



Research Report
2006/2007

Max Planck Institute for
Human Cognitive and
Brain Sciences
Leipzig

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Research Report 2006/2007

The photograph on this page was taken in summer 2007, depicting the building works at our Institute. It makes the point that much of our work during the past two years has been conducted, quite literally, beside a building site. Happily, this essential work, laying the foundations for our future research, has not interfered with our scientific progress.

There were two phases of construction. The first results from the merger of both Institutes and will accommodate two new Departments including offices and multi-function laboratories (see right hand side of the photograph). We currently expect to be able to move into the new extension building in autumn 2008, which will mark the end of the building work and the provisional room arrangements with which we have now been living for some time. The second phase of building works saw the completion of the NMR building for the Institute's new 7 Tesla scanner. Although cosmetic finishing touches remain to be applied to the front of the building (see right bottom side of the picture), the scanner has been up and running since September 2007.

During the past two years, the Institute has resembled a building site not only from the outside, but also with regard to its research profile. On the one hand, D. Yves von Cramon has shifted the focus of his work from Leipzig to the Max Planck Institute for Neurological Research in Cologne. On the other hand, we successfully concluded two new appointments. Since October 2006, Robert Turner has been working at the Institute as Director of the newly founded Department of Neurophysics, which has already established itself at international level. In November 2007, Arno Villringer became Director at our Institute, taking over the leadership of the Department of Cognitive Neurology and the supervision of the University Day Clinic for Cognitive Neurology. For 2008/2009, two more appointments focusing on different domains of cognition are planned; an appointment committee has been formed by the Max Planck Section of Social Sciences and Humanities and has taken up work in September 2007.



On a smaller scale, new research groups are coming and going, too. While the Independent Junior Research Group on the Neurocognition of Music has gradually reduced its activity now that its head, Stefan Koelsch, has accepted a position abroad, two new groups have come into existence and are already starting their research: one on Music Cognition and Action (headed by Peter Keller)

and another one on Body and Self (headed by Simone Schütz-Bosbach). Besides the work of Independent Junior Research Groups, this report also covers research by the Max Planck Fellow Group on Attention and Awareness headed by John-Dylan Haynes.

D. Yves von Cramon
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Prof. Dr. D. Yves von Cramon
Director

1

Functional Neuroanatomy of the Frontal Lobe

Department of Cognitive Neurology

Studying the cognitive functions of the frontal lobe is a challenging undertaking. The work group “Functional Neuroanatomy of the Frontal Lobe” engages in this venture, aiming at a functional exploration of the various facets of this brain region in both healthy subjects and neurological patients. The underlying motivation guiding the group’s endeavours is to integrate individual findings into a unified functional framework.

Of the two projects that have investigated social interaction, one aimed to decompose the neuronal network underlying higher order intentionality (1.1.1), while the other focused on intertemporal decision making for oneself as compared to others (1.1.2). In contrast to many laboratory implementations of decision making, daily life often requires intuitive decisions, which draw particularly on orbitofrontal structures (1.1.3), and choices which are only partially determined by ourselves (1.1.4). However, before deciding what to do, we first have to decide whether to engage in an action or to refrain from it (1.1.5). While the dorsal frontomedian cortex plays a role in the intentional inhibition of action, transcranial magnetic stimulation (TMS) over the inferior frontal junction area induced disturbances in task set formation during a task switching paradigm (1.1.6).

However, even when we know what we want to do, we often make errors due to time constraints. Awareness of making errors was found to modulate insular activity reflecting autonomic reactions, whereas posterior frontomedian regions remained unmodulated (1.1.7). Interestingly, individual differences in such performance monitoring can be related to a genetic polymorphism associated with variable dopamine receptor density. Indeed, genetic differences were found to have a significant impact on the ability to learn from errors (1.1.8). The vital role of becoming aware of our own errors is to trigger adaptive behavior. The same applies for unexpected events which we observe but do not initiate ourselves. Indeed, the neural correlates of expectancy violation were found to be heavily dependent on the specific nature of

expectations (1.1.9). Such findings indicate a critical role played by the premotor system in rule-based predictive contexts, which is in line with a new framework that proposes to generalize a predictive account of the motor system from action to event perception (1.1.10). Pointing towards the same direction, motor planning and cognitive planning implemented within a modified Raven Matrices paradigm, were found to both engage comparable frontopolar as well as lateral premotor areas (1.1.11). Similar domain-general computational mechanisms were also suggested by the findings of an fMRI study in which the difficulty of goal inference was manipulated in an action observation task (1.1.12). Two further projects addressed the issue of regional differentiation within the premotor cortex. One project focused on the anatomical and functional parcellation of the precentral gyrus by combining DTI and fMRI (1.1.13). The other project investigated functional gradients within the mesial and lateral premotor cortex for anticipatory processes in the domains of action and perception (1.1.14). Furthermore, behavioral studies demonstrated that the motor and the perceptual domain are linked via timing preferences, aspects of which are intriguingly modulated by the presence of certain personality traits (1.1.15).

A systematic quantitative meta-analysis of frontotemporal dementia was placed in a framework of cognitive neuropsychiatry (1.2.1). Frontal dysfunction was investigated in three further patient studies. One project considered

its relation to neurovascular coupling impairments using functional near-infrared spectroscopy in patients suffering from cerebral microangiopathy (1.2.2). Another study used a switching paradigm together with a Stroop task and demonstrated increased distractibility and/or frequent switching between uncompleted tasks in adults with attention-deficit/hyperactivity disorder (ADHD), thereby corroborating the hypothesis of a lateral prefrontal deficit in this syndrome (1.2.3).

Finally, frontal impairments in early multiple sclerosis was found to be associated with a higher degree of cognitive control - probably as a compensatory mechanism (1.2.4). Two other clinical ERP studies investigated semantic processing using an implicit task in patients with anterior temporal lesions and found that the right, but not left, anterior temporal cortex is crucial for semantic categorization (1.2.5). In contrast, the intactness of both the right and the left anterior temporal lobe were found to be decisive for successful lexical-semantic processing of novel sounds (1.2.6).

All in all, the adoption of multiple methodologies together with varied experimental paradigms has enabled a clearer conception of the functional specialization of different anatomical regions in the frontal lobe. The mounting evidence helps outline not only the unique functional profile of each frontal region but also its role relative to other brain areas.

- (a) German Research Foundation (DFG)
- (b) European Union
- (c) University of Leipzig
- (d) Federal Ministry of Education and Research (BMBF)
- (e) Schering Deutschland GmbH
- (f) Young Academy at the Berlin-Brandenburg Academy of Science and Humanities and the German Academy of Natural Scientists Leopoldina
- (m) Erxleben (Visiting) Professorship, Institute for Psychology II, Otto von Guericke University Magdeburg, 01/10/2006 – 30/09/2007
- (n) Max Planck Institute for Neurological Research, Cologne
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1.1

Decision Making and Control

The neural underpinnings of higher order intentionality

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Imaging research over the past decade has consistently revealed the involvement of a number of neural regions when engaging in mental state reasoning. However, what remains a matter of considerable debate is the precise function of each area. The objective of the current study was to explore this issue by focusing on the relational nature of mental or intentional states.

We developed an fMRI experimental paradigm where the stimuli for the intentional or mental state condition (M) involved mental state relations between people, whereas that of structurally similar non-intentional conditions entailed spatial relations between persons sitting in a theatre (P) or objects in a room (O). We were thus able to tease apart which areas of the brain are recruited when a scenario involves intentional (mental state) relations relative to non-intentional (spatial) relations (M versus PO) from those that are responsive to the mere presence of persons (P versus O). The degree of structural complexity of the representations was also varied (2nd order: M2, P2 and O2 versus 3rd order: M3, P3 and O3).

The findings revealed that the processing of intentional information was associated with medial prefrontal cortex (mPFC) and bilateral temporal pole activity, whereas processing information containing persons (intentional and nonintentional) was associated with increased response in the precuneus, left temporo-parietal junction (TPJ) and anterior superior temporal sulcus (aSTS). The right TPJ, in

contrast, was selectively responsive to the processing of non-intentional information referring to persons in space. There was also an effect of complexity with the right TPJ being associated with higher activations for more complex stimuli whereas the mPFC showed the opposite pattern. These findings add new dimensions to the theory of mind domain and highlight the need to take into account the critical roles played by an extensive network of neural regions to fully appreciate complex social cognition.

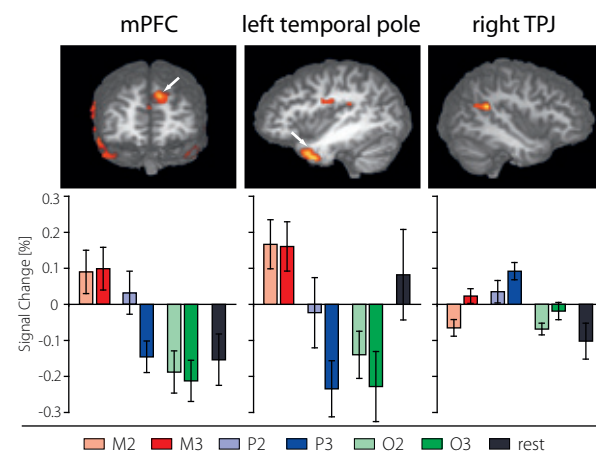


Figure 1.1.1 Group-averaged statistical maps and percentage signal change plots of significantly activated areas in the mPFC and left temporal pole for intentional representations (M>PO) and in the right TPJ for person-in-space representations (P>O).

Neural differences in decision-making for self and other

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Behavioral studies have found that humans behave inconsistently, preferring to be impatient when making trade-offs in the present but patient when making trade-offs in the future. McClure et al. (McClure, Laibson, Loewenstein, & Cohen, 2004, Science, 306, 503-507) inves-

tigated the neural basis of intertemporal preferences and found that people, offered the choice between a smaller, sooner and a larger, later monetary reward, showed different brain activation patterns depending on the date at which the sooner reward was made available. Only

choice sets that included an immediate reward were accompanied by activation in the dopaminergic reward system. The current study tested the hypothesis that there would be less activation in the dopaminergic reward system when subjects make intertemporal decisions for others. Adapting the experiment implemented (McClure, Laibson, Loewenstein, & Cohen, 2004, *Science*, 306, 503-507), we asked our subjects to make intertemporal choices for themselves and for other subjects. We found that when subjects faced choice sets with an immediate reward, intertemporal choices made for oneself were accompanied by activation in highly reward-related and self-related brain areas, whereas none of these regions showed elevated activation when subjects made choices for another person (Fig. 1.1.2). While this confirmed our hypothesis about the brain correlates of intertemporal choices for self and other, we did not find any behavioral differences in the choices that participants made for themselves and for others. In both cases, subjects chose the sooner reward more often if it was available immediately. To investigate the influence of impulsivity, we split our sample into two groups, depending on the subjects' individual dis-

count values (Laibson, 1997, *Q J Econ*, 112, 443-477). Only within the group of strongly discounting (i.e., highly impulsive) subjects, we could find the same differences in neural activation patterns between self and other as before. In accordance with these activation differences, we also found behavioral differences between decisions for self and other in this group of subjects: They more often chose the immediate reward for themselves than for the other person.

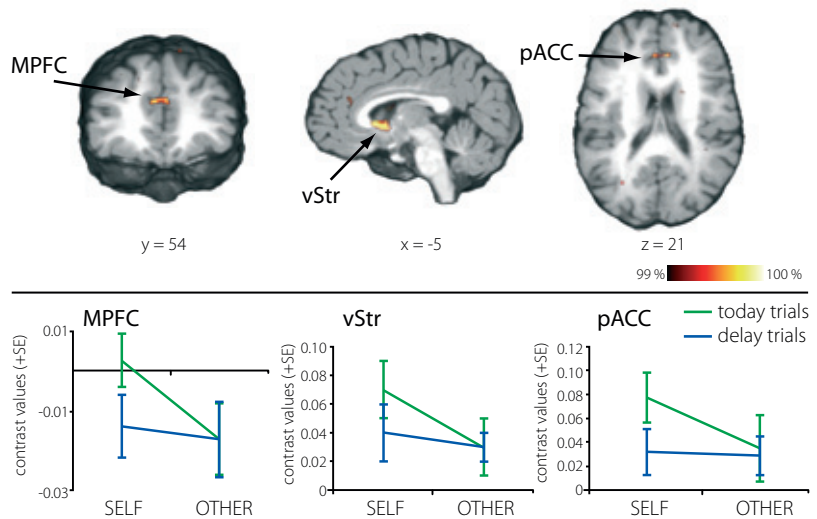


Figure 1.1.2 An interaction contrast of temporal distance (trials containing immediate option x trials containing no immediate option) and receiver (self vs. other) show activation differences within the medial prefrontal cortex (MPFC), ventral striatum (vStr) and pregenual anterior cingulate cortex (pACC). Contrast values indicate that these activation differences are mainly due to elevated activation in today trials in SELF.

1.1.3 What neuroscience can tell about intuitive processes in the context of auditory discovery

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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 responses appear as ideas or feelings that subsequently guide thoughts, behavior, and inquiry. It is proposed that people continuously, without conscious attention, recognize patterns in the stream of sensations that impinge upon them. What exactly is being recognized is not yet clear, but we assume that people detect potential content based on only a few aspects of the input, i.e., the gist of the situation. The result is a

vague perception of coherence embodied in a "gut feeling" and experienced as an initial guess, which subsequently biases thought and behavior accordingly. In the visual domain, it has recently been suggested that the orbitofrontal cortex (OFC) serves as a fast detector and predictor of potential content resting upon coarse facets of the input (Bar, Kassam, Ghuman, Boshyan, Schmid, Dale, et al., 2006, *P Natl Acad Sci USA*, 103, 449-454; Volz & von Cramon, 2006). To investigate whether the OFC is crucial in biasing task-specific processing and hence sub-serves intuitive judgments in various modalities, we repeated

our study in the auditory domain. Participants were presented with short sequences of non-verbal environmental sounds, which were hard to recognize due to distortion manipulations. Their task was to indicate for each item whether or not it involved a coherent meaningful sound. Our imaging results revealed anterior and posterior later-

al OFC activation to be responsive to the requirement of auditory intuitive judgments. By means of a conjunction analysis between the present results and those from a previous study on visual intuitive judgments, it revealed that the only region commonly activated in both tasks was the posterior OFC. Hence, we conclude that OFC activation during intuitive judgments in various modalities sub-serves the detection of potential content based on only coarse facets of the input.

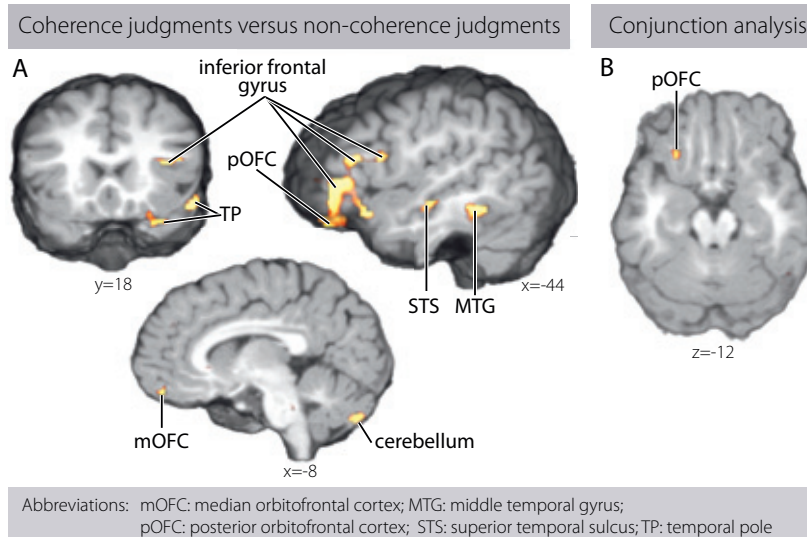


Figure 1.1.3 Group-averaged activations are shown on coronal, sagittal, and axial slices taken from an individual brain normalized and aligned to the Talairach stereotactic space. Panel A shows the direct contrast between trials participants judged to be coherent with trials participants judged to be incoherent. Panel B shows the conjunction analysis between auditory (cf. panel A) and visual coherence judgments. The latter contrast is taken from a previous study on visual coherence judgments (Volz & von Cramon, 2006).

When the choice is ours: context and agency modulate the neural bases of decision-making

1.1.4

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The option to choose between several courses of action is often associated with the feeling of being in control. Yet, in certain situations, one may prefer to decline such

agency and instead leave the choice to others. In the present functional magnetic resonance imaging (fMRI) study, we provide evidence that the neural processes involved

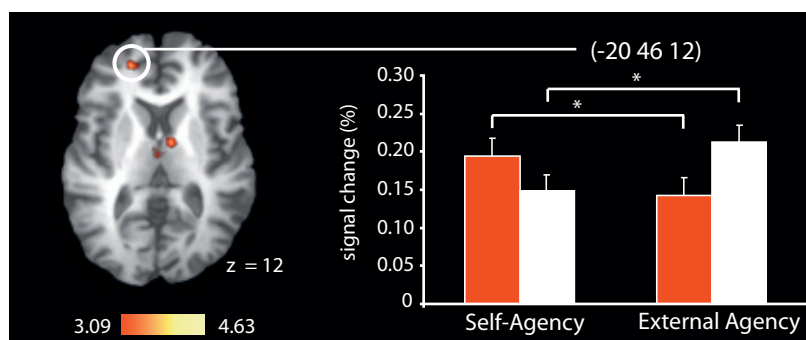


Figure 1.1.4.1 The interaction of agency and context in the anterior frontomedian cortex. Red bars = free context; white bars = determined context.

in decision-making are modulated not only by who controls our choice options (agency: self vs. external), but also by whether we have a say as to who is in control (context: free vs. determined). The fMRI results are noteworthy in that they reveal specific contributions of the anterior fronto-medial cortex (viz. BA10 extending into BA 9; Fig. 1.1.4.1) and the rostral cingulate zone (RCZ; Fig. 1.1.4.2) in decision-making processes. The RCZ

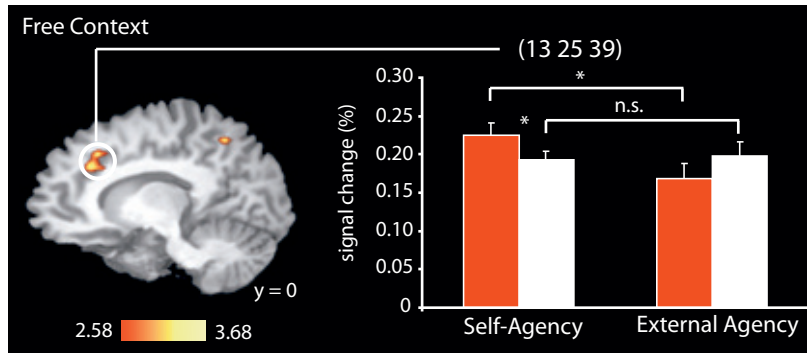


Figure 1.1.4.2 The conditional main effect of agency on RCZ activation depending on choice context.

is engaged when conditions clearly present us with the most choice options. BA 10 is particularly engaged when the choice is completely our own, as well as when it is completely up to others to choose for us, suggesting that both self-attributions and other-attributions arise from this cortical region. After all, it does not only matter whether we have any options to choose from, but also who decides on a given option.

