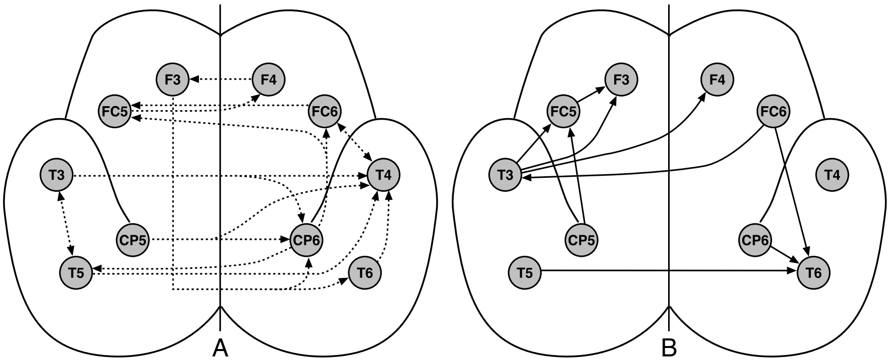

Figure 7.13 Figure A on the left displays significant coherence increases in beta-frequency range for meaningless pictures (as compared to meaningful pictures) within the time window of the N400 (meaningless > meaningful), and B on the right shows coherence increases for recognizable objects compared to unrecognizable objects (meaningful > meaningless). The arrows indicate the direction of information transfer. For all: significance level $p < 0.05$.

7.3.4 Lexical memory search during N400: Cortical couplings in auditory comprehension

Supp, G.G.[1,2,3], Schlögl, A.[2], Gunter, T.C.[1], Bernard, M.[2,4], Pfurtscheller, G.[2] & Petsche, H.[5]

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Event-related potentials (ERPs) have repeatedly informed cognitive neuroscientists about the time course of language comprehension. Semantic processing, for instance, is reflected in a negative ERP component peaking around 400 ms post-stimulus (N400). The amplitude of the N400 varies systematically with the processing of potentially meaningful stimuli at the level of meaning. The N400 is smaller for words when compared to pseudo-words, suggesting a more extensive search in semantic memory for the pseudo-words (Kutas & Federmeier, 2000).

The N400 response is generally addressed as an index of semantic processes reflecting temporally restricted brain activity that results from interlinked sets of brain areas in both hemispheres, each providing a distinct contribution. However, standard ERP methods focused on amplitude changes of the ongoing EEG are restricted to local changes of the voltage fields and, consequently, do not detect coupling changes between two (or more) concurrently measured EEG signals. Only methods such as partial-directed coherence (PDC) analysis (and other coupling measures) directly quantify the coupling level between EEG signals shedding light on the questions of transient cortical connections (Varela et al., 2001; Baccala & Sameshima, 2001).

In the present study, we applied such an EEG coupling measure to characterize cortical interactions that are established during the N400 time window in response to spoken stimuli. Specifically, we investigated whether the processing differences between words and pseudo-words are reflected by specific changes of cortical networks of information transfer, established within the time window of the N400. In a lexical decision task, twelve native speaking German subjects were confronted sequentially with two-syllabic concrete German nouns and phonologically legal pseudo-words (mean articulatory duration: 470 ms +/– 70 ms), while their EEG was recorded. The ERP epochs were averaged separately for both conditions from stimulus onset to 1000 ms post-stimulus, relative to a 200 ms pre-stimulus baseline. According to visual inspection and subsequent ANOVA analysis the N400 effect occurred in the interval of 550–700 ms (F (1,11) = 20.93, $p < 0.0008$), evenly distributed over both hemispheres. Next, we carried out a partial-directed EEG-coherence (PDC) analysis that provide information on both, the neural cooperation level and the direction of information flow, established during the time window of the N400.

The most striking finding is the prominent coherence increase in the beta-frequency band (13–30 Hz) between temporal, parietal and frontal areas restricted to the left hemisphere for pseudo-words, while word processing is associated with an almost exclusive increase of inter-hemispheric interactions. We conclude that this network of coherence changes may reflect search processes within the semantic memory (Supp et al., 2004).

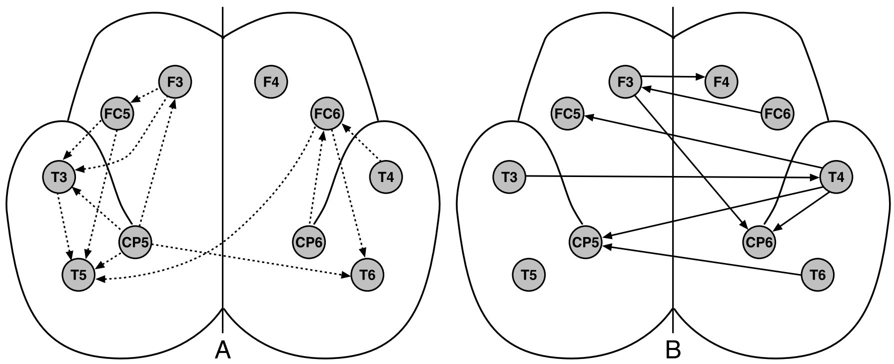

Figure 7.14 Figure A on the left: Coherence increases for auditory pseudo-words (in relation to auditory words) within the time window of the N400 (meaningless > meaningful) for the beta-frequency range (13–30 Hz). The arrows indicate coherence increase and the direction of information transfer for pseudo-words in relation to words. Figure B on the right: Coherence increases for words in relation to pseudowords (meaningful > meaningless). The arrows depict coherence increase and the direction of information transfer. For all: significance level $p < 0.05$.

7.3.5 Effects of musical expertise and boundary markers on phrase perception in music

Neuhaus, C., Knösche, T.R. & Friederici, A.D.

The Closure Positive Shift ('music CPS') is a neural correlate for phrase boundary perception in music. It has recently been identified in musicians and has an equivalent in speech perception. The aim of the current ERP and MEG study was to examine if musical expertise and systematic variation of local acoustic cues at the phrase boundary modify CPS amplitude and latency (Figure 7.15).

Twelve musicians and 12 non-musicians listened attentively to binary-phrased melodies and their continuous counterparts. Phrased versions evoked a CPS and a CPSm in musicians, but an early negativity and a less pronounced CPSm in non-musicians. Apparently, both subject groups use different perceptual strategies. While musicians probably perceive phrased melodies in a structured manner, non-musicians seem to react to discontinuity in the melodic input.

Furthermore, all subjects had higher amplitude values for long boundary tones combined with long pauses ('strong phrase boundary') than for short boundary tones combined with short pauses ('weak phrase boundary'). Separate manipulation of pause length (original: 498 ms, long pause: 942 ms, short pause: 112 ms) elicited a CPS for original and long pauses in musicians and an early negativity for original pauses in non-musicians. All participants revealed a similar CPSm with different amplitude values for different pause lengths.

We suggest that ERP and MEG methods are sensitive to different aspects within phrase perception. In ERP, we observe qualitatively different components for musicians and non-musicians (CPS and early negativity), which may indicate a top-down activation of different phrasing schemes. In MEG, results of both subjects groups differ only quantitatively from each other, which may reflect gradual differences in the bottom-up processing of acoustic cues.

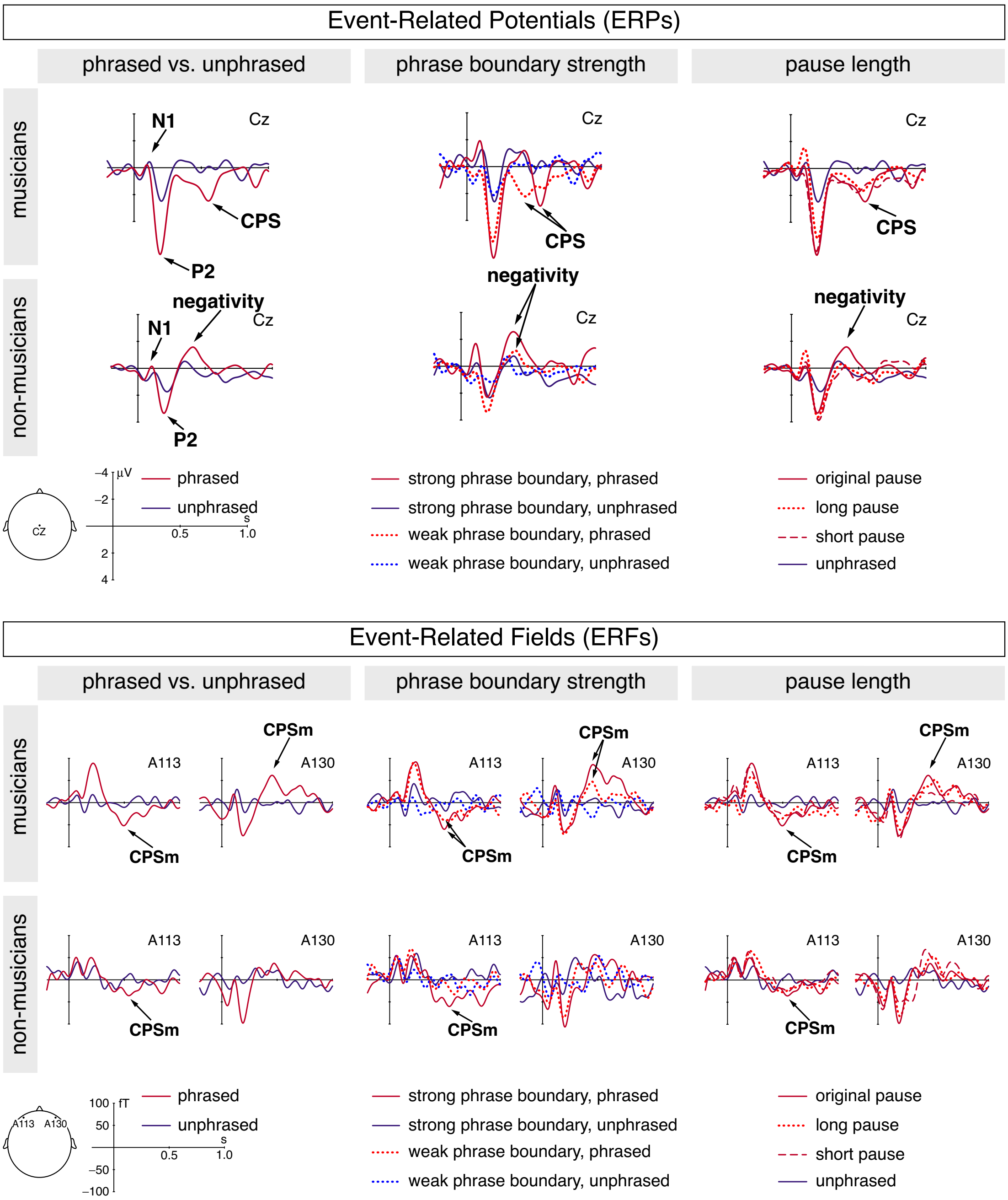

Figure 7.15 Grand average event-related potentials (ERPs) und event-related fields (ERFs) of musicians and non-musicians. Trigger point is the very onset of the second phrase.

7.3.6 The perception of music phrase structure: A cross-cultural event-related brain potentials study

Nan, Y., Knösche, T.R. & Friederici, A.D.

With EEG, the neural correlates for the phrase boundary perception of Western and Chinese musicians were compared in both Western and Chinese music listening conditions. The early components such as a positive deflection in the time window 100–300 ms (P2) and a negative deflection in the time window 300–500 ms (N2b) varied as a function of musical styles and subject group. This difference was significant between two musician groups in the time window of 300 to 500 ms (N2b), with German musicians showing larger activities compared to Chinese musicians in Chinese music condition only. We propose that phrase perception in music as registered by EEG is composed of several distinct components. The early components (P2 and N2b) are sensitive to musical styles and cultural backgrounds, while CPS is indicative for a general phrasing process, which appears to be independent of musical styles and acculturation effects.

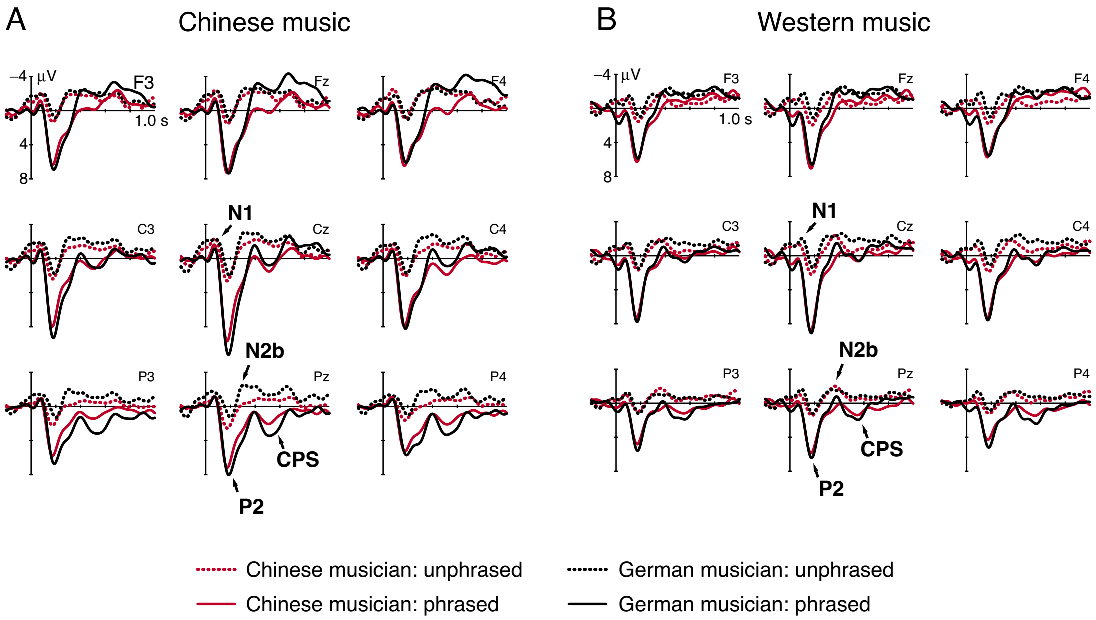

Figure 7.16 Time courses of the grand average ERPs for the main experiment. Red lines: Chinese musicians; black lines: German musicians; solid lines: *phrased* melodies, dotted lines: *unphrased* melodies.