1.1.5 To do or not to do: The neural signature of self-control

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Voluntary action is fundamental to human existence. To date, research on voluntary action has primarily focused on the selection when to perform a specific action or how to select between alternative movements. The aim of the present study was to investigate the fundamental, though neglected, decision whether to act or not. This decision process is crucial in daily life because it allows us to avoid impulsive behavior. In the present experiment participants were asked to press a button on a keyboard. However, in some trials they could freely choose to withhold the planned action in the last moment. Participants were asked to report the time when they decided to execute the button press by reporting the position of a clock hand. By contrasting brain activity for trials in which participants planned and then withheld the action with

brain activity in trials where they planned and then executed the action, we could show that a region in the dorsal fronto-median cortex (dFMC) is involved in intentional inhibition of action (see Fig. 1.1.5). Furthermore, the hemodynamic response in this area was positively correlated with the frequency of inhibition trials, indicating that participants with stronger dFMC activation tended to inhibit more frequently. Our data suggest that the intentional inhibition of action involves brain areas that are distinct from areas involved in deciding when and how to act. Furthermore, the data suggest that the dFMC might be involved in those aspects of behavior and personality that reflect 'self-control' (Brass & Haggard, 2007, p. 9141-9145).

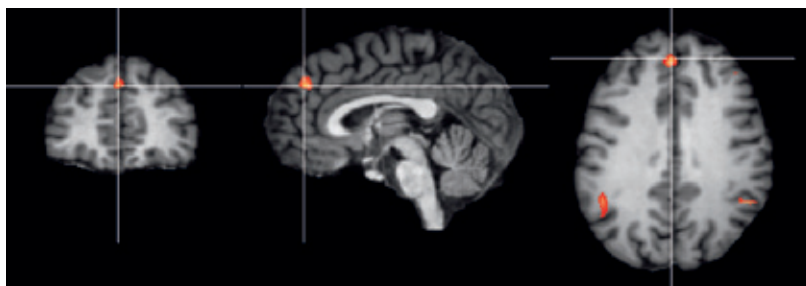


Figure 1.1.5 Activation in the dorsal fronto-median cortex (dFMC) for the contrast of inhibition versus action trials. The z-map is thresholded at $z > 3.09$ ($p < .001$).

Testing the role of the inferior frontal junction area in cognitive control

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Previous fMRI research has demonstrated consistent activation of the left inferior frontal junction (IFJ, crossing point of precentral and medial frontal sulci) in task switching experiments (Brass & Heyes, 2005, *Cogn Sci*, 9, 489-495). However, fMRI cannot prove the indispensability of a brain area for a specific cognitive process. While patient data support the role of the left frontolateral cortex in cognitive control, they lack the neuroanatomical specificity to show the functional significance of a brain region as circumscribed as the IFJ.

Transcranial magnetic stimulation (TMS) offers a tool to transiently block the function of a well-defined cortical area (approx. 1cm diameter), thereby overcoming the weaknesses of patient studies. Here, we used TMS to interfere with cognitive processing during task-switching: Subjects switched on a trial-by-trial basis between classifying a number between 1 and 9 according to whether it was smaller or larger than 5 (magnitude task) or whether it was odd or even (parity task), respectively. Two cues were associated with each conditions. In each trial, the digit to be evaluated was preceded by two cues, which could either be identical (cue repetition, CRP), different but indicating the same task (cue switch, CSW), or different and indicating a different task (task switch, TSW). TMS was applied pseudo-randomly after the second cue in

half of the double cue trials. To ensure encoding of the first cue, the digit was preceded by only one cue in a further manipulation.

Results show that TSW trials are affected differently by TMS as compared to the other conditions (Fig. 1.1.6). Error rates rose significantly in TSW, whereas CSW remained unchanged and CRP showed a trend toward less errors ($p=.08$). Conversely, there was a significant reduction in reaction times in TSW trials, while the other conditions remained unchanged.

Apparently, participants disengage from the first task-set successfully in TSW, but are not capable of establishing the alternative task-set correctly under TMS, ultimately leading to a tendency to answer by chance (high error rates). The reaction time speeding indicates that this "state without task-set" is apparently not conflict-loaded. Since it is not necessary to disengage from the task in CSW or CRP, these conditions are not as prone to the effects of TMS to the IFJ. Our results mimic findings in frontal lobe patients, who also tend to react prematurely (and incorrectly), especially if adaptive action is afforded.

In conclusion, we postulate that the IFJ plays a vital role in establishing new task-sets, while other mechanisms of task-switching, especially inhibition of competing tasks, remain intact.

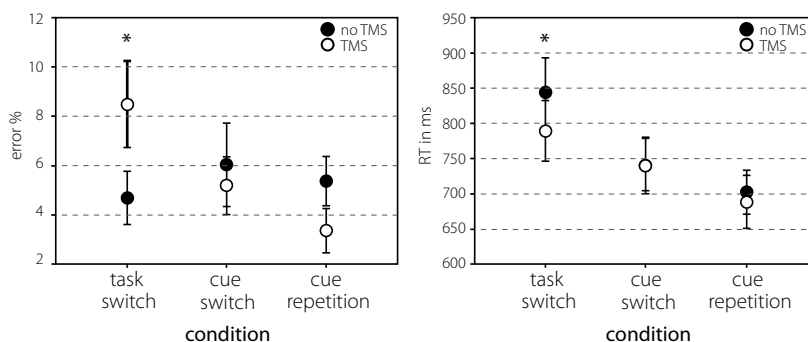


Figure 1.1.6 Mean error rates and reaction times for TSW, CSW, and CRP. Black circles indicate trials without TMS, white circles with TMS. Error bars show mean standard error. * indicates $p < .05$

1.1.7 Genetically determined differences in learning from errors

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Dopamine has been suggested to play a major role in monitoring negative action outcomes and appropriately adjusting behavior in the service of outcome optimization. We made use of a human genetic polymorphism (DRD2 TAQ 1A) associated with D2 receptor density changes to test the role of dopaminergic transmission in learning from feedback. Using a probabilistic learning task (Frank, Seeberger, & O'Reilly, 2004, *Science*, 306, 1940-1943) in a functional magnetic resonance imaging (fMRI) study, we revealed a diminished capacity for learning to avoid actions with negative consequences in A1-allele carriers (A1+ group) known to have a reduced dopamine D2 receptor density. They show a reduced response to negative action

outcomes in the posterior frontomedian cortex (pFMC), an area signaling the need for adjustments (Fig. 1.1.7 A). Interestingly, only in the non A1-allele carriers (A1- group) the time course of response certainty – reflecting learning progress – shows a positive correlation with activity in the posterior hippocampus bilaterally (Fig. 1.1.7 B), whereas no such correlation was found in A1+ participants. Furthermore, we found for the A1- participants an interaction between performance monitoring in the pFMC and the hippocampus, a structure involved in learning. This interaction changes over the course of learning – it is largest in the beginning of the experiment and reduces when response certainty increases (see Fig. 1.1.7 C).

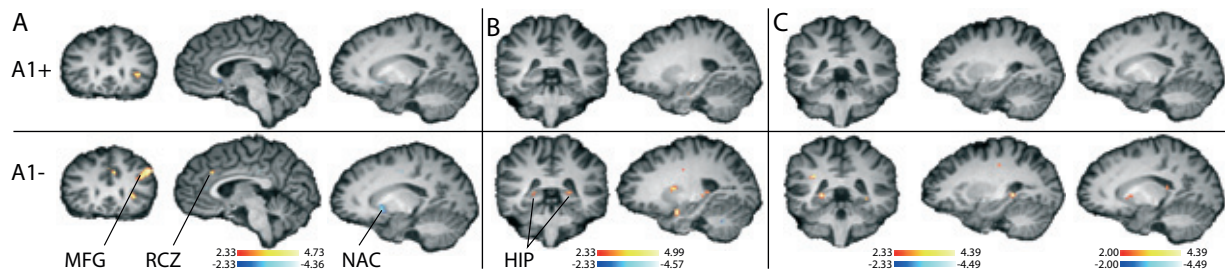


Figure 1.1.7 (A) Contrast "negative (red) vs. positive (blue) Feedback". MFG = middle frontal gyrus, RCZ = rostral cingulate zone, NAC = nucleus accumbens. (B) Parametric within subject fMRI analysis using the certainty of the given response. HIP = Hippocampus. (C) Psychophysiological Interaction Analysis between RCZ ($x = 4, y = 24, z = 33$) and other brain areas. Red: stronger interaction in the first third than in the last third of the experiment; blue: stronger interaction in the last than in the first third.

1.1.8 Neural correlates of error awareness

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Error processing results in a number of consequences on multiple levels. The posterior frontomedian cortex (pFMC) is involved in performance monitoring and signaling the need for adjustments, which can be observed as post-error speed-accuracy shifts at the behavioral level. Furthermore autonomic reactions to an error have been reported. We examined the neural correlates of conscious error perception in a functional magnetic resonance imaging (fMRI) study. An antisaccade task

known to yield sufficient numbers of aware and unaware errors was used (Nieuwenhuis, Ridderinkhof, Blom, Band, & Kok, 2001, *Psychophysiology*, 38, 752-760). Results from a meta-analysis were used to guide a region of interest (ROI) analysis of the fMRI data. Consistent with previous reports, error-related activity in the rostral cingulate zone (RCZ), the pre-supplementary motor area (pre-SMA) and the insular cortex bilaterally was found (see Fig. 1.1.8). Whereas the RCZ activity did not differentiate between

aware and unaware errors, activity in the left anterior inferior insular cortex was stronger for aware as compared to unaware errors. This could be due to increased awareness of the autonomic reaction to an error, or the increased autonomic reaction itself. In accordance with this interpretation, O'Connell, Dockree, Bellgrove, Kelly, Hester, Garavan, et al. (2007, *Eur J Neurosci*, 25, 2571-2579)

recently reported a higher skin conductance response to aware as compared to unaware errors. The data suggest that the RCZ activity alone is insufficient to drive error awareness. Its signal appears to be useful for post-error speed-accuracy adjustments only when the error is consciously perceived.

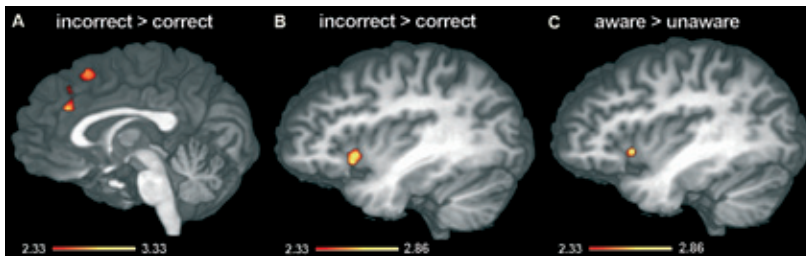


Figure 1.1.8 fMRI results. A and B: General error-related brain activity revealed by the contrast error vs. correct response. C: Activations related to conscious error perception revealed by the contrast aware vs. unaware error.

Violation of expectation: Neural correlates reflect bases of prediction

1.1.9

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Setting perceptual expectations can be based on different sources of information which determine the functional networks involved in implementing preparatory top-down influences and dealing with situations in which expectations are violated. The present study addressed the process of forming and violating expectations based on information of different origin, type and specificity within two types of task contexts. In the serial prediction task participants monitored ordered perceptual sequenc-

es for predefined sequential deviants, while the target detection task entailed a presentation of stimuli which had to be monitored for predefined non-sequential deviants. Detection of sequential deviants triggered an increase of activity in lateral and mesial premotor and cerebellar areas which were initially supporting regular sequence processing. This pattern of activity is suggested to reflect detection of a mismatch between the expected and presented stimuli and updating of the underlying sequence representation (i.e., forward model).

Presented violations additionally triggered activations in frontal areas initially not involved in sequence processing, reflecting the subsequent elaboration of the violation. In contrast, detecting non-sequential deviants triggered primarily bilateral activations within parietal and posterior temporal areas with an additional involvement of right

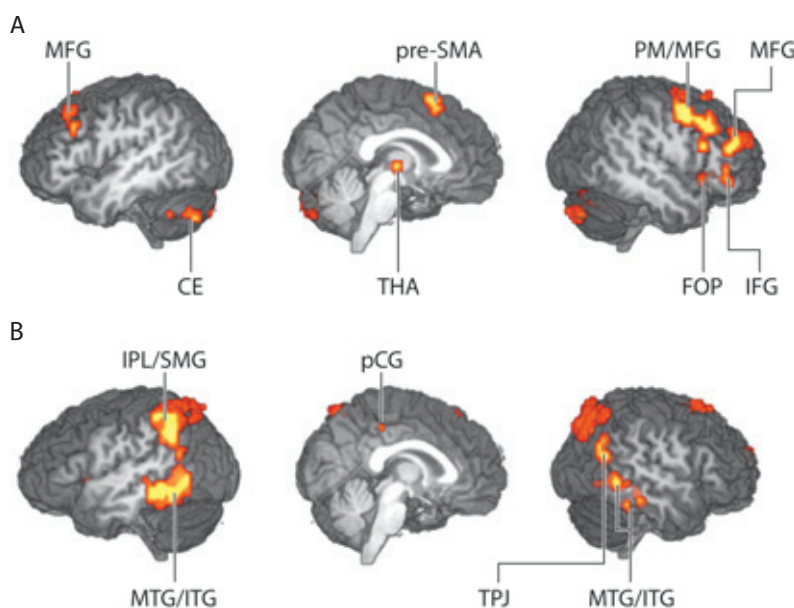


Figure 1.1.9 (A) Brain correlates of detecting sequential deviants (Violated vs. Ordered sequence). From left to right: parasagittal sections ($x=-46$; $x=0$; $x=46$). (B) Brain correlates of detecting non-sequential deviants (Target trial vs. No-target trial). From left to right: parasagittal sections ($x=-52$; $x=0$; $x=52$).

superior and middle frontal gyrus, reflecting an increase in perceptual and attentional processing evoked by the non-sequential deviant. This pattern of results is comparable to the network involved in detecting rare events in the oddball paradigm which is similar to the target detection task used in this study (Blendowski, Prvulovic, Hoechstetter, Scherg, Wibrall, Goebel & Linden, 2004, J Neurosci, 24, 9353-9360; Linden, Prvulovic, Formisano, Vollinger, Zanella, Goebel & Dierks, 1999, Cereb Cortex, 9, 815-823).

The results of the presented study indicate involvement of distinct networks in detecting different types of events deviating from a standard context defined by stability or continuity of presented events. This suggests that brain correlates of detecting different types of deviants reflect the nature of expectations being violated which are closely related to the nature of the deviant.

1.1.10 Prediction of external events with our motor system: Towards a new framework

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We cannot, in the proper sense, imitate or re-enact inanimate events, such as ocean waves rolling, or even non-human animate ones, such as dogs walking. However, we can anticipate the way they change and recent studies show that our motor system becomes involved while doing so. A novel framework is presented that accounts for these findings by generalizing a predictive account of the motor system from action to event perception. At first glance, there seems to be a striking difference between our prediction of other humans' behavior and our prediction of, for example, the rhythm of ocean waves or of an unfolding sequence of abstract stimuli on a computer screen. This difference is due to our ability to reproduce (re-enact) what we see or hear in the case of

humans but not in the case of ocean waves or abstract sequences. However, this difference does not impede the usage of the motor system to support prediction of events that are not actions. It is put forward here that we predict events that we cannot reproduce ourselves by exploiting an audiomotor or visuomotor representation that never amounts to a real action because it lacks proprioceptive and other interoceptive information. When we learn the structure of an event, these representations set up a forward model that can be used for prediction in a simulation mode. But which part of the motor system simulates an inanimate event? A possible answer to this question is provided by the Habitual Pragmatic Event Map (HAPEM; former-

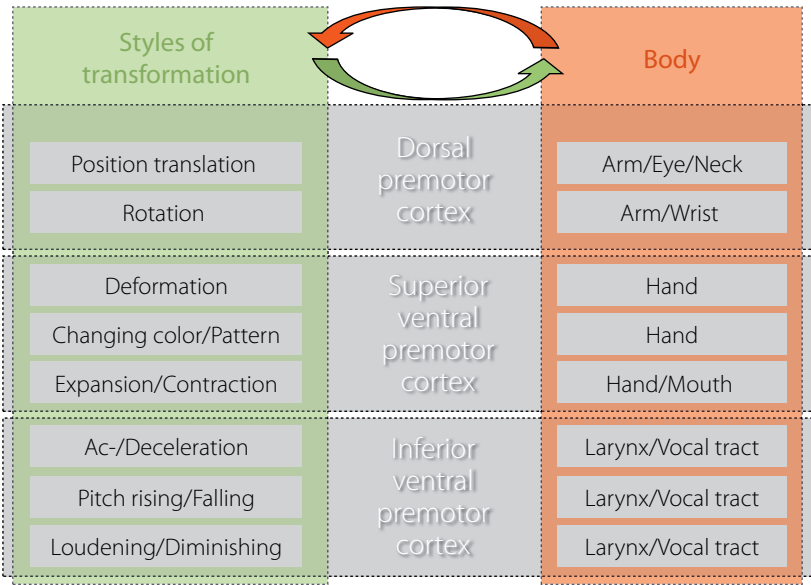


Figure 1.1.10 The premotor cortex houses sensorimotor forward models that are neuroanatomically ordered according to the styles of transformations they describe. For instance, a spatially defined event (e.g., a rotation) will be simulated using the premotor-parietal loop for reaching because an arm-action plan amounts to the expectation of a sequence of mostly spatially defined perceptions. This terminology avoids the reference to action, which seems inadequate for most events, and can be applied to both the environment and the body.

ly Habitual Pragmatic Body Map) framework (Schubotz & von Cramon, 2003, *Neuroimage*, 20, 120-131). It holds that, by default, the prediction of an event that is structured with regard to a property P engages the area of the lateral premotor cortex that is best adapted to specify its motor output in terms of property P. It is assumed that a subset of sensorimotor neurons in action controlling areas is exploited in a rudimentary simulation mode. This simulation suffices to predict some of the relevant dynamics of the observed event, but it cannot serve as an exhaustive event description.

A terminology that describes the role of the premotor cortex in the simulation of action and in the simulation of

events in a unifying framework is possible (see Fig. 1.1.10) because forward models for events are not categorically different from forward models for actions. Forward models for events are just a fraction of forward models for actions, a fraction that misses the full-blown interoceptive and exteroceptive description of action models. Note that this is not to claim that event prediction is a motor function. It is partially realized by a brain network that has so far been named motor system, but it could turn out that prediction system is a more appropriate label.

Abstract and motor planning – an fMRI investigation of relational reasoning

1.1.11

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The aim of the study was to elucidate the role of two frontal areas – frontopolar cortex (FPC) and premotor cortex (PMC) – in planning and relational thinking. To differentiate the correlates of relational processes in the motor and abstract domains, brain activation was measured using fMRI. A reasoning paradigm adapted from the Raven's Progressive Matrices was employed. Subjects performed an "abstract" condition – in which the stimuli were graphical images – and an "action" condition in which the stimuli were photographs of object-directed hand actions. Furthermore, in both of these conditions, correctly solving the matrices either required integration of relations or not.