7.3.7 Counting in everyday life: Discrimination and enumeration

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Enumerating the number of items in a set accurately and quickly is a basic mathematical skill. This ability is especially crucial in the more real-life situations, where relevant items have to be discriminated from irrelevant distracters. Although much work has been done on the brain mechanisms and neural correlates of the enumeration and/or discrimination process, no agreement has been reached yet. We used event-related potentials (ERP) to show the time course of brain activity elicited by a task that involved both enumeration and discrimination at the same time. We found that even though the two processes run to some extent in parallel, discrimination seems to take place mainly in an earlier time window (from 100 ms after the stimulus onset) than enumeration (beyond 200 ms after the stimulus onset). Moreover, electrophysiological evidence based on the N2 and P3 components make it reasonable to argue for the existence of a dichotomy between *subitising* (for sets of less than four items) and *counting* (for sets of four and more items). Source estimation suggests that *subitising* and *counting*, though distinct brain processes, do recruit similar brain areas.

Visualization of EEG/MEG volume currents in anisotropic head models

7.3.8

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Anwander, A.[1], *Wolters, C.H.*[2,3], *Tricoche, X.*[3], *Weinstein, D.*[3], *Koch, M.A.*[4] & *MacLeod, R.S.*[3]

The influence of structural and electrical anisotropy in both the skull and the white matter on the EEG and MEG source reconstruction is not well understood. We report on a study of the sensitivity to tissue anisotropy of the EEG/MEG forward problem for deep and superficial neocortical sources with differing orientation components in an anatomically accurate model of the human head. The white matter fiber directions were measured with diffusion-weighted MRI. The goal of the study was to gain insight into the effect of anisotropy of skull and white matter conductivity through the visualization of field distributions, isopotential surfaces, and return current flow and through statistical error measures. One implicit premise of the study is that factors that affect the accuracy of the forward solution will have a stronger influence on solutions than the associated inverse problem. Major findings of the study include (1), anisotropic white matter conductivity causes return currents to flow in directions parallel to the white matter fiber tracts; (2), skull anisotropy has a smearing effect on the forward potential computation; and (3), the deeper a source lies and the more it is surrounded by anisotropic tissue, the larger the influence of this anisotropy on the resulting electric and magnetic fields. Therefore, for the EEG, the presence of tissue anisotropy both for the skull and white matter compartment substantially compromises the forward potential computation and as a consequence, the inverse source reconstruction. In contrast, for the MEG, only the anisotropy of the white matter compartment has a significant effect. Finally, return currents with high amplitudes were found in the highly conducting cerebrospinal fluid compartment, underscoring the need for accurate modeling of this space.

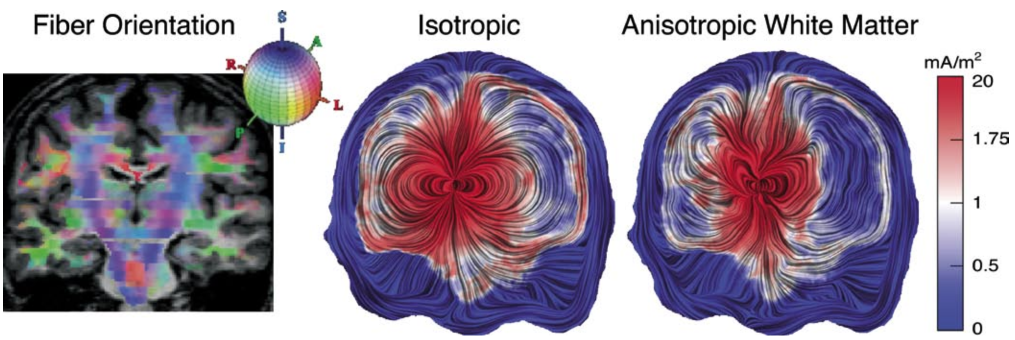

Figure 7.17 Visualization of the white matter fiber orientation measured by diffusion-weighted MRI overlaid on a coronal slice of a T_1-MRI (left). Red color indicates mediolateral, green anteroposterior and blue superoinferior orientation according to the red-green-blue sphere. Return currents for a source in the left thalamus on a coronal cut through the isotropic model (middle) and the model with 1:10 anisotropic white matter compartment (right): The return current directions are indicated by the texture and the magnitude is color coded.

7.3.9 Connectivity-based parcellation of Broca's area

Anwander, A., Tittgemeyer, M., von Cramon, D.Y., Friederici, A.D. & Knösche, T.R.

It is generally agreed that the cerebral cortex can be segregated into structurally and functionally distinct areas. Anatomical subdivision of Broca's area has been achieved using different microanatomical criteria, such as cytoarchitecture and distribution of neuroreceptors. However, for the function of cortical areas, anatomical connectivity is most relevant. Hence, connectivity forms a sensible criterion for the functio-anatomical segregation of cortical areas. Diffusion-weighted MR imaging offers the opportunity to use this criterion in the individual living subject. Probabilistic tractographic methods provide excellent means of extracting the connectivity signatures from these data sets. The correlations between these signatures are then used by an automatic clustering method to identify cortical regions with mutually distinct and internally homogeneous connectivity. We use this principle to parcellate Broca's area and to identify the typical connectivity patterns of putative BA 44, BA 45, and the deep frontal operculum. These results are discussed in the light of previous evidence from other methods in both human and non-human primates. We conclude that plausible results can be achieved by the proposed technique, which cannot be obtained by any other method in vivo. For the first time, there is a possibility to investigate the anatomical subdivision of Broca's area in the individual living human subject.

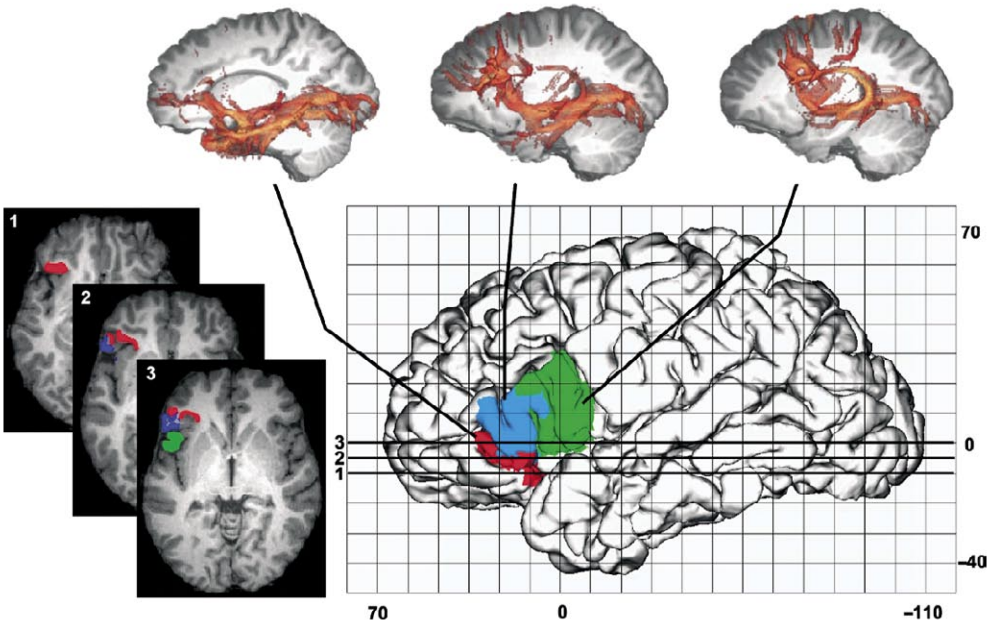

Figure 7.18 Parcellation of the left inferior frontal cortex into three clusters and corresponding signatures for a representative subject plotted on the Talairach-scaled cortical surfaces. Insets show axial slices at three different levels that cut through the parcellated area.

7.3.10 Rapidly induced changes in neuromagnetic fields following repetitive hand movements

Woldag, H.[1], Waldmann, G.[1], Knösche, T.R.[2], Maess, B.[2], Friederici, A.D.[2] & Hummelsheim, H.[1]

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Sensory feedback plays a major role in movement execution and motor learning, particularly in motor rehabilitation. While elaborating therapeutic strategies, it is of interest to visualize the effect of a therapeutic intervention at the moment of its application. Therefore, we analyzed the effect of repeated execution of a simple extension and flexion movement of the wrist on the sensorimotor cortex of seven healthy subjects using magnetoencephalography. Current dipoles were used to quantify the strength of cortical activation. Our results showed an increase of dipole magnitude reflecting activity of efferent neurons even after 15 minutes, whereas the dipole magnitude of proprioceptive afferent neurons was not affected. Since only dipole magnitudes of efferent activity increased, it is likely that this reflects phenomena of long-term potentiation.

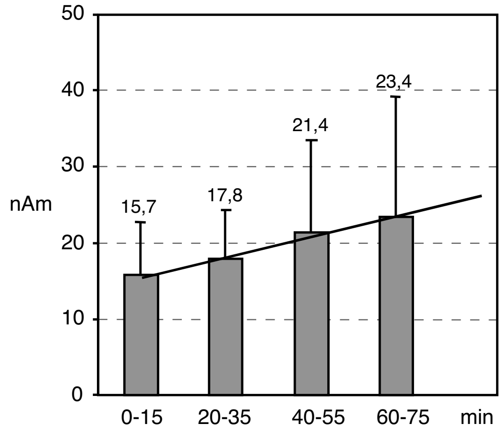

Figure 7.19 Motor field mean power in dipole position corresponding to the region of the primary motor area over 4 blocks in one session of repetitive sensorimotor training. The line indicates the increasing trend of the dipole power.

CONGRESSES 8.1

2004

14th Evoked Potentials International Conference (EPIC XIV)
A.D. Friederici[1], T.C. Gunter[1], T. Gruber[2], C.S. Herrmann[3], T. Jacobsen[2], J.D. Jescheniak[2], M.M. Müller[2], E. Schröger[2] & A. Widmann[2]
University of Leipzig, Germany, March 28–31

[1] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig · Munich, Germany
[2] Institute for Psychology I, University of Leipzig, Germany
[3] Department of Psychology, Otto von Guericke University, Magdeburg, Germany

EuroScience Open Forum (ESOF) 2004
A.D. Friederici (Member of the Program Committee)
Stockholm City Conference Center, Sweden, August 25–28

2005

The Neurosciences and Music II – From Perception to Performance
E. Altenmüller[1], G. Avanzini[2], A.D. Friederici[3], S. Koelsch[3], M. Majno[4] & C. Pantev[5]
Westin Hotel, Leipzig, Germany, May 5–8

[1] University for Music and Drama, Hanover, Germany
[2] National Neurologic Institute "C. Besta", Milan, Italy
[3] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig · Munich, Germany
[4] Fondazione Pierfranco e Luisa Mariani, Milan, Italy
[5] Institute for Biomagnetism and Biosignalanalysis, Münster University Hospital, Germany

6th Schloessmann Seminar on Cognitive Neuroscience of Human Ontogeny
U. Lindenberger[1] & A.D. Friederici[2]
Hotel Döllnsee-Schorfheide, Großdölln/Berlin, Germany, June 4–12

[1] Max Planck Institute for Human Development, Berlin, Germany
[2] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig · Munich, Germany

European Science Foundation Workshop 'Person Perception during Infancy: Integrating Developmental and Comparative Psychology, Cognitive Neuroscience, Psychology of Language and Communication'
T. Striano[1,2] & V.M. Reid[2]
Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany, June 26–30

[1] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig · Munich, Germany
[2] Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

X[th] International Congress for the Study of Child Language (IASCL)

D. Bittner[1], B. Höhle[2], N. Gagarina[1], C. Kauschke[3], G. Klann-Delius[3] & J. Weissenborn[4]

Henry Ford Building, Freie Universität Berlin, Germany, July 25–29

[1] Centre for General Linguistics, Typology and Universals Research, Berlin, Germany
[2] Linguistics Department, University of Potsdam, Germany
[3] Department of Philosophy and Humanities, Freie Universität Berlin, Germany
[4] Department of German Language and Linguistics, Humboldt University, Berlin, Germany

IX[th] International Conference on Neuroscience (ICON9)

A.D. Friederici (International Scientific Committee Member)

Cuban Neuroscience Center, Havana City, Cuba, September 5–10

Anniversary of the Centre for Cognitive Sciences (ZfK) at the Centre for Advanced Study (ZHS) of the University of Leipzig

A.D. Friederici[1,2], M. Middell[2], E. Schröger[3], T. Jacobsen[3], J.D. Jescheniak[3], M.M. Müller[3], R. Rübsamen[3], D.Y. von Cramon[1,3] & G. Zybatow[3]

Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany, October 27

[1] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig · Munich, Germany
[2] Centre for Cognitive Sciences, Centre for Advanced Study, University of Leipzig, Germany
[3] Centre for Advanced Study, University of Leipzig, Germany

2004

Symposium 'Making Minds'
P. Hauf[1], F. Försterling[2], G. Knoblich[1] & W. Prinz[1]
Kloster Irsee, Germany, January 29 – Feburary 1

[1] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig · Munich, Germany
[2] Ludwig Maximilians University, Munich, Germany

Symposium 'On Willing and Doing' [Sponsored by the Volkswagen Foundation]
T. Vierkant[1], S. Maasen[2] & W. Prinz[1]
Max Planck Institute for Human Cognitive and Brain Sciences, Munich, Germany, February 17–19

[1] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig · Munich, Germany
[2] University of Basel, Switzerland

Workshop 'Textverstehen und Textproduktion bei Aphasie: Diagnostik und Therapie'
E. Ferstl[1] & B. Engell[2]
February 28 (7. Würzburger Aphasie-Tage, Würzburg, Germany, February 26–28)

[1] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig · Munich, Germany
[2] Department of Psychology, RWTH Aachen University, Germany

Symposium 'Process-Based and Code-Based Interference in Dual-Task Performance'
I. Koch[1], S. Schuch[1] & P. Jolicoeur[2]
Hotel Alpenblick, Ohlstadt, Germany, February 27–29

[1] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig · Munich, Germany
[2] Department of Psychology, University of Montreal, QC, Canada

Post-Conference Workshop 'Language Acquisition'
K. Lindner[1], J. Meibauer[2] & A. Hohenberger[3]
February 28 (26. Kongress der Deutschen Gesellschaft für Sprachwissenschaft (DGfS), Mainz, Germany, February 25–27)

[1] Ludwig Maximilians University, Munich, Germany
[2] Johannes Gutenberg University, Mainz, Germany
[3] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig · Munich, Germany