The results showed a broad, predominantly left-lateralized fronto-parietal network to be activated for relational integration, independent of domain, a finding in agreement with previous studies. Action stimuli specifi-

cally elicited bilateral activation of the inferior frontal, supramarginal and fusiform gyri as well as in an occipito-temporal complex, whereas abstract stimuli primarily activated the cuneus and right intraparietal sulcus. ROI analyses could show that there was a tendency for FPC to be activated more by reasoning with abstract stimuli and for lateral PMC to be activated more by reasoning with action stimuli. Importantly, both brain regions were equally implicated in relational integration, and there was no evidence that FPC was recruited more for integration of abstract relations or that PMC was recruited more for integration of relations in the motor domain, as classical views would suggest. The results provide evidence that PMC, far from having purely motor-preparation related functions, is also relevant for the performance of highly complex cognitive tasks.

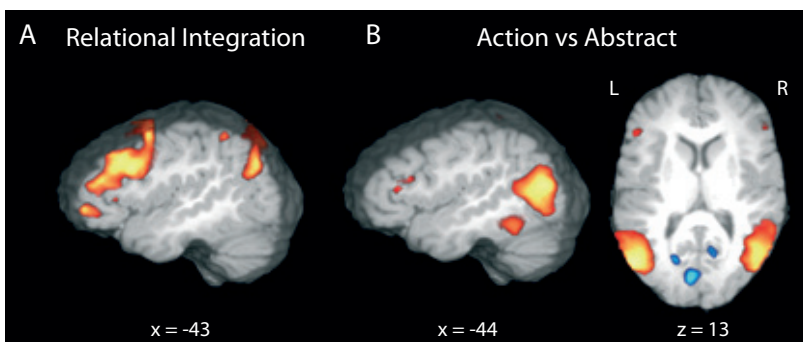


Figure 1.1.11 Brain regions activated for (A) relational integration in both the abstract and motor reasoning domains and (B) reasoning with action stimuli as compared to abstract stimuli (red) and vice versa (blue). Group Z-maps were overlaid onto an individual anatomical reference image and thresholded at $p < .001$ (uncorrected).

1.1.12

Predicting goals from others' actions: The outcome of low-level processing in right inferior parietal and posterior temporal cortex

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Recent behavioral and neuroimaging studies have found that observed actions are directly matched onto the motor representation of an observer. Although direct matching is a very simple mechanism it might be the underlying mechanism of higher order cognitive processes, such as inferring others' action goals. We used fMRI to test which neural circuits are involved in inferring goals from others' actions when these actions do not directly indicate the goals. We compared two conditions, both showing tiny finger lifting movements. In one condition the goal was easy to infer due to the presence of action context (a clamp over the moving finger, see Fig. 1.1.12.1 B). Goal inference in the second condition was difficult due to the lack of action context (see Fig. 1.1.12.1 A). We found three different regions more strongly activated when goal inference was difficult (see Fig. 1.1.12.2): (1) The superior temporal sulcus (not shown), (2) the right inferior

parietal cortex, at the junction with the posterior temporal cortex (TPJ) and (3) the angular gyrus of the inferior parietal lobule. In line with mentalizing accounts of goal prediction, these findings suggest that inferring goals from others' actions is the outcome of a set of lower-level computational processes taking place in parts of superior temporal and inferior parietal cortex. The anatomical location of the TPJ suggests that an attentional shifting function, comparable to the one we found for goal-inference processing, is also needed in low-level attentional tasks, as well as in higher-level TOM tasks. Our findings are framed by two theoretical concepts of goal inference processing differing with respect to the direction of the inference process. Taken together, our findings support the recently proposed view that rather domain-general computational mechanisms are crucial for higher level social cognitive processing (Decety & Lamm, in press).

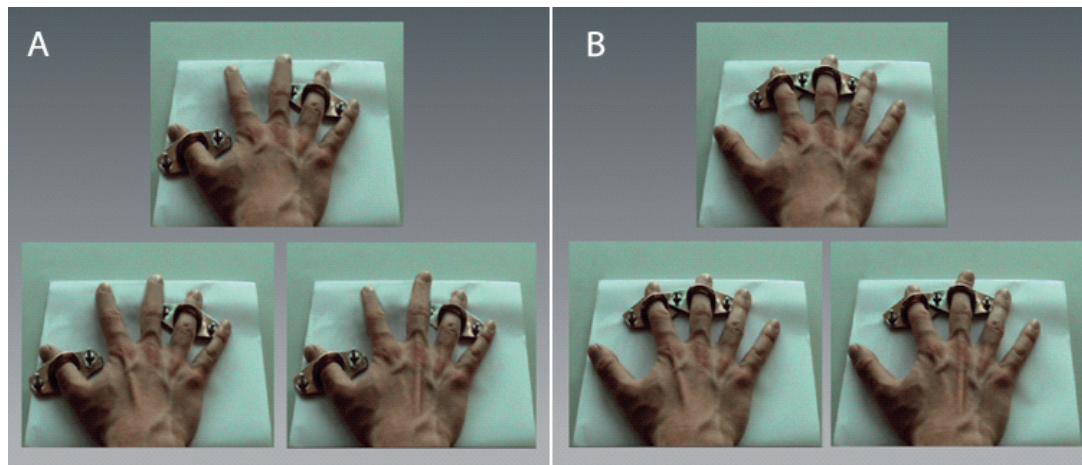


Figure 1.1.12.1 (A) Micro movements and (B) Restraint movements showing a static hand (upper), a hand where either the index finger (left lower) or the middle finger (right lower) was lifted. (A)-(B) reflect the contrast Micro movement-Restraint movement.



Figure 1.1.12.2 Shows the resulting zmap overlaid onto an anatomical reference image for the contrast Micro movement-Restraint movement. The zmap was thresholded at $z=3.09$ which corresponds to an alpha-level of 0.001.

Anatomical and functional parcellation of the human lateral premotor cortex

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The lateral premotor cortex of the macaque monkey is an anatomically multifaceted area which serves multiple sensorimotor and cognitive functions. While evidence for the functional organization of human premotor cortex accumulates, much less is known about the underlying anatomical properties of this brain region. Based on the findings in macaques, we hypothesized the existence of at least two major fields: corresponding to the ventral and the dorsal lateral premotor cortex, the border between which is still a matter of debate in the human brain. Since a further subdivision running orthogonally in rostro-caudal direction has been suggested and often reconfirmed in macaques, we tested whether our data would support four distinct fields on the lateral convexity as well. We used Diffusion Tensor Imaging (DTI) and functional Magnetic Resonance Imaging (fMRI) to investigate whether the supposed-to-be-homologue area in humans can be segregated on the basis of anatomical connectivity and of functional activation in a set of cognitive and motor tasks. DTI data suggested a distinction between ventral and dorsal premotor cortex and a further inferior/superior sub-par-

cellation of both. Functional MRI data corroborated these four areas, showing that anatomical parcellation predicts the distribution of functional activation and vice versa. Functional data from movement of different body parts (Experiment 1), prediction of rhythmic, object-based or spatial sequences (Experiment 2), and observation of different types of movement of an actor (Experiment 3) were largely consistent with the interpretation of the DTI-based parcellation of four sub-regions in the PCG. However, they also showed that functional activations were not sharply restricted to these fields. In line with evidence from macaque research, we therefore suggest that even under optimal signal-to-noise ratio, the contribution of the sub-regions of the PCG are differently weighted for different functional requirements rather than exclusively engaged in only the one or the other function or task.

In sum, results may encourage the application of combining DTI and fMRI in vivo in order to shed light on the correspondence of brain function and anatomy.

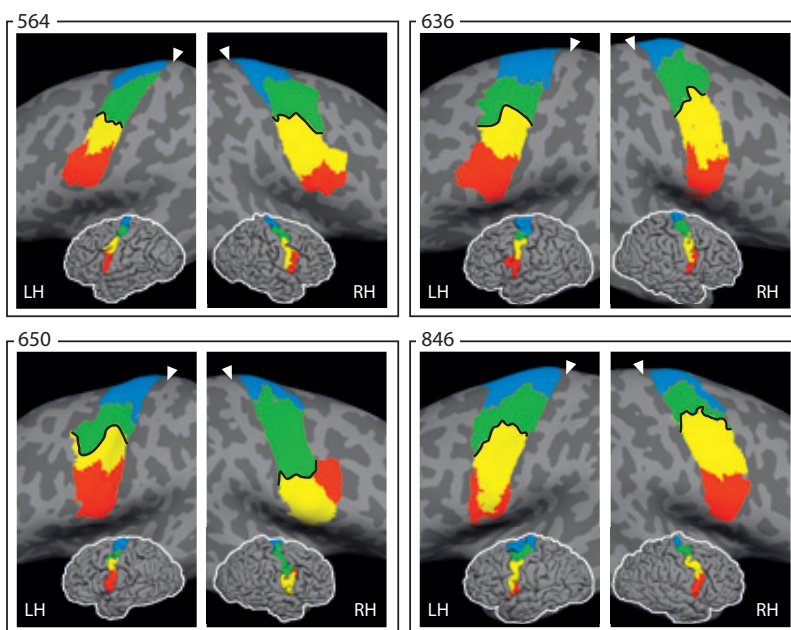


Figure 1.1.13 Connectivity-based parcellation of the precentral gyrus. Results of parcellating the left and the right hemisphere (here: 4 of the 10 subjects) indicate that the precentral gyrus is divided into a superior dorsal (blue), inferior dorsal (green), superior ventral (yellow) and an inferior ventral (red) area. Arrows indicate the central sulcus in each hemisphere; a thick solid line indicates the border between ventral and dorsal areas.

1.1.14

Neural correlates of anticipatory processes in action and perception: fMRI evidence for functional gradients

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The present study aimed at investigating the general overlap and differentiation of anticipatory processes in action and perception on the brain level. To this end, we employed serial prediction tasks that required the anticipation of visuo-spatial stimulus patterns (perceptual prediction) and motor imagery tasks that required the planning of one's own movement sequences (motor prediction).

The fMRI data revealed a functional gradient in the medial frontal cortex, with more anterior regions being preferentially engaged in perceptual prediction and more posterior regions, i.e., the supplementary motor area (SMA), being preferentially engaged in motor prediction (see Fig. 1.1.14). In between these areas, functional overlap was observed in posterior medial frontal cortex comprising the pre-supplementary motor area (pre-SMA) and the rostral cingulate zone (RCZ). In addition, functional overlap of the two domains of prediction was observed in the dorsal part of the anterior insula. We take these findings to reflect that the medial frontal cortex and the dorsal anterior insula share a role in the prospective monitoring of events. For the lateral premotor cortex, a functional differentiation was revealed with more superior parts being pref-

erentially engaged in perceptual (here visual) prediction, and more inferior parts being preferentially engaged in motor prediction. We argue that this differentiation reflects the difference in what is pragmatically relevant about the anticipated events in perception and action on a more global level, i.e., beyond specific properties and movements. Common and pragmatically relevant in all perceptual prediction conditions was the visuo-spatial nature of the to-be-predicted event. In turn, common and pragmatically relevant in all motor prediction conditions was the goal-character of the anticipated or planned events.

Together, the present findings suggest that a functional gradient in the medial frontal cortex oriented along the anterior-posterior axis reflects the different weight of cognitive and motor aspects of the anticipatory processes inherent to perception and action. Furthermore, the functional differentiation in the lateral premotor cortex seems to reflect the event the anticipatory process aims at, i.e., the anticipated content, in terms of its pragmatic relevance.

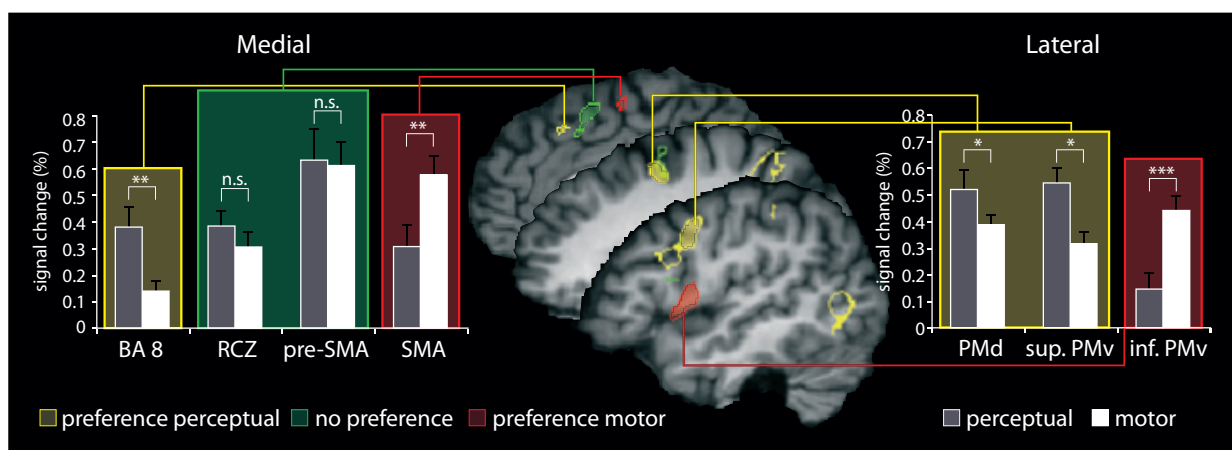


Figure 1.1.14 Middle panel: Overlap (green) and distinctiveness of perceptual (yellow) and motor prediction (red). Left and right panel: Maximal percent signal change values extracted from the peak voxels displaying conjoint or preferential activation in medial frontal cortex and lateral pre-motor cortex, respectively. Significant differences are indicated by asterisks: * $p < .05$, ** $p < .01$, *** $p < .001$.

Exploring individual temporal preferences

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Understanding and producing motor and auditory sequences requires an accurately controlled temporal dimension. Interestingly, our everyday experience and research suggest that individuals differ both in their temporal motor pattern production and in their musical preferences. Various studies identified interindividual temporal differences in locomotion, goal-directed movement, as well as in speech patterns. Throughout the last century, there have been investigations of the relationship between musical preferences and personality, and, in particular, the way, in which musical tempo is associated to age, sex, as well as to individual heart rate, breath, gait and tapping – the so-called “personal tempo”. Recently, several analytical, behavioral and neurocognitive studies provided evidence for a link between movement and auditory temporal perception.

Our studies explored the connection between individual preferences for the auditory temporal factors tempo, meter, beat subdivision and rhythm (N = 30), personality

traits (N = 29) and individual stepping frequency (N = 25) in healthy subjects using behavioral measures and personality testing.

As suggested by the link between temporal aspects of movement and auditory perception, we found that the preferred stepping frequency is related to the preferred temporal grouping of auditory patterns (meter), which extends previous knowledge by the notion of intraindividual parallels in temporal preferences. Additionally, the results point to a personality-based model of individual temporal perceptual and temporal motor preferences. Each aspect of individual temporal preference is related to a specific range of personality factors and facets.

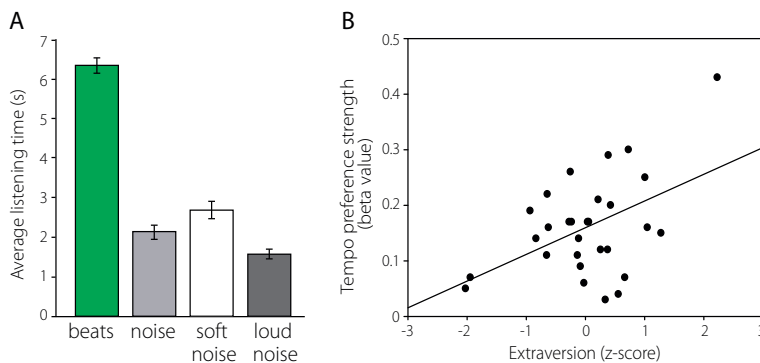


Figure 1.1.15 (A) Subjects listened to beats significantly longer than to white noise ($t = 11.684^{***}$; $p < 0.001$) and to soft white noise significantly longer than to loud white noise ($t = 5.23^{***}$; $p < 0.001$). Thus, listening time is interpreted as an implicit measure of auditory preference. (B) The strength of auditory tempo preference correlates significantly with extraversion.

1.2

Frontotemporal Dysfunction

Losing your self – Neural networks in frontotemporal dementia

1.2.1

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Frontotemporal dementia is the most common form of frontotemporal lobar degeneration. It is characterized by deep alterations in behavior and personality. We conducted a systematic and quantitative meta-analysis to examine its neural correlates and place the disease in a framework of cognitive neuropsychiatry (Schroeter, Raczka, Neumann, von Cramon, in press). MedLine and

Current Contents search engines were used to identify imaging studies investigating frontotemporal dementia between 1980 and 2005. Nine studies were identified reporting either atrophy or decreases in glucose utilization. Overall, the analysis involved 132 subjects. A quantitative meta-analysis was performed. Maxima of the studies resulted in activation likelihood estimates.

The meta-analysis revealed a particularly frontomedian network impaired in frontotemporal dementia (Fig. 1.2.1). Additionally, right anterior insula and medial thalamus were identified. Our study specifies frontotemporal dementia as the frontomedian variant of frontotemporal lobar degeneration. More specifically, the disease affects neural networks enabling self-monitoring, theory of mind capabilities, processing/evaluation of internal mental states, perception of pain and emotions, and sustaining personality and self. Accordingly, our study contributes to placing frontotemporal dementia in cognitive neuropsychiatry.

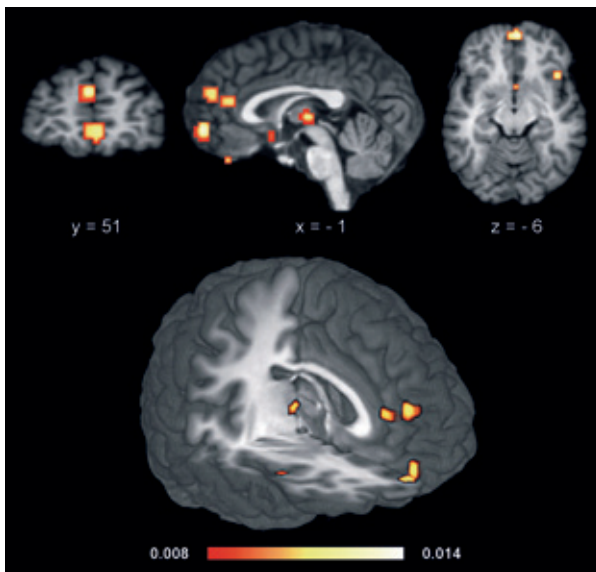


Figure 1.2.1 Results of the quantitative meta-analysis. The activation likelihood estimate (ALE) map displays above-threshold voxels for frontotemporal dementia indicating impaired brain regions in comparison with controls. Results are shown on an individual brain in Talairach space. Left side is left.

Neurovascular coupling is impaired in cerebral microangiopathy – An event-related Stroop study

1.2.2

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Small-vessel disease or cerebral microangiopathy is a common finding in elderly people leading finally to sub-cortical ischemic vascular dementia. Because cerebral microangiopathy impairs vascular reactivity and affects mainly the frontal lobes, we hypothesized that brain activation decreases during an event-related color-word matching Stroop task. 12 patients suffering from cerebral microangiopathy were compared with 12 age-matched

controls (Schroeter, Cutini, Wahl, Scheid, von Cramon, 2007, *Neuroimage*, 34, 26-34). As an imaging method we applied functional near-infrared spectroscopy, because it is particularly sensitive to the microvasculature. The Stroop task led to activations in the lateral prefrontal cortex (Fig. 1.2.2). Generally, the amplitude of the hemodynamic response was reduced in patients in tight correlation with behavioral slowing during the Stroop task and

with neuropsychological deficits, namely attentional and executive dysfunction. Interestingly, patients showed an early deoxygenation of blood right after stimulation onset, and a delay of the hemodynamic response. Whereas the amplitude of the hemodynamic response is reduced

in the frontal lobes also with normal aging, data suggest that impairments of neurovascular coupling are specific for cerebral microangiopathy. In summary, our findings indicate frontal dysfunction and impairments of neurovascular coupling in cerebral microangiopathy.

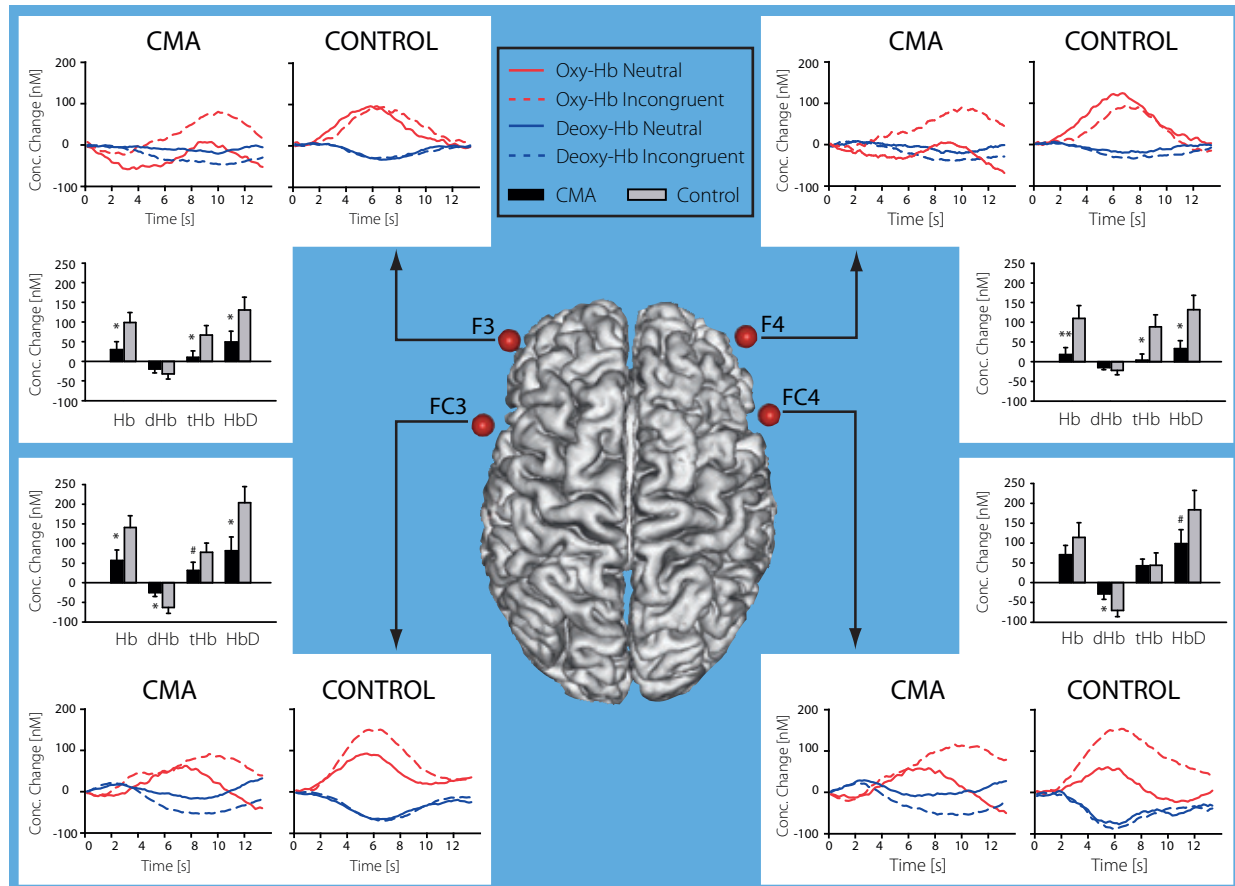


Figure 1.2.2 Time courses for concentrations of oxy- and deoxy-hemoglobin in the dorsolateral prefrontal cortex during the neutral and incongruent conditions of the Stroop task (starting at 0 s). The bar charts illustrate the mean hemodynamic concentration changes. Values during the neutral and incongruent condition were pooled. Average across patients with cerebral microangiopathy (CMA) and control subjects. Hb hemoglobin, dHb deoxy-Hb, HbD Hb difference, tHb total Hb. ** $p < 0.01$; * $p < 0.05$; # $p < 0.1$ ('trend') for controls vs. patients (unpaired one-tailed Student's t-test). Mean+SEM.

1.2.3 Inefficient cognitive control in adult ADHD: Evidence from trial-by-trial Stroop test and cued task switching performance

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Neuropsychological models of attention-deficit/hyperactivity disorder (ADHD) implicate disrupted cognitive control as contributing to disorder-characteristic deficiencies and excesses (e.g., inattention, impulsivity, hyperactivity).

However, such models are child-based and have yet to undergo empirical scrutiny with respect to individuals with persistent ADHD in adulthood. Suggestive of inefficient lateral prefrontal cortex (LPFC) function, adult pa-

tients often complain of such cognitive disturbances as heightened distractibility and/or frequent switching between uncompleted tasks. The current study contrasted the performance of a clinical sample ($n = 22$; 17 male) and a matched control group on two experimental measures with demonstrated sensitivity to LPFC function: a manual trial-by-trial Stroop test and a cued task-switching paradigm. The Stroop test required subjects to respond to the ink color of color-words and meaningless letter-strings. Interference control efficiency was gauged by performance differences between incongruent (e.g., the word “red” printed in green) and neutral trials (e.g., “XXXX” printed in green). The task-switching paradigm required subjects to switch between classification of colored shapes either according to color or to shape in an unpredictable manner. Experimental manipulations allowed for the investigation of transient cognitive flexibility, sustained task-set maintenance, preparatory mechanisms and interference control. Abnormal ADHD group processing of task-irrelevant stimulus features on the task switching paradigm indicated that the interference effects observed on the Stroop test (see Fig. 1.2.3.1) were not merely due to the distracting nature of dominantly represented verbal material. Further analysis of this effect disclosed that the ADHD group interference control impairment was dependent on inefficient task preparation. Group differences in sustained maintenance and transient updating of task-set (see Fig. 1.2.3.2) were also discovered to be dependent on aberrant preparatory processes in the ADHD group. Our findings deliver novel evidence of impaired cognitive control in adult ADHD. Possibly suggestive of inadequate bottom-up engagement of cognitive control, all group differences were found to be dependent on inefficient preparatory mechanisms. The current findings contribute to a better understanding of the development of cognitive control in ADHD.

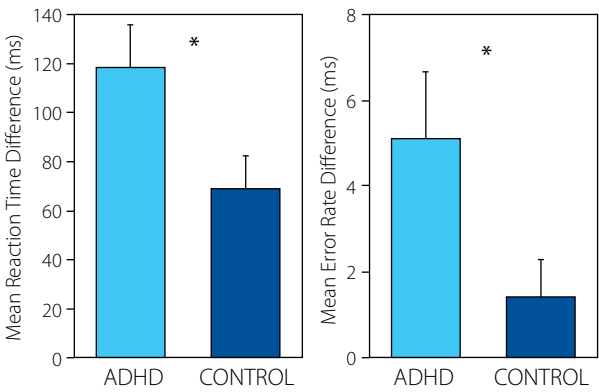


Figure 1.2.3.1 Mean reaction time (left) and error rate percentage (right) differences between incongruent and neutral conditions (i.e., Stroop interference) of the Stroop test for ADHD and control groups. * indicates $p < .05$. Bars represent standard errors of the mean.

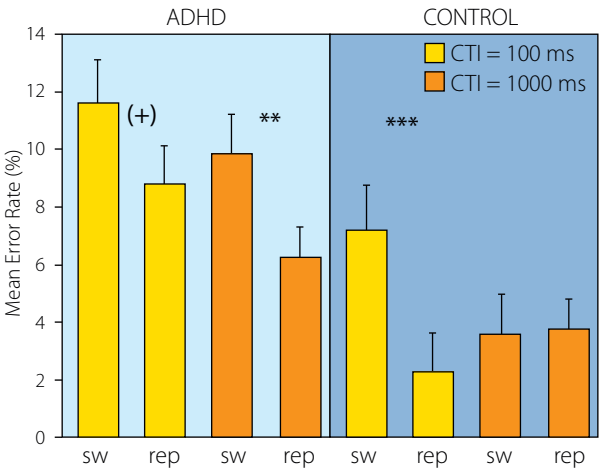


Figure 1.2.3.2 Mean error rates for the ADHD and control groups on mixed block switch and repetition trials as a function of CTI. (+) indicates $p = .07$. ** indicates $p < .01$. *** indicates $p < .001$. Bars represent standard errors of the mean.

Stroop interference in early multiple sclerosis: An event-related fMRI study

1.2.4

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Although cognitive impairment has been recognized as considerable feature in multiple sclerosis, patients especially in the early stage of the disease often demonstrate preserved or only slightly impaired cognitive functioning. Using functional magnetic resonance imaging (fMRI), we investigated the brain activation pattern in early MS

patients and discussed whether possible changes are due to a higher degree of cognitive control to limit the impact of tissue damage on patients' cognitive performance.

Previous research observed task-related changes in functional brain activation in MS patients using the Paced

Auditory Serial Addition Test (PASAT) or the N-back task. We employed an adapted single trial version of the Stroop interference task, which is a classical paradigm to study cognitive control and inhibitory processes. Seven cognitively preserved patients with early relapsing remitting MS were compared with seven healthy controls. The fMRI recording was carried out three times for each patient within a period of approximately three weeks to enhance the validity of the results.

We found no differences in the behavioral performance of both groups. In contrast, fMRI data revealed significantly increased interference-specific activation in brain areas known to be involved in cognitive control (Figure 1.2.4). Especially the observed frontal regions have been shown to be associated with competing task-related information (preSMA) and more specifically with conflict monitoring (posterior inferior frontal sulcus, pIFS). Increased brain activation in the intraparietal sulcus (aIPS) has been related to the updating of relevant task representations which is a crucial process involved in Stroop interference. The results support the hypothesis that patients with early MS must increase the degree of cognitive control to maintain their behavioral performance level. Further we conclude that fMRI parameters sensitively detect early compensatory processes in MS.

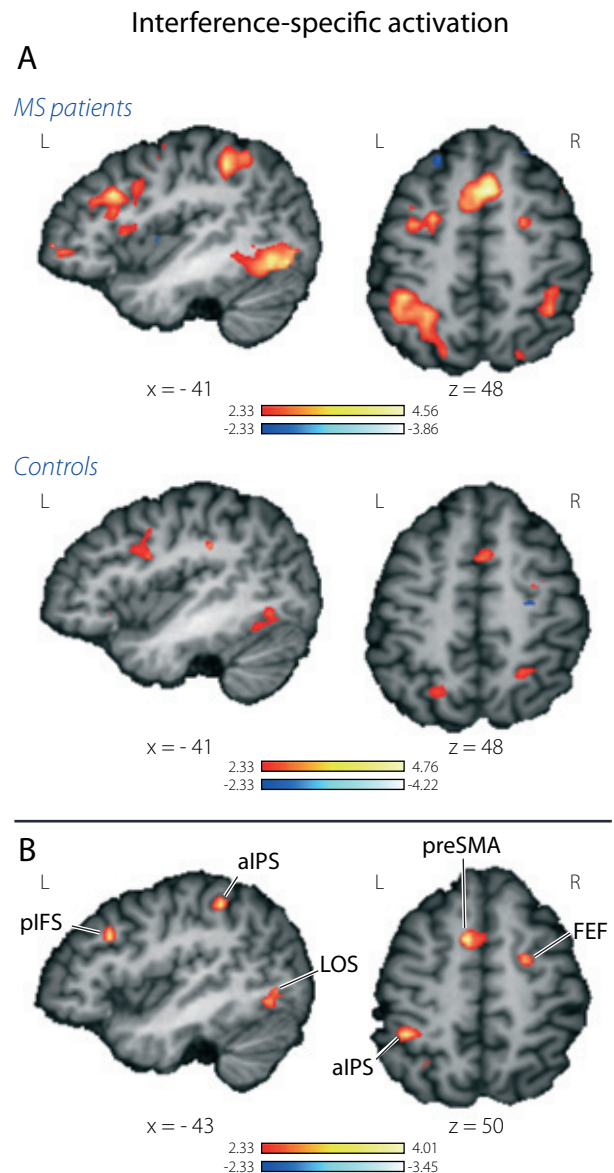


Figure 1.2.4 (A) Main activations for the contrast incongruent vs. neutral condition for MS patients and controls. Statistical threshold: $z = 2.33$ ($p < 0.01$). During the incongruent condition both groups demonstrated activations in Stroop relevant brain areas. (B) Group specific activations for the contrast MS patients vs. controls (incongruent vs. neutral condition). Statistical threshold: $z = 2.33$ ($p < 0.01$). The figure presents brain areas with a statistically significant activation increase in the patient group during the incongruent condition (critical interference condition).

1.2.5 Categorization of semantic memory – ERP evidences for the processing of animacy in patients with anterior temporal lesions

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Since the 1970s category specific deficits have been investigated in neuropsychological research. Most commonly, a deficit for animate (animals) vs. inanimate (objects) categories has been described in the literature, although the opposite has been observed. One critical aspect that may have contributed to the diverse results is the use of explicit categorization tasks that may con-

found the process at stake. Therefore we conducted a visual ERP experiment using a lexical decision semantic paradigm that allows to test semantic processing implicitly. We tested six patients with a left (ATL-patients, 47-71 years, mean: 56 years), six patients with a right anterior temporal lesion (ATR-patients, 43-65 years, mean: 55.8) and six age-matched controls (46-72 years, mean: 55.7

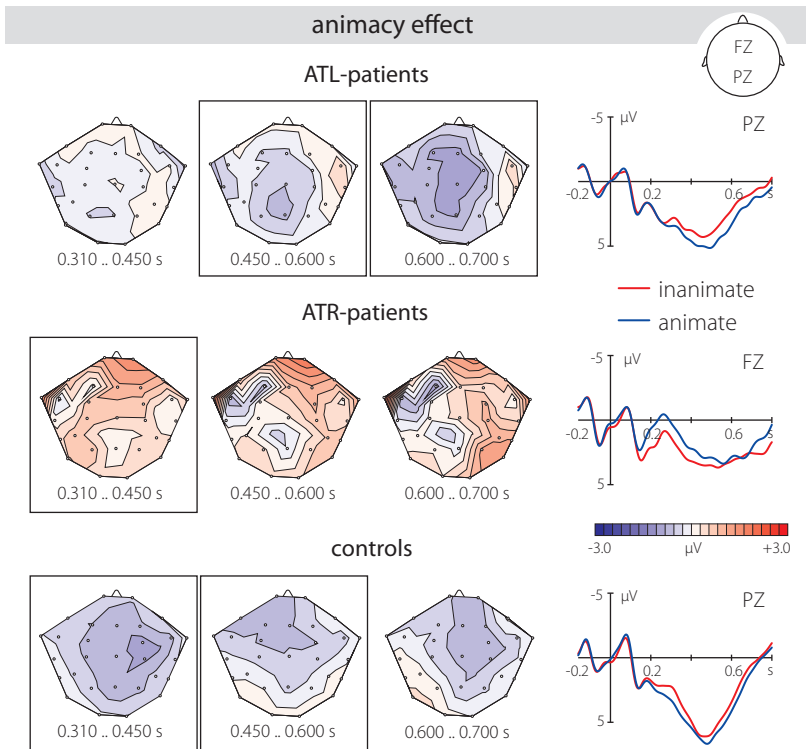


Figure 1.2.5 Selected electrodes and distribution of effects for the factor animacy (animate vs. inanimate).

ERP effects of meaningful and non-meaningful sound processing in anterior temporal patients

1.2.6

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The role of the anterior portion of the temporal lobe has recently received renewed attention in language comprehension research. While this brain area is clearly affected in semantic dementia (Patterson & Hodges, 2000), Damasio and colleagues state that particularly the medial anterior portion of the temporal lobe may not be critical for semantic knowledge representation per se, but may rather be engaged in lexical access (Patterson & Hodges, 2000, *Semantic dementia: One window on the structure and organization of semantic memory*, In: Cermak (Ed.), *Revised handbook of neuropsychology: memory and its disorders*, 289-309, Amsterdam: Elsevier; Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996, *Nature*, 380, 499-505). If this view is valid, it should not only hold for the processing of words, but also for the processing of meaningful sounds. Here, we tested patients with prima-

ry lesions in the anterior portion of the left (ATL) and right (ATR) temporal lobe in comparison with healthy controls (HC) in an event-related brain potential (ERP) experiment to examine the effect of meaningful and non-meaningful novel sound processing in a novelty P3 oddball paradigm. HCs and both patient groups displayed a normal target P3b as well as a novelty P3a. In addition, while HCs differentiated non-meaningful and meaningful novel sounds in the novelty P3a at posterior lateral and midline electrode-sites, all patients showed this effect only at midline sites. Lastly, the P3a effect was followed by a larger N400 amplitude rise for meaningful compared to non-meaningful novel sounds in HCs, but not in either patient group. The present data indicate that both the left and right anterior temporal lobe is crucial for lexical-semantic processing of novel sounds.