Symposium 'Processing Words and Sentences: ERP Evidence from Patients'
S.A. Kotz
March 31 (14th Evoked Potentials International Conference (EPIC XIV), University of Leipzig, Germany, March 28–31)

Symposium 'Emotional Perception'
A. Schirmer
March 31 (14th Evoked Potentials International Conference (EPIC XIV), University of Leipzig, Germany, March 28–31)

Symposium 'Objektrepräsentation und Kategorisierung'
M. Graf[1] & M. Kiefer[2]
April 7 (46. Tagung experimentell arbeitender Psychologen (TeaP), Justus Liebig University, Gießen, Germany, April 4–7)

[1] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig · Munich, Germany
[2] Department of Psychiatry III, University of Ulm, Germany

Symposium 'Reaktionskonflikt und Handlungsauswahl'
I. Koch & A.M. Philipp
April 7 (46. Tagung experimentell arbeitender Psychologen (TeaP), Justus Liebig University, Gießen, Germany, April 4–7)

Symposium 'Munich Encounters in Cognition and Action (MECA VIII): The Homunculus in Action Control'
I. Koch
Max Planck Institute for Human Cognitive and Brain Sciences, Munich, Germany, May 7

Symposium 'Interaction between Perception and Action in Infancy'
P. Hauf & G. Aschersleben
May 8 (14th Biennial International Conference on Infant Studies, Chicago, IL, May 5–8)

Symposium 'Handlungsrepräsentationen in einfachen und komplexen Bewegungsaufgaben – Von den Grundlagen zur Praxis'
M. Weigelt[1] & F. Engel[2]
May 21 (36. Jahrestagung derArbeitsgemeinschaft für Sportpsychologie, Halle/Saale, Germany, May 20–24)

[1] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig · Munich, Germany
[2] Deutsche Sporthochschule, Cologne, Germany

LEDA Workshop on Electrodermal Activity
C. Kaernbach[1] & S. Koelsch[2]
Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany, May 26

[1] Computational Psychology, Karl Franzens University, Graz, Austria
[2] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig · Munich, Germany

Workshop 'Neuro-Cognitive Bases of Task Control'
M. Brass[1], I. Koch[1] & N. Meiran[2]
Kloster Nimbschen, Grimma, Germany, June 3–6

[1] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig · Munich, Germany
[2] Ben-Gurion University of the Negev, Beer-Sheva, Israel

Expert Symposium 'Kognitionsforschung'
W. Prinz, D.Y. von Cramon & A.D. Friederici
Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany, June 7–8

Workshop 'Action Representation'
G. Rapinett, M. Rieger & W. Prinz
Max Planck Institute for Human Cognitive and Brain Sciences, Munich, Germany, June 15

Workshop 'Intention and Action'
M. Grosjean[1] & H. Bekkering[2]
Max Planck Institute for Human Cognitive and Brain Sciences, Munich, Germany, July 20

[1] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig · Munich, Germany
[2] Nijmegen Institute for Cognition and Information (NICI), University of Nijmegen, The Netherlands

Symposium 'The Cognitive and Neural Substrates of Action Control: Part I'
M. Weigelt[1] & E. Hazeltine[2]
Max Planck Institute for Human Cognitive and Brain Sciences, Munich, Germany, July 30

[1] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig · Munich, Germany
[2] Department of Psychology, University of Iowa, Iowa City, IA

Workshop 'Brain Correlates of Emotional Perception in Communication'
S.A. Kotz & A. Schirmer
Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany,
September 2–5

Symposium 'Munich Encounters in Cognition and Action (MECA IX): Ago Ergo Sum – The Development of Action Understanding'
P. Hauf & G. Aschersleben
Max Planck Institute for Human Cognitive and Brain Sciences, Munich, Germany, November 5

Berichtstreffen des DFG-Schwerpunktprogramms 'Exekutive Funktionen'
I. Koch & A.M. Philipp
Max Planck Institute for Human Cognitive and Brain Sciences, Munich, Germany, December 2–5

2005

Workshop '(In-)Determinisms in Language Acquisition'
A. Hohenberger[1], C. Plaza Pust[2] & A. Peltzer-Karpf[3]
February 23 (27. Kongress der Deutschen Gesellschaft für Sprachwissenschaft (DGfS),
Cologne, Germany, February 23–25)

[1] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig · Munich, Germany
[2] Johann Wolfgang Goethe University, Frankfurt/Main, Germany
[3] Karl Franzens University, Graz, Austria

Workshop 'Gestalttheorie und neue Befunde der Gehirnforschung – Geht das zusammen?'
F. Mechsner
February 26 (14. Wissenschaftliche Arbeitstagung der Gesellschaft für Gestalttheorie und ihre
Anwendungen (GTA), Graz, Austria, February 24–27)

Workshop 'Gestalttheorie und Sport'
F. Mechsner
February 27 (14. Wissenschaftliche Arbeitstagung der Gesellschaft für Gestalttheorie und ihre
Anwendungen (GTA), Graz, Austria, February 24–27)

Colloquium 'Forschungsplanung 2005–2010'
W. Prinz
Kloster Irsee, Germany, March 8–10

Workshop 'Crosstalk Meeting'
W. Prinz
Max Planck Institute for Human Cognitive and Brain Sciences, Munich, Germany, March 11

Symposium 'Cross-Domain Longitudinal Study of Infant Cognition and its Relation to Mother/Child Interaction'
G. Aschersleben[1], A. Hohenberger[1], S. de Schonen[2], M. Elsabbagh[3] & A. Karmiloff-Smith[3]
March 30 (Quinquennial Conference of the British Psychological Society, Manchester, England, UK, March 30 – April 2)

[1] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig · Munich, Germany
[2] Developmental Neurocognition Group, Centre National de la Recherche Scientifique (CNRS), Paris, France
[3] Neurocognitive Development Unit, Institute of Child Health, London, England, UK

Symposium 'Pragmatik und Kontext: Neurowissenschaftliche Studien zum Textverstehen'
E.C. Ferstl[1] & F. Schmalhofer[2]
April 6 (47. Tagung experimentell arbeitender Psychologen (TeaP), Regensburg, Germany, April 4–6)

[1] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig · Munich, Germany
[2] Faculty of Sciences, University of Osnabrück, Germany

Symposium 'Neurokognition von Sprache'
D. Koester[1] & C.K. Friedrich[2]
April 6 (47. Tagung experimentell arbeitender Psychologen (TeaP), Regensburg, Germany, April 4–6)

[1] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig · Munich, Germany
[2] Department of Linguistics, University of Konstanz, Germany

Symposium 'Untersuchung von Verhaltenshemmung mit dem Go/No-Go Paradigma'
A.M. Philipp[1] & S. Karch[2]
April 6 (47. Tagung experimentell arbeitender Psychologen (TeaP), Regensburg, Germany, April 4–6)

[1] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig · Munich, Germany
[2] Psychiatric Hospital, Ludwig Maximilians University, Munich, Germany

Symposium on Argument Comprehension from a Cross-Linguistic Perspective – Part I: Hindi and Turkish [Co-Sponsored by the MPI-NWO Grant 'Incremental Interpretation of Case and Prominence']
I.D. Bornkessel[1] & M. Schlesewsky[2]
Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany, April 25–26

[1] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig · Munich, Germany
[2] Junior Research Group Neurolinguistics, Department of Germanic Linguistics, University of Marburg, Germany

4th Sino-German Workshop [Leipzig Part]
A.D. Friederici & S.-A. Rüschemeyer
Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany, May 7–9

Workshop 'Effects of Warning Signals and Accessory Stimuli'
W. Prinz
Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany, May 9–10

Symposium 'Munich Encounters in Cognition and Action (MECA X): The Secret Life of the Somato-sensory Cortex'
R. Laboissière
Max Planck Institute for Human Cognitive and Brain Sciences, Munich, Germany, May 20

Symposium 'Interactions between Perception and Action'
M. Grosjean & W. Prinz
July 4 (9th European Congress of Psychology, Granada, Spain, July 3–8)

Symposium 'The Cognitive and Neural Substrates of Action Control: Part II'
M. Weigelt[1] & O. Oullier[2]
Max Planck Institute for Human Cognitive and Brain Sciences, Munich, Germany, July 8

[1] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig · Munich, Germany
[2] Centre National de la Recherche Scientifique (CNRS), Marseille, France

Workshop 'Sequential Structure in Perception and Action'
I. Koch[1] & R. Radach[2]
Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany, July 26

[1] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig · Munich, Germany
[2] Department of Psychology, Florida State University, Tallahassee, FL

Workshop 'A Psychological Approach to Human Voluntary Movements: Issues, Problems, and Controversies'
F. Mechsner[1], T. Schack[2] & R. Carson[3]
August 18 (11th World Congress of the International Society of Sport Psychology (ISSP), Sydney, Australia, August 15–19)

[1] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig · Munich, Germany
[2] Deutsche Sporthochschule, Cologne, Germany
[3] School of Human Movement Studies, University of Queensland, Brisbane, Australia

Symposium 'Cross-Domain Longitudinal Study of Infant Cognition and its Relation to Mother/Child Interaction'
G. Aschersleben[1] & S. de Schonen[2]
August 25 (12th European Conference on Developmental Psychology, Tenerife, Spain, August 24–28)

[1] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig · Munich, Germany
[2] Developmental Neurocognition Group, Centre National de la Recherche Scientifique (CNRS), Paris, France

Symposium 'From Action Simulation to Action Prediction'
G. Rapinett
September 1 (14th Conference of the European Society for Cognitive Psychology (ESCoP XIV), Leiden, The Netherlands, August 31 – September 3)

Symposium 'Handlungsverständnis in den ersten zwei Lebensjahren'
B. Jovanovic[1] & T. Hofer[2]
September 15 (17. Treffen der Fachgruppe 'Entwicklungspsychologie' der Deutschen Gesellschaft für Psychologie (DGPs), Ruhr University Bochum, Germany, September 14–16)

[1] Department of Psychology/Developmental Psychology, Justus Liebig University, Gießen, Germany
[2] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig · Munich, Germany

Symposium 'Exekutivfunktionen'
R.I. Schubotz
October 7 (20. Jahrestagung der Gesellschaft für Neuropsychologie (GNP), University of Bremen, Germany, October 6–9)

Symposium of the Hannover and Leipzig Music Groups
Independent Junior Research Group 'Neurocognition of Music'[1] & Research Group around Eckart Altenmüller[2]
Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany, December 9–12

[1] Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig · Munich, Germany
[2] Institute of Music Physiology and Musicians' Medicine, Hannover University of Music and Drama, Germany

DEGREES 9.1

Professorships

2004

Dr. Günther Knoblich	Appointment to Associate Professor of Psychology Department of Psychology, Rutgers University, Newark, NJ
Dr. Harald E. Möller	Appointment to Professor of Experimental Magnetic Resonance (C3) Institute for Clinical Radiology, University of Münster, Germany
Dr. Jochen Müsseler	Appointment to Head of Research Group Institute for Occupational Physiology (IfADo), University of Dortmund, Germany
Dr. Edmund Wascher	Appointment to Professor for Ergonomics (C4) Leibniz Research Center for Working Environments and Human Factors, University of Dortmund, Germany

2005

Dr. Gisa Aschersleben	Appointment to Full Professor of Developmental Psychology (W3) Department of Psychology, Saarland University, Saarbrücken, Germany
Dr. Iring Koch	Appointment to Professor für Allgemeine Psychologie und Arbeitsphysiologie (W3) Department of Psychology, RWTH Aachen University, Germany

Habilitations

2004

Dr. Günther Knoblich — Ludwig Maximilians University, Munich, Germany
Repräsentation eigener und fremder Handlungen

Dr. Stefan Koelsch — University of Leipzig, Germany
Spatio-temporal aspects of processing syntax and semantics in music

Dr. Ricarda I. Schubotz — University of Leipzig, Germany
Human premotor cortex: Beyond motor performance

Dr. Andreas Wohlschläger — Ludwig Maximilians University, Munich, Germany
The ideomotor principle in imitation and action perception

2005

Dr. Margret Hund-Georgiadis — University of Leipzig, Germany
Die Organisation von Sprache und ihre Reorganisation bei ausgewählten neurologischen Erkrankungen gemessen mit funktioneller Magnetresonanztomographie – Einflüsse von Händigkeit, Läsion, Performanz und Perfusion

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Doctoral Degrees

Dr. med. = Doktor der Medizin/Medical Doctor
Dr. rer. nat. = Doktor der Naturwissenschaften/Doctor of Science
Dr. phil. = Doktor der Philosophie/Doctor of Philosophy

2004

Patric Bach — Dr. phil., Ludwig Maximilians University, Munich, Germany
Space and function in action comprehension

Franziska Biedermann — Dr. rer. nat., University of Leipzig, Germany
Auditorische Diskriminationsleistungen nach unilateralen Läsionen im Di- und Telenzephalon

Simone Bosbach — Dr. phil., Ludwig Maximilians University, Munich, Germany
Der Einfluss visueller Bewegungswahrnehmung auf die Steuerung von Handlungen

Katja Fiehler — Dr. rer. nat., University of Leipzig, Germany
Temporospatial characteristics of error correction

Heiko Hoffmann — Dr. rer. nat., University of Bielefeld, Germany
Unsupervised learning of visuomotor associations

Claudia Hruska	Dr. rer. nat., University of Leipzig, Germany Einflüsse kontextueller und prosodischer Informationen in der auditorischen Satzverarbeitung: Untersuchungen mit ereigniskorrelierten Hirnpotentialen
Monika Kiss	Dr. phil., Ludwig Maximilians University, Munich, Germany Searching for a color singleton among new items: No preliminary suppression of old distractor locations
Dirk Koester	Dr. rer. nat., University of Leipzig, Germany Morphology and spoken word comprehension: Electrophysiological investigations of internal compound structure
Michael Öllinger	Dr. phil., Ludwig Maximilians University, Munich, Germany Die Rolle von Einstellungseffekten und Heuristiken beim Lesen von Einsichtsproblemen
Hannes Ruge	Dr. rer. nat., University of Leipzig, Germany Eine Analyse des raum-zeitlichen Musters neuonaler Aktivierung im Aufgabenwechselparadigma zur Untersuchung handlungssteuernder Prozesse
Marc Schönwiesner	Dr. rer. nat., University of Leipzig, Germany Functional mapping of basic acoustical parameters in the human central auditory system
Stefanie Schuch	Dr. phil., Ludwig Maximilians University, Munich, Germany Task-specific coding of actions: Evidence from dual-task paradigms
Natalie Sebanz	Dr. phil., Ludwig Maximilians University, Munich, Germany You are always on my mind: Representing others' actions and intentions
Daniel Senkowski	Dr. rer. nat., University of Leipzig, Germany Neuronal correlates of selective attention: An investigation of electrophysiological brain responses in the EEG and MEG
Britta Stolterfoht	Dr. phil., University of Leipzig, Germany Processing word order variations and ellipses: The interplay of syntax and information structure during sentence comprehension
Robert Trampel	Dr. rer. nat., University of Leipzig, Germany Perfusions-Bildgebung mittels arteriellem Spin-Labeling
Kirsten G. Volz	Dr. rer. nat., University of Leipzig, Germany Brain correlates of uncertain decisions
Clemens von Zerssen	Dr. med., University of Leipzig, Germany Bewusstes Erinnern und falsches Wiedererkennen: Eine funktionelle MRT-Studie neuroanatomischer Gedächtniskorrelate