Patients

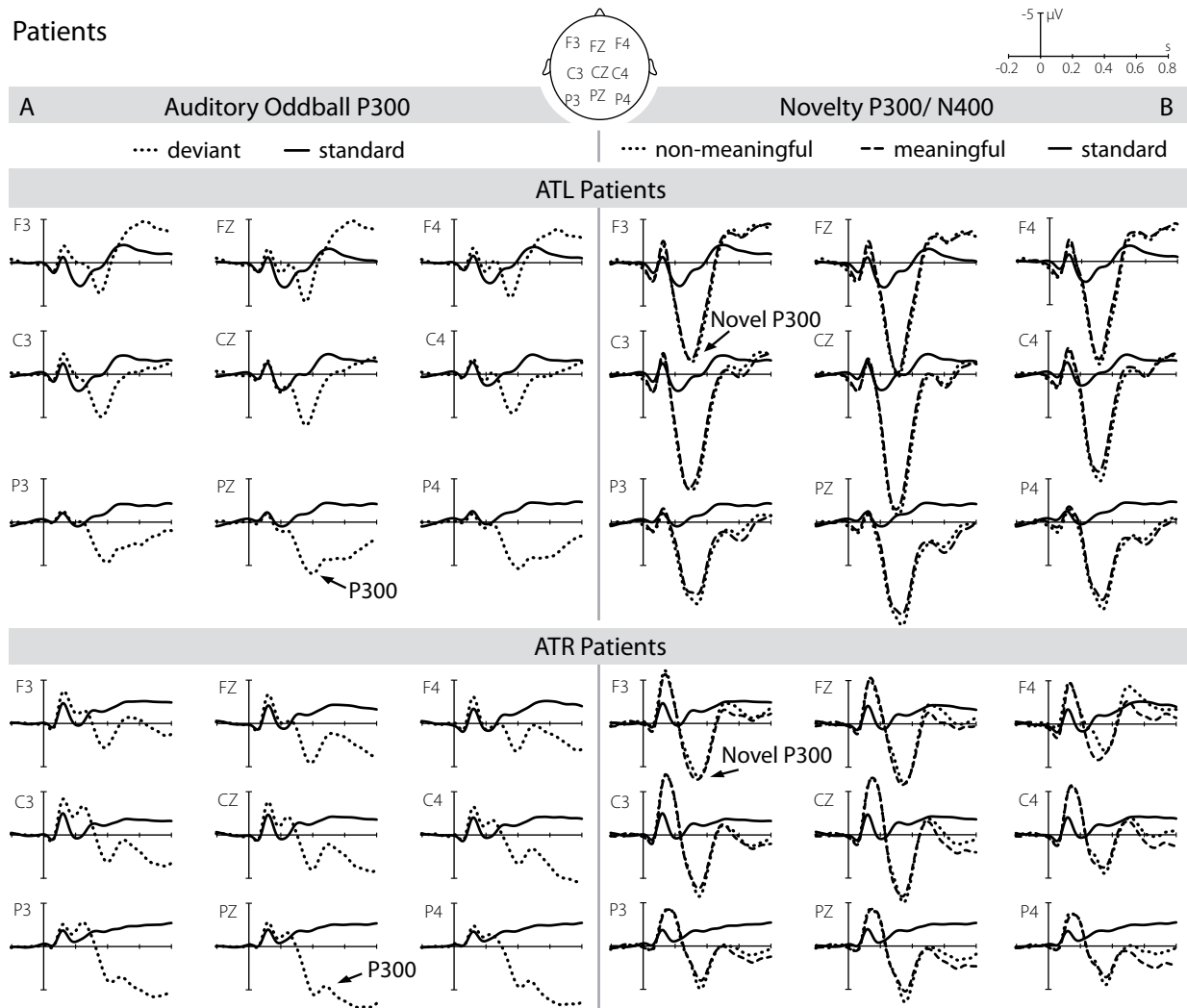


Figure 1.2.6 A (left panel) displays the P300 oddball effect in patients (top panel = ATL, bottom panel = ART). The solid line represents the standard tones, the dotted line the deviant tones. B (right panel) the novelty P300 effect followed by the N400 effect is depicted at selected electrode-sites. Again solid lines represent ERPs elicited by standard tones, dotted; lines and dashed lines indicate the brain response to the non-meaningful and the meaningful sounds, respectively.

Congresses, Workshops, and Symposia

Graf, M., Rapinett, G., Schubotz, R. I., & Prinz, W. (February). *Embodied Simulation*. Symposium. Kloster Irsee, Germany. ■ 2006

Schroeter, M., & Fallgatter, A. J. (November). *Optische Bildgebung mit Nah-Infrarot Spektroskopie (NIRS) zur Hirnfunktionsmessung bei psychiatrischen Patienten: Grundlagen und Anwendungsmöglichkeiten*. [Optical imaging with near-infrared spectroscopy in psychiatry]. Symposium. Annual Meeting DGPPN, Berlin, Germany. ■

Liepelt, R. (December). *Evolution, Development, and Intentional Control of Imitation (NEST 012929-EDICI)*. Conference. Schloss Machern, Germany. ■

Springer, A., & Volz, K. G. (January). *Finding culturally (in)dependent levels of self-representation: The case of emotions*. Workshop. Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany. ■ 2007

Ferstl, E. C., van den Broek, P., & van Berkum, J. (February). *Brain Mechanisms and Cognitive Processes in the Comprehension of Discourse*. Workshop. Lorentz Center, Leiden University, the Netherlands. ■

Schubotz, R. I. (June). *Other Minds – Perspektiven, Einblicke, Fragen* [Other Minds – Perspectives, Insights, Questions]. Workshop. Otto von Guericke University Magdeburg, funded by the Young Academy at the Berlin-Brandenburg Academy of Science and Humanities and the German Academy of Natural Scientists Leopoldina. Schönebeck, Germany. ■

Ullsperger, M., & Debener, S. (June). *New Avenues for Simultaneous EEG/fMRI Recordings: From Feasibility to Practice*. Workshop. 13th annual meeting of the Organization for Human Brain Mapping, Chicago, IL, USA. ■

Volz, K. G., & Springer, A. (September). *Dissociating Levels of Emotional Self-Representation*. Workshop. Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany. ■

Schroeter, M. L., & Fallgatter, A. J. (November). *Diagnostische Aspekte frontotemporaler Demenzen* [Diagnosis of frontotemporal dementia]. Symposium. Annual Meeting DGPPN, Berlin, Germany. ■

Appointments

Brass, Marcel. *Research Professorship funded by the Special Research Fund of Ghent University*. Ghent University, Belgium. ■ 2006

Ferstl, Evelyn C. *Senior Lectureship for Cognitive Neuroscience*. University of Sussex, Brighton, United Kingdom. ■

Schubotz, Ricarda I. *W2 Visiting Professorship ("Erleben-Professur")*. Otto-von-Guericke-University Magdeburg, Germany. ■

Ullsperger, Markus. *Leader of the Independent Junior Research Group "Cognitive Neurology"*. Max Planck Institute for Neurological Research, Cologne, Germany. ■

Degrees

Habilitations

- 2006** ■ Ferstl, E. C. *The functional neuroanatomy of text comprehension*. Faculty of Biology, Pharmacy and Psychology, University of Leipzig, Germany.
- Müller, K. *Die Anwendung von Spektral- und Waveletanalyse zur Untersuchung der Dynamik von BOLD-Zeitreihen verschiedener Hirnareale [Using spectral and wavelet analysis to investigate the BOLD dynamics of different brain regions]*. Faculty of Medicine, University of Leipzig, Germany.
- Schroeter, M. L. *Optische Bildgebung in der kognitiven Neurowissenschaft [Enlightening the brain – optical imaging in cognitive neuroscience]*. Faculty of Medicine, University of Leipzig, Germany.
- 2007** ■ Brass, M. *Das inferior-frontale Kreuzungsareal und seine Rolle bei der kognitiven Kontrolle unseres Verhaltens [The role of the inferior frontal junction area in cognitive control]*. Faculty of Biology, Pharmacy and Psychology, University of Leipzig, Germany.
- Ullsperger, M. *Functional neuroanatomy of performance monitoring: fMRI, ERP and patient studies*. Faculty of Medicine, University of Leipzig, Germany.

PhD Theses

- 2006** ■ Bahlmann, J. *Neural correlates of the processing of linear and hierarchical artificial grammar rules: Electrophysiological and neuroimaging studies*. University of Leipzig, Germany.
- Forstmann, B. U. *Behavioral and neural correlates of endogenous control processes in task switching*. University of Leipzig, Germany.
- Kupka, T. A. *Funktionelle Nahinfrarotspektroskopie in den kognitiven Neurowissenschaften – Multimodale Bildgebung und ereigniskorrelierte Stimulationsdesigns [Functional near-infrared spectroscopy in cognitive neurosciences – Multimodal imaging and event-related stimulation tasks]*. University of Leipzig, Germany.
- Siebörger, F. T. *Funktionelle Neuroanatomie des Textverstehens: Kohärenzbildung bei Witzen und anderen ungewöhnlichen Texten [Functional neuroanatomy of text comprehension: Coherence building in jokes and other peculiar texts]*. University of Leipzig, Germany.
- Tewes, A. *Perzeptuelle Sequenzverarbeitung im lateralen prämotorischen Kortex – eine Untersuchung mit repetitiver transkranieller Magnetstimulation (rTMS) [Perceptual sequence processing in lateral premotor cortex – an investigation using repetitive transcranial magnetic stimulation (rTMS)]*. University of Leipzig, Germany.
- Walter, K. *Entwicklung und Evaluation eines interaktiven Gedächtnissystems für hirngeschädigte Patienten mit Beeinträchtigung des prospektiven Erinnerns [Development and evaluation of an interactive memory system for patients with brain damage and prospective memory impairment]*. University of Leipzig, Germany.
- Wolfensteller, U. *Habituelle und arbiträre sensomotorische Verknüpfungen im lateralen prämotorischen Kortex des Menschen [Habitual and arbitrary sensorimotor mappings in human lateral premotor cortex]*. University of Leipzig, Germany.
- 2007** ■ Konrad, S. *Die Rolle des anterior-präfrontalen und des inferior-parientalen Kortex bei der nichtartikulatorischen Aufrechterhaltung und Manipulation verbaler Information in Arbeitsgedächtnisaufgaben. Ergebnisse aus zwei funktionell-magnetresonanz-tomographischen Studien unter parametrischer Variation von Gedächtnislast,*

artikulatorischer Suppressionsintensität und Manipulationsanforderung [The role of the anterior prefrontal and inferior parietal cortex in non-articulatory maintenance and manipulation of verbal information in working memory tasks. Findings from two functional magnetic resonance imaging studies employing parametric variation of memory load, articulatory suppression intensity and manipulation demand.]. University of Leipzig, Germany.

Awards

Brass, M. Heisenberg Forschungsstipendium [Heisenberg Fellowship]. German Research Foundation (DFG). ■ 2006

Ferstl, E. C. Fellowship (9 months) at the Hanse-Institute for Advanced Study. Delmenhorst, Germany. ■

Hoffmann, S. Best oral presentation given by young investigators at the 22nd Congress of the European Committee for Treatment and Research in Multiple Sclerosis. Madrid, Spain. ■

Ullsperger, M. Junior Fellow Research Grant. Max Planck International Research Network on Aging (MaxNetAging). ■

Volz, K. G. Posterpreis für herausragende wissenschaftliche Leistungen auf dem Gebiet der Medizin und Biowissenschaften [Poster award for outstanding scientific performances in medicine and life sciences]. 5th Leipzig Research Festival for Life Sciences, Leipzig, Germany. ■

Klein, T. A. Travel Award of the Organization for Human Brain Mapping. Organization for Human Brain Mapping. ■ 2007

Publications

Books and Book Chapters

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

Brass, M., Derrfuß, J., & von Cramon, D. Y. (2007). The role of the posterior frontolateral cortex in task-related control. In S. A. Bunge, & J. D. Wallis (Eds.), *Neuroscience of Rule-Guided Behavior* (pp. 177-197). Oxford: Oxford University Press.

Brass, M., & Spengler, S. (in press). The inhibition of imitative behavior and attribution of mental states. In T. Striano, & V. M. Reid (Eds.), *Social cognition: Development, neuroscience and autism*. Oxford: Blackwell.

Brass, M., & von Cramon, D. Y. (in press). How motor-related is cognitive control? In P. Haggard, Y. Rossetti, & M. Kawato (Eds.), *Sensorimotor foundations of higher cognition* (Attention + Performance, Vol. 22). Oxford: Oxford University Press.

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Ferstl, E. C., & Siebörger, F. T. (2007). Neuroimaging studies of coherence processes. In M. Schwarz-Friesel, M. Consten, & M. Knees (Eds.), *Anaphors in Text: Cognitive, formal and applied approaches to anaphoric reference* (SLCS = Studies in Language Companion Series, Vol. 86, pp. 225-240). Amsterdam: Benjamins.

Forstmann, B. U. (2006). *Behavioral and neural correlates of endogenous control processes in task switching* (MPI Series in Human Cognitive and Brain Sciences, Vol. 70). Leipzig: Max Planck Institute for Cognitive and Brain Sciences.

Hübsch, T., & Tittgemeyer, M. (2007). Multi-Scale Analysis of Brain Surface Data. In A. Deutsch, R. Bravo de la Parra, R. J. de Boer, O. Diekmann, P. Jagers, E. Kisdi, et al. (Eds.), *Mathematical Modeling of Biological Systems* (pp. 279-287). Boston: Birkhäuser.

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Lohmann, G., von Cramon, D. Y., & Colchester, A. C. F. (2006). Investigating cortical variability using a generic gyral model. In J. Sparring, M. Nielsen, & J. Sparring (Eds.), *Medical Image Computing and Computer-Assisted Intervention – MICCAI 2006* (Lecture Notes in Computer Science, pp. 109-116). Berlin: Springer.

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Schroeter, M. L. (2006). *Enlightening the Brain – Optical Imaging in Cognitive Neuroscience* (MPI Series in Human Cognitive and Brain Sciences, Vol. 72). Leipzig: Max Planck Institute for Human Cognitive and Brain Sciences.

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Schubotz, R. I., & von Cramon, D. Y. (in press). Funktionelle Neuroanatomie und Pathologie der Exekutivfunktionen [Functional neuroanatomy and pathology of executive functions]. In M. Eimer, & T. Goschke (Eds.), *Kognitive Neurowissenschaft. Enzyklopädie der Psychologie*. Göttingen: Hogrefe.

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Published Papers

Abraham, A. (2007). Can a neural system geared to bring about rapid, predictive and efficient function explain creativity? *Creativity Research Journal*, 19(1), 19-24.

Abraham, A., von Cramon, D. Y., & Schubotz, R. I. (in press). Meeting George Bush versus meeting Cinderella: The neural response when telling apart what is fictional in the context of our reality. *Journal of Cognitive Neuroscience*.

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Abraham, A., & Windmann, S. (2007). Creative cognition: The diverse operations and the prospect of applying a cognitive neuroscience perspective. *Methods*, 42(1), 38-48.

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Amunts, K., & von Cramon, D. Y. (2006). The anatomical segregation of the frontal cortex: What does it mean for function? *Cortex*, 42(4), 525-528.

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- Boecker, M., Bücheler, M. M., Schroeter, M., & Gauggel, S. (2007). Prefrontal brain activation during stop-signal response inhibition: An event-related functional near-infrared spectroscopy study. *Behavioral Brain Research*, 176, 259-266.
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- Brass, M., Schmitt, R., Spengler, S., Gergely, G. (in press). Understanding action understanding. *Current Biology*.
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- Debener, S., Ullsperger, M., Siegel, M., & Engel, A. K. (2006). Single-trial EEG-fMRI reveals the dynamics of cognitive function. *Trends in Cognitive Sciences*, 10(12), 558-563.
- Debener, S., Ullsperger, M., Siegel, M., & Engel, A. K. (in press). Towards single-trial analysis in cognitive brain research. A reply to C. Bledowski et al. *Trends in Cognitive Sciences*.
- Derrfuß, J., Brass, M., von Cramon, D. Y., Lohmann, G., & Amunts, K. (in press). Neural activations at the junction of the inferior frontal sulcus and the inferior precentral sulcus: Interindividual variability, reliability and association with sulcal morphology. *Human Brain Mapping*.
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- Friederici, A. D., von Cramon, D. Y., & Kotz, S. A. (2007). Role of the corpus callosum in speech comprehension: Interfacing syntax and prosody. *Neuron*, 53(1), 135-145.
- Führer, D., Zysset, S., & Stumvoll, M. (in press). Brain activity in hunger and satiety: an fMRI study. *Obesity*.
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Figure 1.2.1

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Prof. Dr. Angela D. Friederici
Director

2 Neurocognition of Language

Department of Neuropsychology

The department's research agenda is to identify the neural basis of language processing in the mature and the developing brain. The theoretical view guiding our research is that the human language faculty can be decomposed into linguistically relevant subdomains which have specific representations in the brain. We take it as a challenge to not only localize these subdomains, but also to uncover how they interact in real-time.

Based on our findings, we have formulated a Neurocognitive Model of Auditory Language Comprehension in the adult which describes the time course and neuroanatomy of syntactic, thematic and lexical as well as prosodic processes. The former processes are located as separable networks in the left hemisphere, while those associated with the processing of prosody are located in the right hemisphere. Our recent research has focused on further specifying the neural basis of the syntactic and prosodic processes and delineating the time course and neural underpinnings of their interaction. Moreover, we have explored the relationship between language and other systems relevant to communication such as Emotion, Action and Music.

Research in the domain of language development has allowed us to specify the neurophysiological markers reflecting early phonological, lexical and syntactic processes, and to describe their course of maturation. Our studies suggest that, once developed, these processes and their neural underpinnings are qualitatively similar to those of the adult system, but quantitatively different. Thus their time course is slowed, and their localization is less segregated.

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2.1

Neurocognition of Language Processing

In recent years, our research has been dominated by investigations into the neural basis of syntax and prosody as well as how the two systems interact. Functionally, we have investigated the role of Broca's area in syntactic processing in a number of fMRI experiments involving: (a) a context-free grammar (2.1.1), (b) an artificial grammar mimicking the phrase structure rules of a natural grammar (2.1.2), and (c) a natural language, i.e. Japanese, which has a particularly interesting morphological system (2.1.3). A progressive shift of activation in Broca's region, from a more posterior activation to a more anterior activation, was observed across the three experiments, 2.1.1, 2.1.2 and 2.1.3. These findings suggest functional differentiation within this region. A structural segregation of the prefrontal cortex was further demonstrated on the basis of connectivity patterns (Friederici, Bahlmann, Heim, Schubotz, & Anwender, 2006). Here, we report a segregation based on a receptorarchitectonic analysis (2.1.4). The interaction between syntax and prosody during language processing was studied at the functional and the structural level (2.1.5, 2.1.6, Friederici, von Cramon, & Kotz, 2007, *Neuron*, 53, 135-145), and during the learning of rule-based structured sequences (2.1.7).

The processing of emotional prosody (2.1.8, 2.1.9, 2.1.10) revealed the involvement of the right hemisphere and the amygdala. Emotion in form of positive and negative information encoded lexically was investigated at the level of word recognition (2.1.11) and at the level of news reports (2.1.12). Additional studies focused on the processing of irony (2.1.13, 2.1.14). Finally the relation between language and motor systems during language comprehension was investigated for the special case of co-speech gestures (2.1.15, 2.1.16, 2.1.17).

A core interest of research at the institute has been, and still is, the relationship between language and music. The interrelation between language and music processing was demonstrated in joint experiments with the Neurocognition of Music group (see Jentschke, Koelsch, & Friederici, 5.1.3 and Sammler, Koelsch, & Friederici, 5.1.4). Similarities and hemispheric differences in the brain activation for instrumental and sung sequences (2.1.18) and for music and speech items (2.1.19) provided interesting insights into the neural representation of language and music. The processing of native and non-native music pieces revealed differences in the lateralization of the neural network of music processing (2.1.20).

2.1.1 The role of Broca's area in hierarchical processing: fMRI evidence from a context-free grammar

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The processing of hierarchical structures has recently been claimed to be a human-specific trait of the language faculty. The question of whether this trait has a specific neural basis was addressed in the present study using two types of artificial grammar. Here we demonstrated that the brain region identified as processing grammar is specialized for the processing of structural hierarchies. This was done by making a direct comparison of the brain activation during the processing of hierarchical versus linear rules. Two types of syllable category were generated. Categories were segregated according to vowel type (A = e/i; B = o/u) and consonant type (A1 – B1 = b – p; A2 – B2 = d – t; A3 – B3 = g – k). Linear syllable sequences followed the rule (AB)_n, in which simple transitions between two types of syllable category were generated (e.g. A1B1A2B2; “be po di tu”). The hierarchical

syllable sequences followed the rule AnBn, generating a centre-embedded structure (e.g. A2A3B3B2; “de gi ku tu”) such that the last elements were predicted by the first elements. The chunking of the two categories, and the maintenance of the particular elements in working memory until the matching category occurred produced long distance dependencies of embedded syllable sequences. When comparing the processing of hierarchical sequences to linear sequences, significantly higher activations were observed in Broca's area and in several other cortical and subcortical regions. The present study thus provides evidence for the notion that Broca's area is part of a neural circuit that is associated with the processing of embedded structures and the resultant hierarchical dependencies.