Christiane Weber — Dr. phil., University of Potsdam, Germany
Rhythm is gonna get you: Electrophysiological markers of rhythmic processing in infants with and without risk for specific language impairment

Matthias Weigelt — Dr. phil., Ludwig Maximilians University, Munich, Germany
Target-related coupling in bimanual coordination

Kathrin Wiegand — Dr. phil., Ludwig Maximilians University, Munich, Germany
Differentielle Effekte der Überlappung räumlicher Reiz- und Reaktionsmerkmale

2005

Diana Böttger — Dr. med., University of Leipzig, Germany
Aktivität im Gamma-Frequenzbereich des EEG: Einfluss demographischer Faktoren und kognitiver Korrelate

Claudia Danielmeier — Dr. rer. nat., University of Leipzig, Germany
Neuronale Grundlagen der Interferenz zwischen Handlung und visueller Wahrnehmung

Moritz de Greck — Dr. med., University of Leipzig, Germany
Die Aktivierung des motorischen Kortex bei der Verarbeitung von visuellen räumlichen Hinweisreizen

Jan Derrfuss — Dr. rer. nat., University of Leipzig, Germany
Functional specialization in the lateral frontal cortex: The role of the inferior frontal junction in cognitive control

Ulrich Drost — Dr. phil., Ludwig Maximilians University, Munich, Germany
Sensory-motor coupling in musicians

Kai Engbert — Dr. phil., Ludwig Maximilians University, Munich, Germany
Intentional action in temporal binding

Manon Grube — Dr. rer. nat., University of Leipzig, Germany
The where and when of auditory space: Evidence from patients with acquired brain lesions

Tanja Hofer — Dr. phil., Ludwig Maximilians University, Munich, Germany
Infant action understanding in the first year of life

Thies H. Jochimsen — Dr. rer. nat., University of Leipzig, Germany
Metabolic characterization of neuronal activation in the human brain by nuclear magnetic resonance

Kerstin Leuckefeld	Dr. phil., University of Potsdam, Germany The development of argument processing mechanisms in German: An electrophysiological investigation with school-aged children and adults
Susan Morgenstern	Dr. med., University of Leipzig, Germany Magnetresonanztomographische Messungen der Dicke des menschlichen Neokortex
Jutta L. Mueller	Dr. rer. nat., University of Leipzig, Germany Mechanisms of auditory sentence comprehension in first and second language: An electrophysiological miniature grammar study
Ann Pannekamp	Dr. rer. nat., Humboldt University, Berlin, Germany Prosodische Informationsverarbeitung bei normalsprachlichem und deviantem Satzmaterial: Untersuchungen mit ereigniskorrelierten Hirnpotentialen
Andrea M. Philipp	Dr. phil., Ludwig Maximilians University, Munich, Germany The cognitive representation of tasks: Exploring the role of response modalities using the task-switching paradigm
Sonja Rossi	Dr. rer. nat., University of Salzburg, Austria The role of proficiency in syntactic second language processing: Evidence from event-related brain potentials in German and Italian
Shirley-Ann Rüschemeyer	Dr. rer. nat., University of Leipzig, Germany The processing of lexical semantic and syntactic information in spoken sentences: Neuroimaging and behavioral studies of native and non-native speakers
Andrea Schankin	Dr. phil., Ludwig Maximilians University, Munich, Germany Wie entsteht visuelles Bewusstsein? Eine EKP-Studie zum Zusammenhang zwischen Aufmerksamkeit und Bewusstsein
Nikolai Steffenhagen	Dr. med., University of Leipzig, Germany Modulation von Arbeitsgedächtnisfunktionen durch Modafinil
Ulrike Toepel	Dr. phil., University of Potsdam, Germany Contrastive topic and focus information in discourse – Prosodic realisation and electrophysiological brain correlates
Michael von Mengershausen	Dr. rer. nat., University of Leipzig, Germany 3 D diffusion tensor imaging in the human brain with nuclear magnetic resonance
Selina Wriessnegger	Dr. phil., Ludwig Maximilians University, Munich, Germany Processing visual information for different purposes: An application of the sustained-transient approach to visual masking

2004

S.A. Kotz	German Research Foundation (DFG) Scientific Network "The structure of the left periphery in Germanic languages: CP- and IP-related elements in normal and impaired language" (Network member; travel, presentation and lodging for 3 years)
T. Riemer, H.E. Möller, W. Driesel & F. Seifert	Award "Förderung der Medizintechnik – Innovationswettbewerb 2004", Federal Ministry of Education and Research (BMBF)
M. Sebanz	Heinz Heckhausen Young Scientist Award, German Society of Psychology
R.I. Schubotz	Poster Award, 49th Annual Meeting of the German Society for Clinical Neurophysiology and Functional Imaging, Jena, Germany, September 2004
K.G. Volz	Best Paper Award, 2nd Conference on NeuroEconomics, Münster, Germany, May 2004
M. Weigelt	Graduate Student Research Award, North American Society for the Psychology of Sport and Physical Activity (NASPSPA)

2005

I.D. Bornkessel & M. Schlesewsky	Humboldt Research Award to Robert D. Van Valin, Jr., jointly nominated/hosted by the Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany and the University of Marburg, Germany
S. Bosbach	Otto Hahn Medal for Junior Scientists, Max Planck Society (MPG)
W. Driesel, T. Mildner & H.E. Möller	Poster Award "Honorable Mention", 13th Scientific Meeting of the International Society for Magnetic Resonance in Medicine (ISMRM)
E.C. Ferstl & T. Guthke	Promotion of Young Scientist Prize to thesis graduand Tina Jentzsch, Society for Neuropsychology (GNP)
B.U. Forstmann	Travel Award for the Society for Neuroscience Meeting, German Research Foundation (DFG), Washington, DC

G. Knoblich	Distinguished Scientific Award for Early Career Contribution to Psychology, American Psychological Association
J.L. Mueller	Schloessmann Scholarship, Max Planck Society (MPG)
S. Rossi	Poster Award, Rovereto Workshop on Bilingualism, Rovereto, Italy, October 2005
U. Toepel	Schloessmann Prize, Max Planck Society (MPG)
M. Ullsperger	Junior Fellow, Max Planck International Research Network on Aging (Maxnet Aging)
M. Weigelt	Karl Feige Prize, German Society of Sport Psychology
M. Weigelt, T. Stöckel & C. Hartmann	3rd Poster Prize, 37th Annual Meeting of the German Society of Sport Psychology

BOOKS AND BOOK CHAPTERS 10.1

Alter, K. (2004). **Neurophysiologische Grundlagen der Sprachverarbeitung.** In B. Gmelin & H. Weidinger (Eds.), *Die Erforschung des letzten Kontinents: Aktuelle Ergebnisse der Hirnforschung. Atzelsberger Gespräche der Nürnberger Medizinischen Gesellschaft, Vol. 9* (pp. 21-36), Nürnberg: Helmut Seubert.