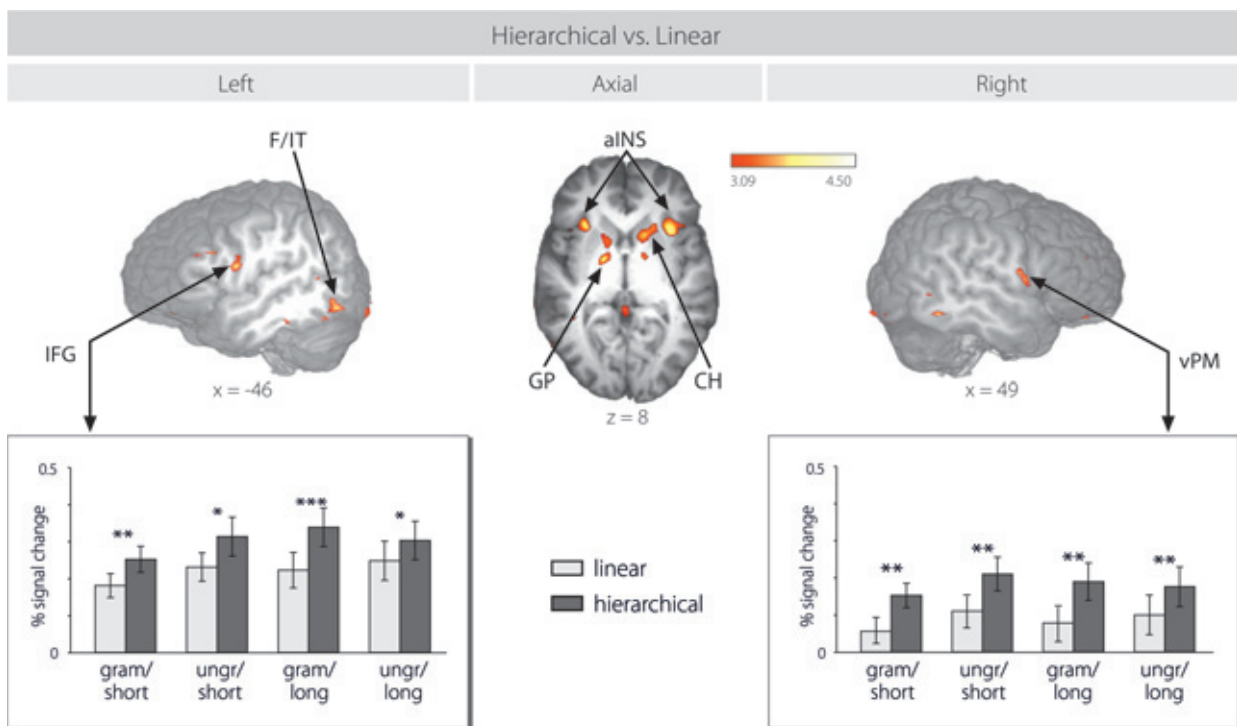


Figure 2.1.1 Left diagram: ROI analysis of the different variables obtained in the left BA 44/6. Right diagram: ROI analysis in the right BA 6. Hierarchical sequences (dark gray) show a higher BOLD response than linear sequences (light gray) in bilateral BA 44/6, in grammatical, short sequences (gram/short); ungrammatical, short (ungr/short); grammatical, long (gram/long); and ungrammatical, long items (ungr/long). Left-hemispheric ROIs revealed a higher hemodynamic response in comparison to right-hemispheric ROIs. IFG = inferior frontal gyrus; F/IT = fusiform/inferior temporal gyrus; aINS = anterior insula; GP = globus pallidus; CH = caudate head; vPM = ventral premotor cortex. N = 14, * $p < .05$, ** $p < .01$, *** $p < .001$.

Neural basis of processing sequential and hierarchical syntactic structures

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Language learning partly relies on a rule-based mechanism that is mediated by the frontal cortex. Interestingly, the actual structure involved within the frontal cortex varies with the kind of rule being processed. Using functional MRI, we investigated the neural underpinnings of rule-based language processing using an artificial language that allowed direct comparison between local phrase structure dependencies and hierarchically structured

long-distance dependencies (see Fig. 2.1.2.1). Participants were trained on the artificial grammar two days prior to scanning. During scanning, grammatically correct and incorrect sentences were presented. A word verification task after each sentence was administered to maintain the participants' attention. A first fMRI data analysis contrasted sentences containing local violations with correct sentences and those containing long-distance violations

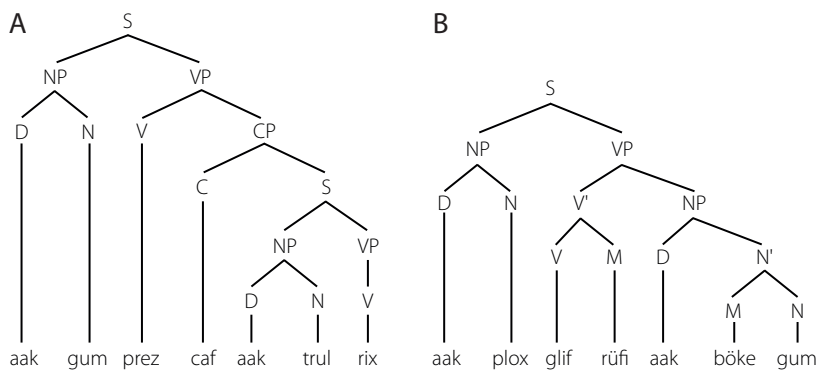


Figure 2.1.2.1 Examples of the hierarchical structure (A) and local dependencies (B) of the grammar system. D, determiner; A, adjective; N, noun; V, verb; M, verb modifier; C, complementizer.

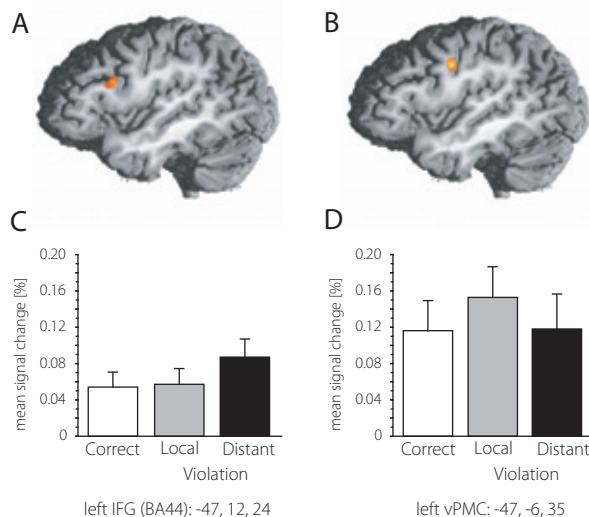


Figure 2.1.2.2 Regions in the frontal cortex demonstrating increased activity to violations as compared to correct sentences. A: The left IFG (BA 44) is selectively more engaged in processing long-distance violations as compared to local violations or correct sentences. B: The vPMC shows more activity for local as compared to long-distance violations and correct sentences. C,D: Brain activity (mean % signal change of the BOLD response of three consecutive time points around the peak $\pm$ SE of the mean across participants) for both violation conditions compared to correct sentences.

with correct sentences. Local violations led to increased activity in a number of brain areas including the hippocampus and the left ventral premotor cortex (vPMC). Long-distance violations compared to their correct counterparts only gave rise to activation in a few brain areas. A second analysis, which took into account the individual differences in learning, i.e. proficiency, found clear differences between sentences with long-distance violations and correct sentences in two brain areas: the opercular part of the IFG (BA 44 as part of Broca's area) and the vPMC (see Fig. 2.1.2.2).

Thus, activation in the left vPMC was related to the local character of rule change, whereas long-distance dependencies activated the opercular part of the inferior frontal gyrus (Brodmann's area (BA) 44). These results suggest that the brain's involvement in syntactic processing is determined by the type of rule used, with Broca's area playing an important role during language processing when long-distance dependencies are processed, and with the ventral PMC subserving the processing of local dependencies.

2.1.3 The neural correlates of thematic reanalysis during sentence comprehension

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The present auditory fMRI study focused on investigating the brain region responsible for “thematic reanalysis”. This particular type of linguistic process is required when the comprehenders’ initial assignment of the thematic roles in a sentence must be revised during on-line processing of the sentence. Japanese causative and passive constructions were tested in the current study. In these two constructions, in Japanese the critical morphemes (causative *sase* and passive *rare*) attach to the verb in the sentence final position and induce a thematic reanalysis (see Fig. 2.1.3.1). The passive construction additionally requires a structural reanalysis. This process is illustrated in Fig. 2.1.3.1.

The results from the study indicated that thematic reanalysis (causative vs. active) elicited an increased activation in the left inferior frontal gyrus (BA 45) while a combination of thematic and structural reanalyses (passive vs. active) activated both left IFG (BA 45) and PSTG/STS (see Fig. 2.1.3.2). Thus, we conclude that BA 45 is crucially associated with thematic reanalysis. The current study provides direct evidence for a functional neuroanatomical basis for thematic reanalysis as well as providing further evidence for the supporting role of Broca’s area in language processing.

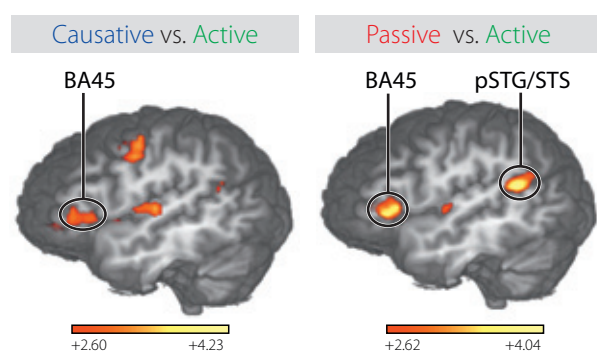


Figure 2.1.3.2 Brain regions sensitive to thematic and structural reanalysis. The comparison Causative vs. Active (left) demonstrates that BA45 is sensitive to thematic reanalysis for Causative. The comparison Passive vs. Active (right) indicates that BA45 is responsible for thematic analysis as well as that a combination of thematic and structural reanalysis induces an activation of STG/STS for Passive.

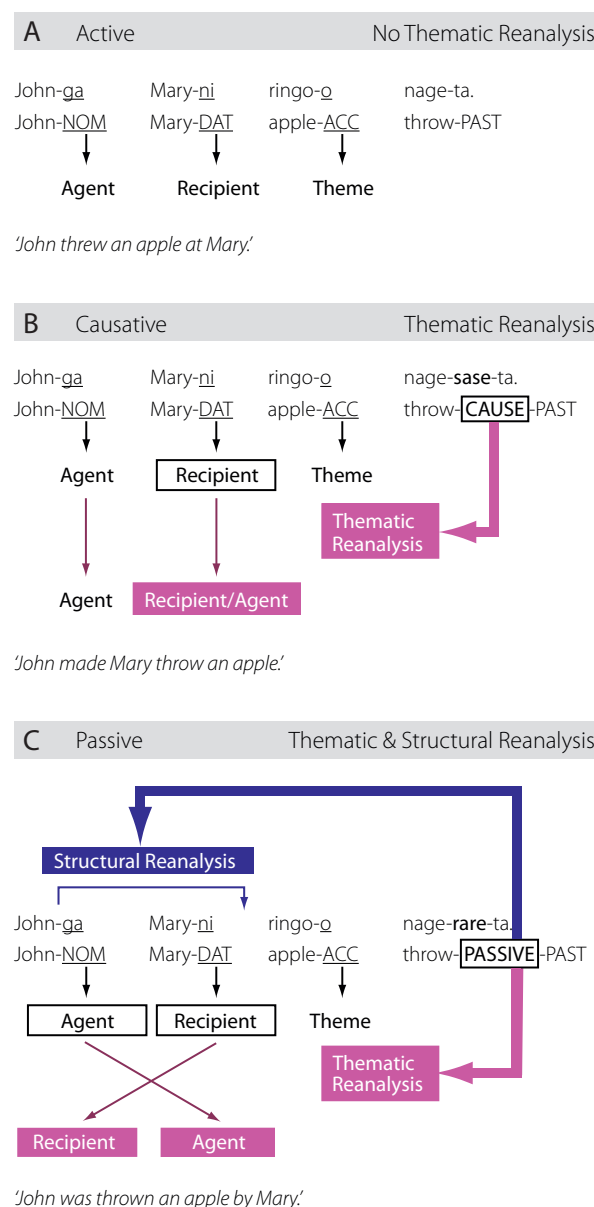


Figure 2.1.3.1 Predicted thematic and structural reanalysis. Black arrows indicate a default assignment of thematic roles, pink arrows thematic reanalysis, and blue arrows structural reanalysis.

Receptor architectonics of Broca's region and the frontal operculum

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Previously published probabilistic cytoarchitectonic maps (Amunts, Schleicher, Bürgel, Mohlberg, Uylings, & Zilles, 1999, *J Comp Neurol*, 412, 319-341) and functional imaging studies (Heim & Friederici, 2003, *Neuroreport*, 14, 2031-2033; Indefrey, Brown, Hellwig, Amunts, Herzog, Seitz, & Hagoort, 2001, *Proc Natl Acad Sci USA*, 98, 5933-5936; Friederici, Rüschemeyer, Hahne, & Fiebach, 2003,

Cereb Cortex, 13, 170-177) suggest a more detailed parcellation of the posterior inferior-frontal cortex than has been demonstrated so far. To increase our understanding of the functional and anatomical nature of Broca's region and neighbouring areas in the posterior inferior-frontal cortex, a multimodal parcellation was conducted to create the foundation for a reliable localization of functional activations. For this purpose, cytoarchitectonic mapping was combined with quantitative receptor autoradiography – a method reflecting the distributional patterns of neurotransmitter receptors in the brain (Zilles, Schleicher, Palomero-Gallagher, & Amunts, 2002, In Toga, & Mazziotta (Eds.), *Brain Mapping: The Methods* (pp. 573-602), Elsevier Science; Zilles, Palomero-Gallagher, & Schleicher, 2004, *J Anat*, 205, 417-432). The present study gives the first complete, comprehensive receptor architectonic description of the posterior inferior-frontal cortex and includes the receptor architectonic characterization of Broca's region and its right hemispheric homologue, i.e. BA 44 and BA 45, as well as the receptor architectonic definition of three new areas bordering on Broca's region: area dtc (dysgranular transitional cortex) and areas op (opercular) 8 and op 9. Analysis of receptor distribution patterns revealed a clear differentiation between the opercular areas and the remaining posterior inferior-frontal areas. Additionally, the receptor architectonic organization of the inferior-frontal areas showed strong resemblances between Broca's region (BA 44 and BA 45) and premotor area (BA 6), indicating common functions of these areas.

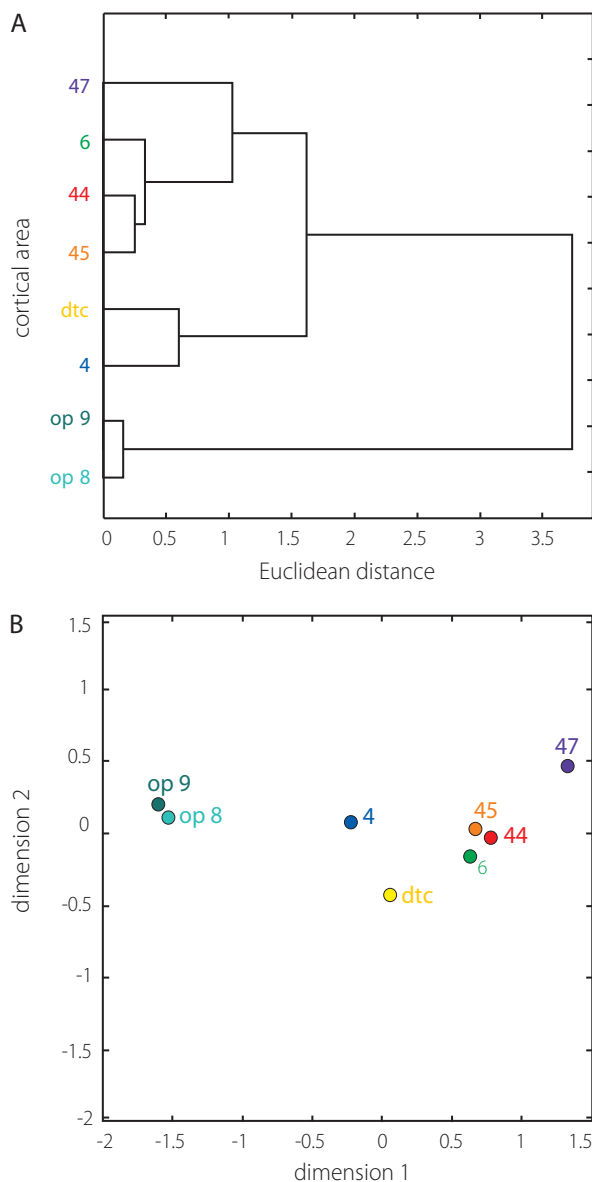


Figure 2.1.4 Hierarchical cluster analysis and multidimensional scaling (MDS) of the posterior inferior-frontal areas based on receptor architectonic data. The normalized receptor density values are used as feature vectors for the different areas. The Euclidean distance between the feature vectors of two cortical areas is a measure of similarity. The similarity information was visualized by (A) hierarchical cluster analysis and (B) MDS. In the hierarchical cluster analysis, areas are grouped according to their Euclidean distances. The MDS was applied as a means of presenting the similarity pattern in a two-dimensional plot. A short distance indicates a high similarity of the receptor distribution patterns and hence a similar receptor architectonic organization.

2.1.5 ERP-Evidence for initial interaction of syntax and prosody in speech comprehension

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In a recent ERP-study designed to investigate the time course of processing of phrasal prosody and phrasal syntax, we observed an interaction between both types of information which took place during a late integrative stage of speech processing. The aim of the present ERP-study was to specify whether a first mapping between prosody and syntax had already occurred during the very early stage of phrase-structure building.

To this end, we fully combined a prosodic and a syntactic incongruity in a 2 x 2 design yielding four experimental conditions. The challenge of having two critical information types available at different times was managed by using words, in which the (suprasegmental – “slow”) prosodic information was provided already at the word’s stem, whereas the (segmental – “fast”) syntactic information was available not before the word’s suffix.

In the present study we replicated our earlier observation of a right anterior negativity (RAN) following a mere prosodic incongruity. This supports our interpretation of the RAN as a correlate of linguistic processing at the prosodic representation level. It reflects a mismatch between expectancies built up on the basis of prior prosodic information and the actual prosodic properties of the speech input. The appearance of the RAN occurring even before syntactic information is available is relevant for linguistic theory, as it provides evidence that, in principle, prosodic information can be processed independently of basic syntactic information.

Second, the syntactic violation yielded a frontotemporal negativity resembling the ELAN. This is known, from various previous studies with comparable syntactic ma-

nipulations, to be a correlate of initial phrase structure building. Interestingly, in the present study, the ELAN was restricted to the left hemisphere when the prosodic phrase structure was congruent (see Fig. 2.1.5 A). In contrast, a bilateral E(L)AN, equally distributed over both the left and the right hemispheres, was observed for the combined syntactic and prosodic incongruity (see Fig. 2.1.5 B). This modulation of the topography of the ELAN suggests that prosodic information does indeed influence the course of early syntactic phrase structure building, and that an interaction between prosodic and syntactic information takes place even at this very initial stage of speech processing.

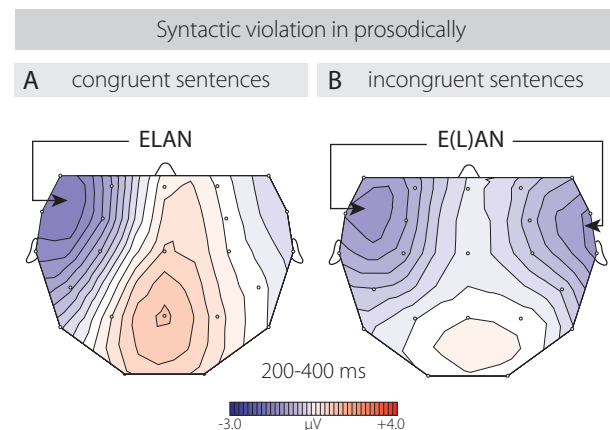


Figure 2.1.5 Topographical distribution of the ERP effects on the critical word’s suffix calculated by the subtraction of the fully correct baseline condition from (A) the syntactic alone violation condition and by the subtraction of prosodically alone incongruent sentences from (B) the combined syntactically and prosodically incongruent sentences.

2.1.6 Processing prosodic boundaries in natural and hummed speech: An fMRI study

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Speech contains prosodic cues such as pauses between different phrases of a sentence. These intonational phrase boundaries (IPBs) elicit a specific component in event-re-

lated brain potential studies, the so-called closure positive shift. The aim of the present study using functional magnetic resonance imaging techniques was to identify

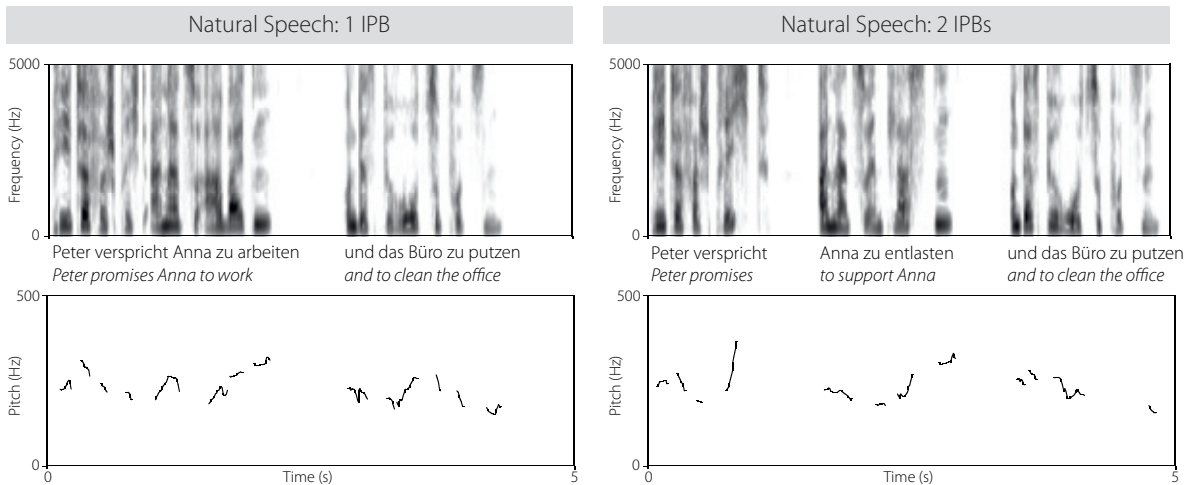


Figure 2.1.6.1 Spectrograms (0-5000 Hz) and fundamental frequency contours (pitch: 0-500 Hz) for sample stimuli of the sentence materials used for all conditions of the experiment. Spectrograms and pitch contours are given for each pair (1 and 2 IPBs) of sentence materials.

the neural correlates of this prosody-related component in sentences containing segmental and prosodic information (natural speech) and hummed sentences (i.e. only containing prosodic information). Sentences with 1 IPB or 2 IPBs were constructed. See Fig. 2.1.6.1 & 2.1.6.2 for examples of natural speech and their acoustic parameters. Participants listened to normal and hummed sentences. Hummed sentences contained one normally spoken word. This permitted the use of the same probe word verification task for both the spoken and hummed conditions. Sentences with 2 IPBs both in normal and hummed speech activated the middle superior temporal gyrus, the rolandic operculum, and Heschl's gyrus more strongly than sentences with 1 IPB (see Fig. 2.1.6.2). The results from a region of interest analysis of auditory cortex and auditory association areas suggest that the posterior ro-

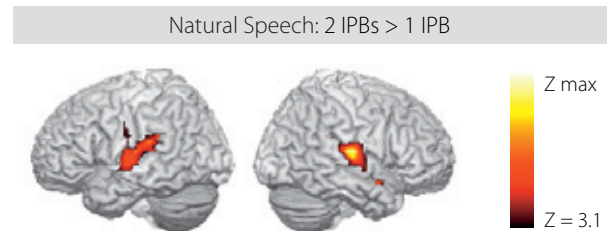


Figure 2.1.6.2

landic operculum bilaterally, in particular, supports the processing IPB information. Interestingly, this rolandic opercular activation is only observed in natural speech but not in hummed speech. This seems to indicate that prosody is an integrated part of natural speech when processing intonational phrase boundaries.

The role of pause cues in language learning: The emergence of ERPs related to sequence processing

2.1.7

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Humans can derive sequential dependencies from unfamiliar artificial speech within several minutes of exposure. However, there is an ongoing debate about the nature of the underlying learning processes. A widely discussed behavioural study suggests that the presence of subtle acoustic cues in the learning input might influence the computational mechanisms during the processing of language-like syllable strings (Peña, Bonatti, Nespore, & Mehler, 2002, *Science*, 298, 604-607). The present study was designed to elicit the electrophysiological

correlates of learning and processing of language-like syllable sequences in 2x2-experimental design. ERPs were measured in response to correct and incorrect phrases consisting of bisyllabic entities after short exposure to either rule-based or random artificial speech streams. Rule-based streams contained dependencies of the form AXC, whereby A elements reliably predicted the C elements while X elements were variable. Participants were exposed to four input and test phases. Two of the input streams were rule-based and contained either only

probabilistic information related to the distribution of the AXC stimuli or an additional acoustic cue indicating the boundaries of relevant units. The other two streams were random variations of the rule-based streams. During the test phase in the condition with pause cues, an early negativity and a later positivity emerged for correct as well as for incorrect items in comparison to their acoustically identical counterparts which were presented after the random control condition. During the test phase in the non-cued condition, only negativities

were seen. The ERP differences between incorrect sequences in the cued and non-cued conditions suggest that different cognitive mechanisms were applied during processing. The early timing of the negativity in the non-cued condition points to sensory-based processes of local deviance detection while the later timing of the negativity in the cued condition suggests application of a morphosyntactic rule. An additional positivity for the cued condition may reflect additional rule integration mechanisms at a later processing stage. In sum, the

results suggest that acoustic cues, such as pauses, crucially influence cognitive operations acquired during exposure to a rule-based syllable string.

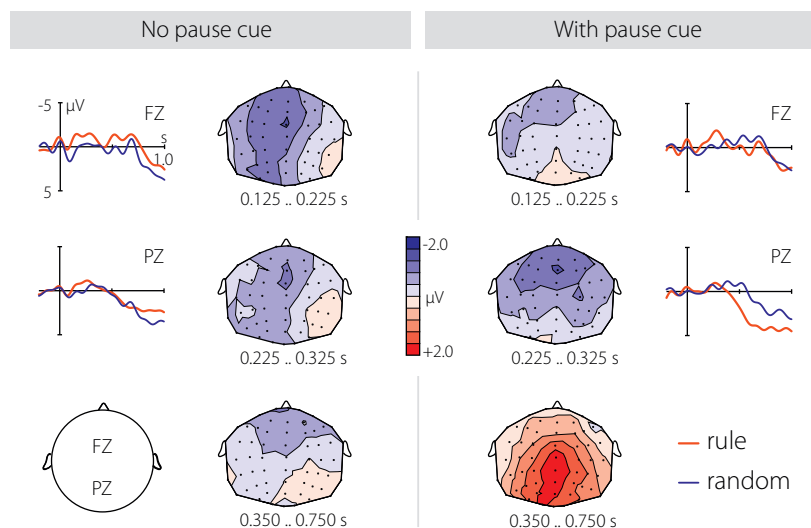


Figure 2.1.7 On the left side of the figure, illustrating the non-cued condition, an early negativity (125-225) can be seen. On the right side of the figure, illustrating the cued condition, a later negativity and an additional positivity were present. Red lines refer to ERPs measured in response to syntactically incorrect items after rule-guided exposure while blue lines refer to ERPs measured in response to the same items after randomly distributed exposure.

2.1.8 Lateralization of emotional prosody

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Research on the lateralization of linguistic and non-linguistic (emotional) prosody has experienced a revival, but neuroimaging and patient evidence do not coherently support the notion of right hemisphere involvement for linguistic and emotional prosody. In particular, recent neuroimaging evidence points to the possibility that methodological aspects may influence findings regarding lateralization effects. Here, we compared the results of a fully event-related design comparing emotionally unintelligible and emotionally intelligible sentences (Kotz, Meyer, Alter, Besson, von Cramon, & Friederici, 2003, *Brain Lang*, 86, 366-376) with results of a mixed design. Unintelligible and intelligible emotional stimuli were presented in blocks, respectively, but within blocks, emotional categories (emotional vs. non-emotional sen-

tences) were presented and analyzed in an event-related manner (Kotz, Meyer, Besson, & Friederici, 2003, *J Cogn Neurosci*, Suppl. 138). As the same stimulus material and task (emotional prosodic categorization) were used in both experiments, the effects of blocked-presentation vs. fully event-related presentation were directly compared. We previously argued (Kotz et al., 2003, *Brain Lang*, 86, 366-376) that the interleaving of stimulus types in an event-related design may promote bilateral and left-accented activation of an emotional prosodic brain network due to the fact that emotional prosodic categorization requires the participants to verbally label prosodic contours. Thus, the swift change from intelligible to unintelligible (filtered) emotional sentences may cause participants to attempt to understand and categorize unin-

telligible emotional sentences. In essence, as also argued by Vingerhoets and colleagues (Vingerhoets, Berckmoes, & Stoobant, 2003, *Neuropsychology*, 17, 93-99), verbally labelling emotional categories may promote semantic

processing and as a result enhance a left-hemisphere effort over a right-hemisphere analysis of emotional prosodic contours. The results confirm this prediction. Using a blocked design, strongly right-lateralized emotion-specific effects were observed, while

data obtained from the event-related study displayed bilateral or left-accented lateralization of emotion-specific effects (see Figure 2.1.8). These findings suggest a strong interaction between language and prosodic processing as a function of task and design.

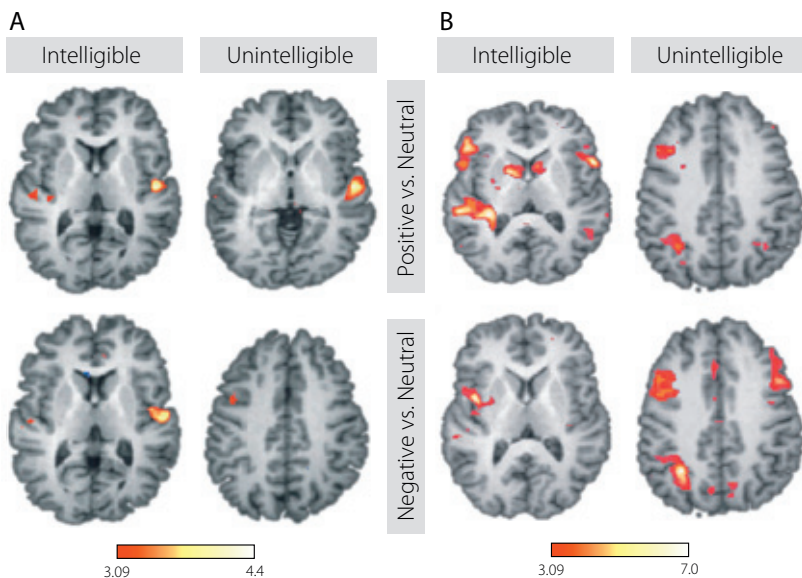


Figure 2.1.8 Displayed are in an axial view (non-radiological convention, left=left; right=right) the activation patterns for intelligible emotional speech (left) and unintelligible emotional speech (right) for positive valence (top) and negative valence (bottom) from (A) the blocked presentation design and (B) event-related design. Functional activation was thresholded at $Z \geq 3.09$ (uncorrected).

Valence and arousal effects on the P200 in emotional prosody processing

2.1.9

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Emotional states are communicated by different channels of expression, i.e. we express emotions through body language, facial expression, and tone of voice. The latter has received increasing attention in the literature over the last years. It has been proposed that emotion-

al prosody decoding is a rapid and highly automatized process in language perception. For example, previous evidence (Paulmann & Kotz, 2005, Poster presented at Proceedings of the ISCA Workshop on Plasticity in Speech Perception, London) revealed that different basic

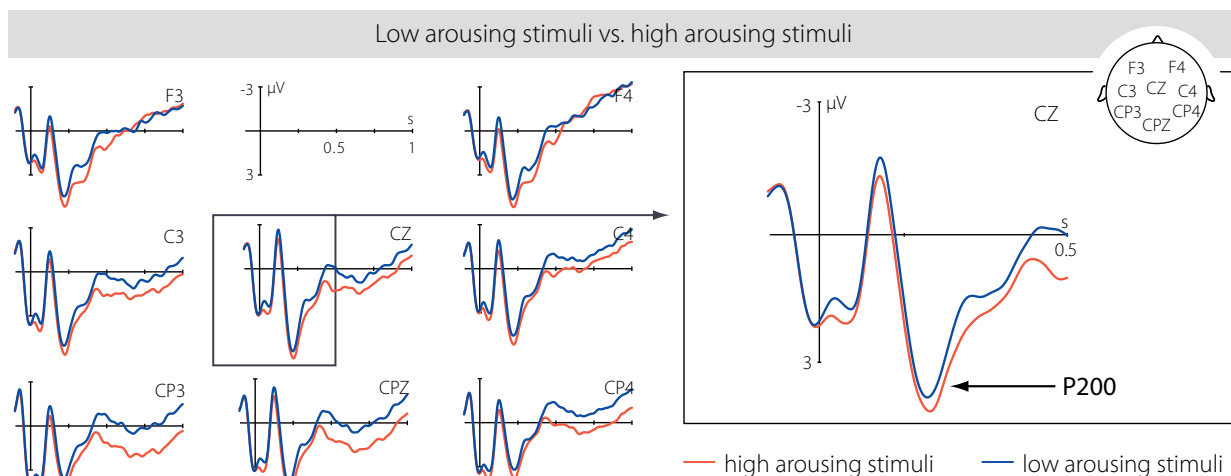


Figure 2.1.9

emotions can be differentiated in an early event-related brain potential (ERP) component, the P200. More specifically, it has been suggested that the P200 is modulated by the valence and intensity of an auditory stimulus, as well as by lexical information. The current study set out to further explore the different factors potentially influencing early emotional prosody processing. To investigate 'pure' emotional prosody processing, we presented pseudo-sentences spoken in six basic emotions plus a neutral baseline. To further explore the influence of arousal, we asked participants to rate the arousal level of a) the speaker or b) their own arousal level. Results confirm that different emotional intonations can be differentiated in a) an early component (P200), and b) a later component (after 500 ms). Analogous to the literature on visual emotional processing, we suggest that the P200 reflects a first emotional encoding of the stimulus including a valence tagging process. This first emotional encoding seems to be

particularly influenced by acoustical variations (Paulmann & Kotz, 2005, Poster presented at Proceedings of the ISCA Workshop on Plasticity in Speech Perception, London) but also by arousal, as different modulations of the P200 component were found for low and high arousing stimuli (see Fig. 2.1.9). The later ERP component is thought to reflect a potentially more elaborate analysis of the emotional stimulus as has been suggested in the visual domain (Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000, *Biol Psychol*, 52, 95-111), a process which is also influenced by arousal level of the participant. In sum, the current results confirm that the processing of emotional prosody is highly automatized and involves several sub-processes including a) early processing of (structural) emotional characteristics of a stimulus as reflected in the P200, and b) a more detailed analysis of the stimulus including an integration of the established context and valence of the emotional prosodic contour.

2.1.10 When vocal emotional processing gets emotional: On the role of interindividual differences and stimulus relevance

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Previous work on vocal emotional processing consistently implicated sensory and cognitive brain regions, but provided little evidence for an involvement of emotional processing areas such as the amygdala or the orbitofrontal cortex (OFC). Here, we sought to specify whether an involvement of these areas depends on the potential relevance that vocal expressions may have for the individual. To this end, we assessed participants' social orientation – a measure of the interest and concern for other individuals and hence the relevance of social signals provided by these individuals. We then presented task-irrelevant syllable sequences that contained rare changes in tone of voice that could be emotional or neutral. Processing differences between emotional and neutral vocal change in the right amygdala and the bilateral OFC were significantly correlated with the social orientation measure. Specifically, higher social orientation scores were associated with enhanced amygdala and OFC activity to emotional as compared to neutral change. This demonstrates that social orientation facilitates basic

emotional responses to unattended changes in speaker tone of voice, and decreases the likelihood that these changes go unnoticed. Moreover, social orientation may serve as a useful predictor for listener responses to vocal emotional cues and explain interindividual variability in vocal emotional processing as introduced by biological and environmental modulators (e.g. sex, culture).

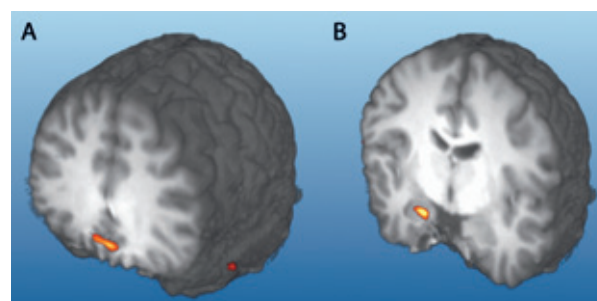


Figure 2.1.10 A positive correlation between social orientation scores and processing differences between rare emotional and rare neutral vocalizations was observed in (A) the bilateral OFC and (B) the right amygdala ($p < 0.001$).

Concrete and abstract emotional word processing

Kanske, P.^{1,2}, & Kotz, S.A.^{1,3}

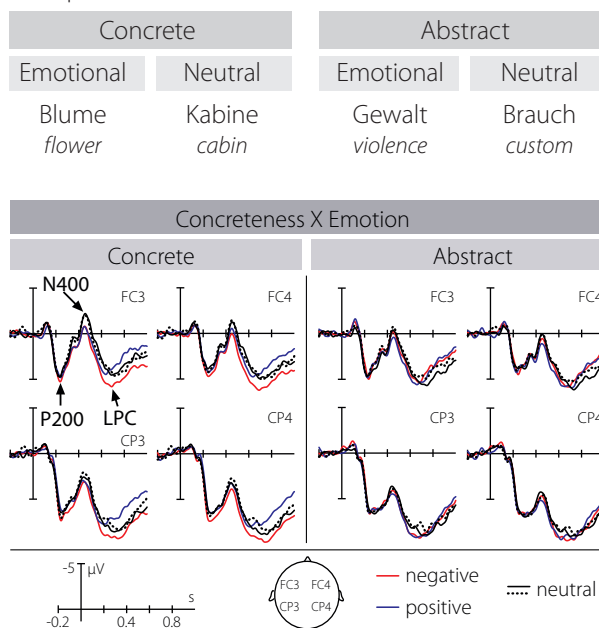
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This project aimed at examining the effects of concreteness and emotionality on visual word processing. Concrete and abstract words of negative, neutral or positive valence, as well as pseudowords were presented in a hemifield lexical decision task.