Aschersleben, G. (in press). **Handlungswahrnehmung in der frühen Kindheit.** In L. Kaufmann, H.-C. Nuerk, K. Konrad & K. Willmes (Eds.), *Kognitive Entwicklungsneuropsychologie,* Göttingen: Hogrefe.

Aschersleben, G., Gehrke, J. & Prinz, W. (2004). **A psychophysical approach to action timing.** In C. Kaernbach, E. Schröger & H. Müller (Eds.), *Psychophysics beyond Sensation: Laws and Invariants of Human Cognition* (pp. 117-136), Mahwah, NJ: Erlbaum.

Biedermann, F. (in press). **Auditorische Diskriminationsleistungen nach unilateralen Läsionen im Di- und Telenzephalon.** In Max Planck Institute for Human Cognitive and Brain Sciences (Ed.), *MPI Series in Human Cognitive and Brain Sciences, Vol. 59,* Leipzig.

Böcker, M. & Schroeter, M.L. (in press). **Signal- und bildgebende Verfahren: Nahinfrarotspektroskopie (NIRS).** In S. Gauggel & M. Herrmann (Eds.), *Handbuch der Neuro- und Biopsychologie,* Göttingen: Hogrefe.

Bornkessel, I. & Schlesewsky, M. (in press). **Generalised semantic roles and syntactic templates: A new framework for language comprehension.** In I. Bornkessel, M. Schlesewsky, B. Comrie & A.D. Friederici (Eds.), *Semantic Role Universals and Argument Linking: Theoretical, Typological and Psycholinguistic Perspectives,* Berlin: Mouton de Gruyter.

Bornkessel, I., Schlesewsky, M., Comrie, B. & Friederici, A.D. (Eds.) (in press). **Semantic Role Universals and Argument Linking: Theoretical, Typological, and Psycholinguistic Perspectives.** Berlin: Mouton de Gruyter.

Bornkessel, I.D. & Friederici, A.D. (in press). **Neuroimaging studies of sentence and discourse comprehension.** In M.G. Gaskell (Ed.), *The Oxford Handbook of Psycholinguistics,* Oxford: Oxford University Press.

Bosbach, S. (Ed.) (2004). **Der Einfluss visueller Bewegungswahrnehmung auf die Steuerung von Handlungen.** Berlin: Wissenschaftlicher Verlag (pp. 180).

Botvinick, M.M., Braver, T.S., Yeung, N., Ullsperger, M., Carter, C.S. & Cohen, J.D. (2004). **Conflict monitoring: Computational and empirical studies.** In M.I. Posner (Ed.), *Cognitive Neuroscience of Attention* (pp. 91-102), New York, NY: Guilford Press.

Bungert, P. (2004). **Zentralnervöse Verarbeitung akustischer Informationen. Signalidentifikation, Signallateralisation und zeitgebundene Informationsverarbeitung bei Patienten mit erworbenen Hirnschädigungen.** In Max Planck Institute for Human Cognitive and Brain Sciences (Ed.), *MPI Series in Cognitive and Brain Sciences, Vol. 41,* Leipzig (pp. 139).

Danielmeier, C. (2005). **Neuronale Grundlagen der Interferenz zwischen Handlung und visueller Wahrnehmung.** In Max Planck Institute for Human Cognitive and Brain Sciences (Ed.), *MPI Series in Human Cognitive and Brain Sciences, Vol. 56,* Leipzig (pp. 91).

Derrfuss, J. (2005). **Functional specialization in the lateral frontal cortex: The role of the inferior frontal junction in cognitive control.** In Max Planck Institute for Human Cognitive and Brain Sciences (Ed.), *MPI Series in Human Cognitive and Brain Sciences, Vol. 64,* Leipzig (pp. 81).

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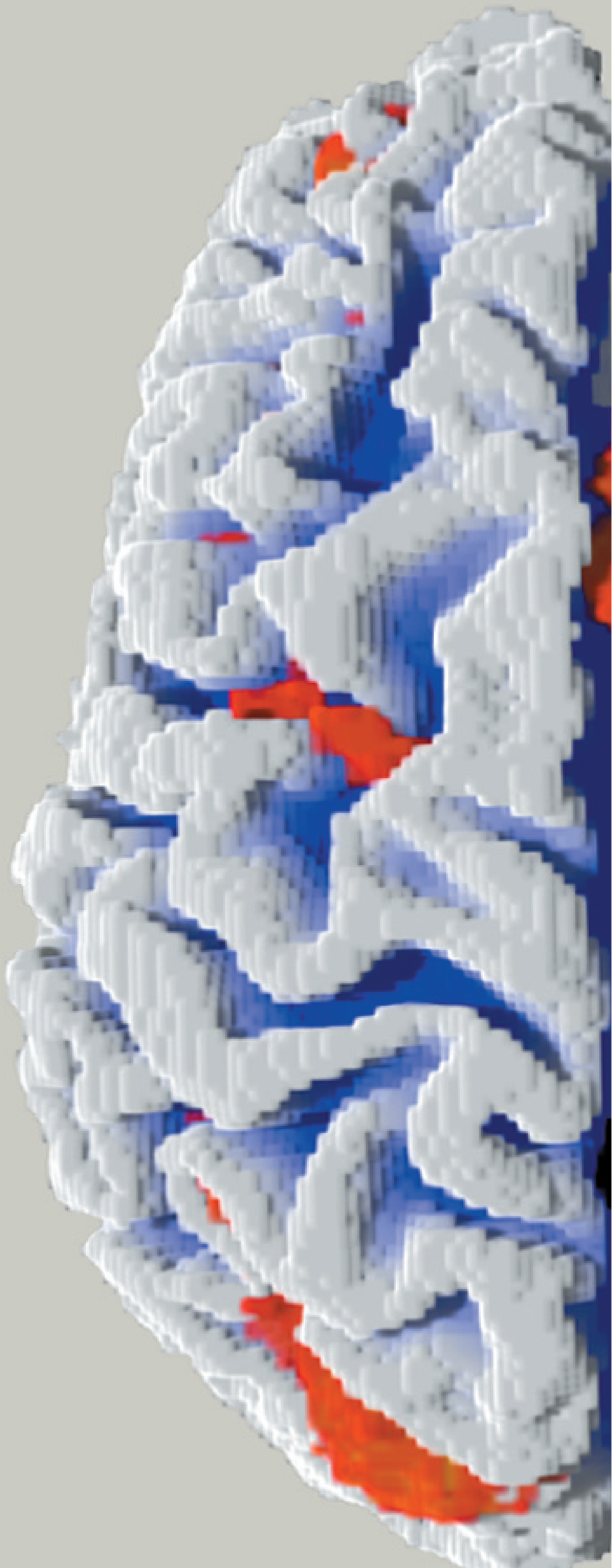

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