Example stimuli are:



Experiment 1 yielded early (P200) and late (N400, late positive component/LPC) emotional word effects. Concreteness also affected the N400 and the LPC. In line with the extended dual coding model and with previous studies (Holcomb, Kounious, Anderson, & West, 1999, *J Exp Psychol Learn*, 25, 721–742; Levy-Drori, & Henik, 2006, *Am J Psychol*, 119, 45–65), the N400 effect represents greater semantic activation, whereas the LPC effect may result from mental imagery being activated by concrete words. Experiment 2 engaged participants in a go/no-go task pressing a button for pseudowords, but not for words to yield an LPC time-window that was not response-confounded. Here, emotionality and concreteness again modulated the N400 independently, but interacted in the LPC time window. Only concrete emotional words differed in the LPC response suggesting that concrete negative words such as “wound” or “bomb” differ from neutral and positive words as a function of mental imagery (Kanske, & Kotz, 2007, *Brain Res*, 1138, 138–148).

Figure 2.1.11 ERPs at selected electrode-sites for concrete emotional and neutral as well as abstract emotional and neutral words in the second experiment.

Exploring the neural basis of public risk perception: Orbitofrontal cortex mediates implicit evaluation of personal relevance

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In a world of sophisticated communication networks we often learn about potentially dangerous events through language, in the absence of direct experience. Evaluation of information about risk for personal relevance is therefore essential to prevent potential harm or loss. To shed light on the neural basis of risk perception, the current functional magnetic resonance imaging (fMRI) experiment was designed to allow for an independent ma-

nipulation of the personal relevance of risk information. We developed a ‘news reception’ design as a model of a real-life risk perception situation where individuals learn about risk through verbal communication. During the scanning session, twenty-two German subjects (11 females) listened to short versions of fabricated but believable news reports about current events that either signaled potential harm/loss (negative reports) or ben-

efit (positive reports). The subjects were told that the reports were derived from real news stories. Critically, high versus low degrees of personal relevance were created by varying the geographical context of the events (Germany versus Great Britain), that is, high relevance for events in the residents' country ('own' condition) and low relevance for events in a distant but culturally comparable country ('other' condition). To assess implicit evaluation of personal relevance, an "oddball" target detection task was applied where subjects were instructed to press a button in response to infrequent target reports about events in a third country (France) that were randomly presented within the series of standard stimuli (Germany and Great Britain). Immediately following the scanning session, subjects performed a self-paced rating task assessing the (1) perceived unpleasantness/pleasantness of the reports, and (2) the probability of being personally affected by potential consequences of the reported is-

ues on visual analog scales. Here we show that among other regions, left orbitofrontal cortex (OFC) and left amygdala are involved in the processing of personally salient threats. Yet, our findings indicate differential roles for the OFC and amygdala in risk perception. Whereas the OFC was implicated in coding transient changes of the personal relevance of the threats, activation of the amygdala covaried with static, individual differences in the risk sensitivity as determined from post-scan ratings. That is, subjects who on average perceived their chances of negative consequences as likely to happen to them more frequently than they did positive consequences (i.e. "pessimists") showed greater activation of the amygdala in response to personally salient threats. Since the news reception paradigm of the present study modeled a primary way humans learn about risk in everyday life, these findings provide insights into the neural basis for public risk perception.

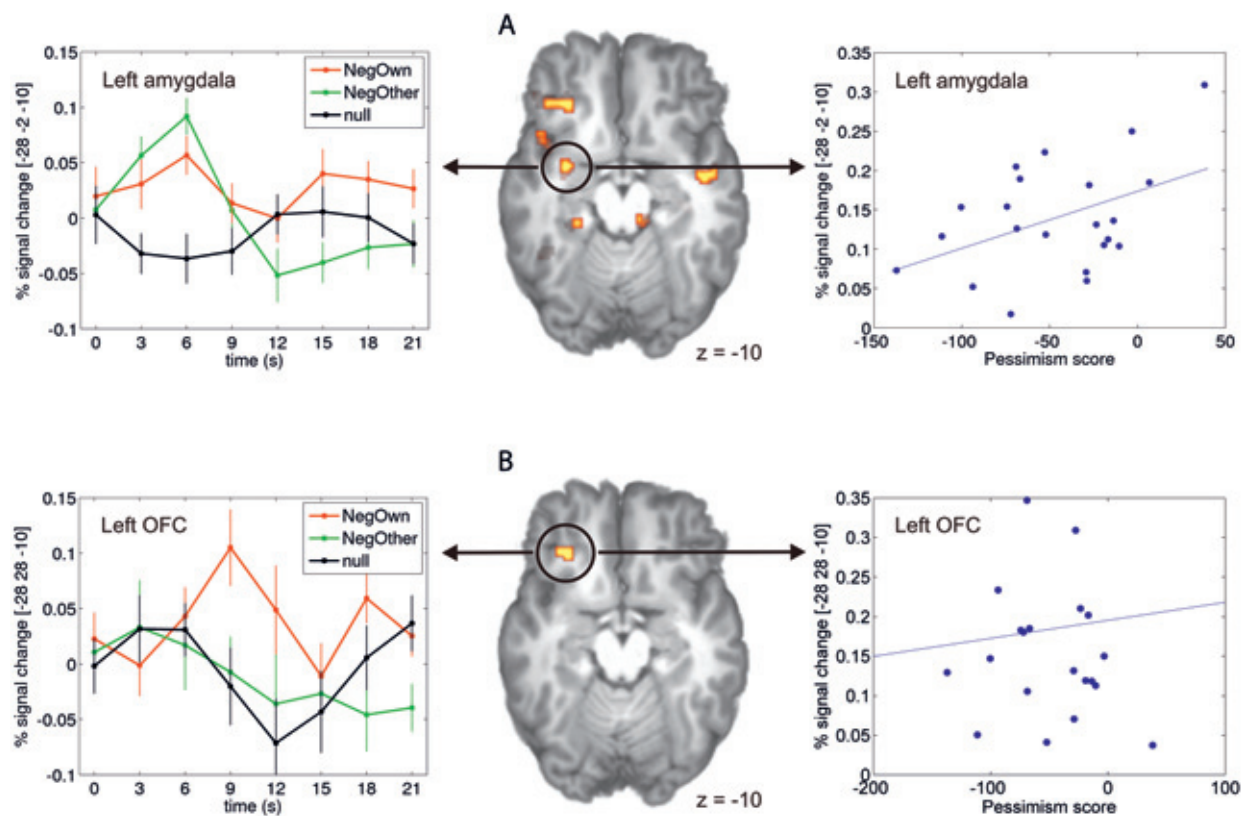


Figure 2.1.12 Differential roles of the OFC and amygdala in risk perception. (A) Brain regions associated with the processing of negative (potential harm/loss) versus positive reports (potential benefit) under conditions of high personal relevance (NegOwn - PosOwn; $P < 0.005$ uncorrected, $k = 10$ voxels). Note that the peak voxel in the left amygdala cluster is not sensitive to changes in the personal relevance of the negative reports as shown by the averaged time courses (% signal change) (left). However, signal change in the amygdala shows significant correlation ($r = 0.44$, $P < 0.05$) with individual differences in risk sensitivity (pessimism) across subjects (right). (B) Brain regions involved in the processing of negative versus positive reports in the high-relevance condition (NegOwn - PosOwn) that show a significant interaction ($P < 0.005$ uncorrected, $k = 10$ voxels) between report type and personal relevance ([NegOwn - PosOwn] - [NegOther - PosOther]). Note that the peak voxel in the left OFC cluster is sensitive to changes in the personal relevance of the negative reports as shown by the averaged time courses (left). However, signal change in the OFC shows no significant correlation ($r = 0.08$, $P = 0.74$) with individual differences in risk sensitivity (pessimism) across subjects (right).

Processing of ironic and non-ironic sentences examined with ERPs

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Irony is one of the most frequently used forms of figurative language and plays an important role in our daily communication. To comprehend ironic sentences, additional (i.e. contextual and pragmatic) information is necessary. The present study investigated the comprehension of visually presented ironic and non-ironic sentences by means of event-related brain potentials (ERPs).

We presented discourses that consisted of a context and a target sentence such as *That's really rich*. Target sentences conveyed an ironic meaning if they referred to a negative event (i.e. receiving a very small dish in a restaurant). By contrast, the same sentences conveyed a non-ironic meaning in reply to a positive event (i.e. receiving an opulent dish).

ERPs in response to the sentence-final word revealed a posteriorly distributed positivity between 500 and 900 ms evoked by ironic sentences. Interestingly, an N400 effect was not present suggesting that semantic processing difficulties were not associated with the comprehension of ironic sentences. Rather, findings suggest that the understanding of irony involves a more demanding inte-

gration process as reflected in the enhanced late positivity. This positivity is thought to reflect difficulty in deriving and integrating an appropriate interpretation in irony.

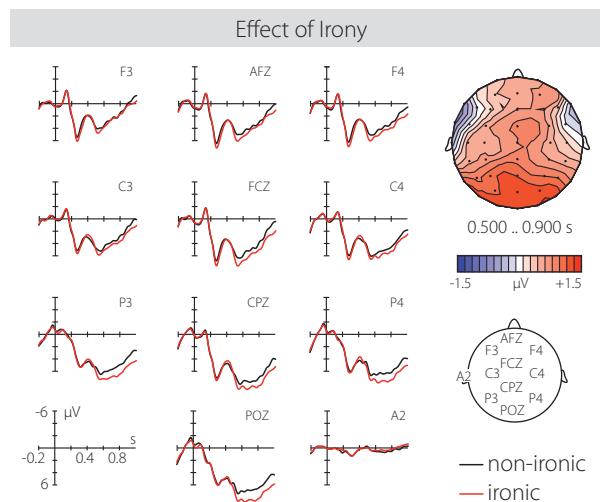


Figure 2.1.13 ERPs at the target sentence-final word for ironic and non-ironic sentence endings. The topographic map illustrates the distribution of the effect.

Irony-related versus syntax-related positivity

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Event-related brain potential (ERP) studies have shown distinct ERP components reliably elicited in response to semantic (N400) and syntactic anomalies (P600). Recent ERP studies have challenged this differentiation in which P600 effects were evoked by semantic manipulations such as semantic expectancy (Gunter, Friederici, & Schriefers, 2000, *J Cogn Neurosci*, 12, 556-568), thematic role violations (Kuperberg, Sitnikova, Kaplan, & Holcomb, 2003, *Cog Brain Res*, 17, 117-129) or semantic reversal anomalies (van Herten, Kolk, & Chwilla, 2005, *Cog Brain Res*, 22, 241-255). ERPs in response to the comprehension of ironic sentences have also shown a late positivity (Regel, Gunter, & Friederici, 2.1.13). These findings raise a question regarding whether the syntax-related P600 effect and the irony-related positivity effect are identical in their electrophysiological characteristics. In the current study, we investigated this question.

Participants read discourses that ended either with an ironic or non-ironic sentence (pragmatic manipulation). Additionally, final words of these sentences were morphosyntactically correct or incorrect since they contained a number or gender disagreement (i.e. *That's really rich*. - *That's really *richs*.).

Findings revealed a sensitivity of the late positivity to syntactic and pragmatic constraints (see Fig. 2.1.14). The P600 elicited by ironic sentences was similar in latency and waveform to the P600 evoked by syntactic anomalies. However, both effects differed in amplitude and morphology, which suggests a dissociation between both late positivities. The absence of an additivity effect on the late positivities' amplitude also supports a functional distinction. We thus conclude that both effects are independently related to the processing of pragmatic and grammatical information. The irony-related positivity

might reflect a more effortful processing related to deriving an appropriate interpretation, whereas the syntax-related P600 may be associated with syntactic repair processes.

Findings are consistent with models of language in which syntax and irony (pragmatics) are treated as representing different aspects of language processing.

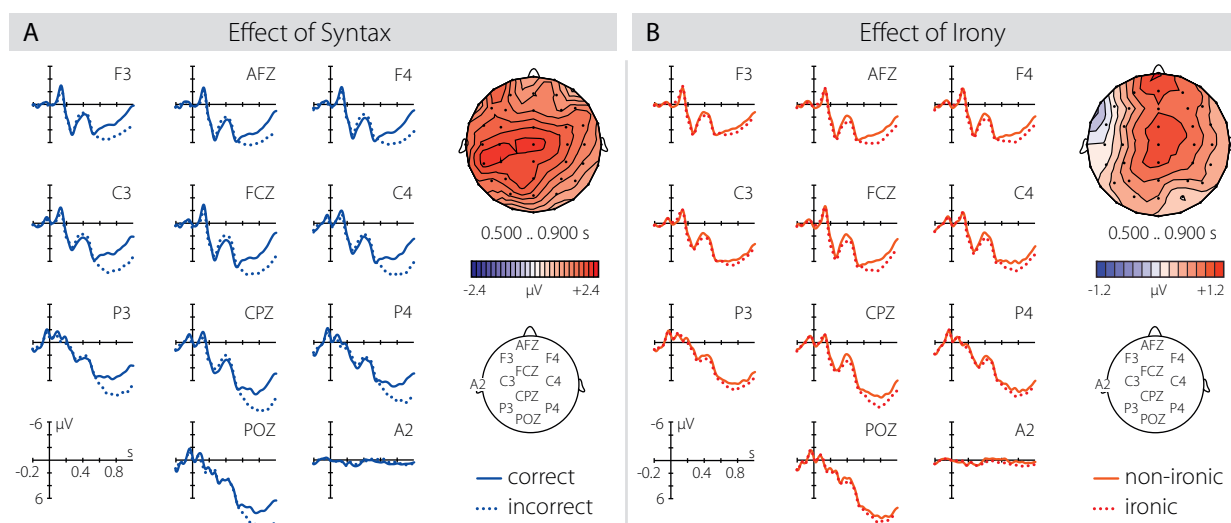


Figure 2.1.14 (A) Morphosyntactically incorrect sentence-final words elicited a broadly distributed positivity that was significant between 500 and 900 ms. (B) Ironic sentences also evoked a late positivity, which was confined to anterior and central brain regions. Compared to the P600 effect of syntax, a clear difference in amplitude and scalp topography of both effects was observed.

2.1.15 Neural correlates of the processing of co-speech iconic gestures

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The neural underpinnings of gestures that speakers spontaneously produce and their relationship to language have attracted increasing interest in recent years. In a previous ERP study (Holle, & Gunter, 2007), we have shown how listeners use the additional information provided by iconic gestures to disambiguate speech. Together with other recent ERP studies, there is now increasing evidence that gesture and speech interact during comprehension (Kelly, Kravitz, & Hopkins, 2004, *Brain Lang*, 89, 253-260; Özyürek, Willems, Kita, & Hagoort, 2007, *J Cogn Neurosci*, 19, 605-616). In the present study, we explored the brain areas involved in these bimodal interaction processes.

To this end, participants were presented with videos of an actress uttering lexically ambiguous sentences (e.g. She touched the mouse). Coincident with the sentence, the speaker produced one of three hand movements: (1) An iconic gesture illustrating the more frequent dominant meaning (e.g. re-enacting picking up a mouse by its tail), (2) An iconic gesture illustrating the less frequent subordinate meaning (e.g. re-enacting a double-click) or

(3) a meaningless grooming movement. The rationale for the experiment was that brain regions involved in the interaction between gesture and speech should show

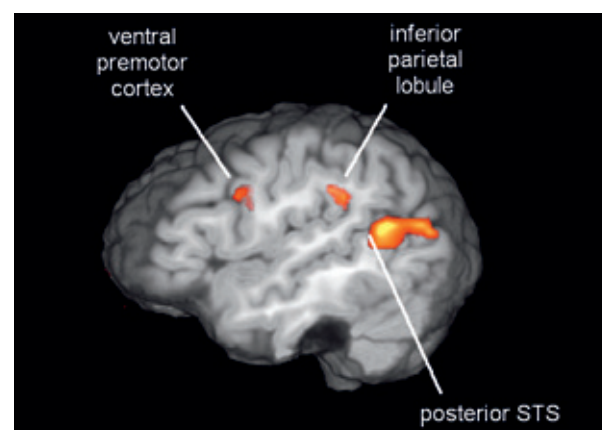


Figure 2.1.15 Brain areas where co-speech gestures elicited greater activation than co-speech grooming. $Z > 3.09$, $p < 0.05$ (corrected), $n = 17$. Note that activations in the vPMC and IPL were bilateral (right hemispheric activations not shown here).

a stronger BOLD response to a gesture-supported sentence than a sentence accompanied by a meaningless grooming movement.

The results showed that the processing of a co-speech gesture elicits greater levels of activation in the left posterior STS than the processing of a co-speech grooming movement. This activation may reflect the interaction between gesture and speech at a conceptual level. Another interesting finding was that gestures elicited greater ac-

tivity in the ventral premotor cortex (vPMC) bilaterally and the inferior parietal lobule (IPL) bilaterally. Given that these areas have been suggested as the core regions of the putative human mirror neuron system, these activations may reflect a mechanism for determining the goal of co-speech hand movements through an observation-execution matching process (Iacoboni, 2005, *Curr Opin Neurobiol*, 15, 632-637).

Exploring the temporal aspects of iconic gesture comprehension

2.1.16

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An increasing number of studies have shown that iconic gestures are of communicative value (e.g. Holle, & Gunter, 2007). While such experiments indicate that listeners can extract additional meaning from iconic gestures, it is still unclear how much of a gesture is needed before it becomes meaningful. In a series of experiments, we tried to clarify this issue.

Gestures can usually be divided into three consecutive time phases: preparation, stroke and retraction. Most researches consider the stroke as the part of a gesture in which meaning is expressed. A gating paradigm was used to determine the amount of gesture information needed to disambiguate a homonym (disambiguation point). For 60 of 96 gestures the content of the preparation phase sufficed, i.e. a gesture already disambiguates before its most informative part is seen. This finding

challenges the widespread notion that gestures are not meaningful prior to the stroke phase.

To check whether the observed disambiguation points carried realistically usable information in a co-speech context, two ERP studies were conducted. In the first one, short videos of an actress uttering sentences ('She was impressed by the BALL, because the GAME/DANCE ...') were shown. The ambiguous noun (BALL) was accompanied by a gesture that was presented up to its disambiguation point and later on disambiguated by a target word (GAME/DANCE). Afterwards, subjects had to judge whether the movement and speech were congruous. The ERP data showed an N400 effect for target words preceded by an incongruous gesture compared to target words preceded by a congruous one. In a second experiment, a more shallow memory task was used to assess

the nature of the process underlying the gesture-speech integration. Here no N400 effect was found.

To sum up, gestures may become meaningful earlier than assumed so far. Yet, the processing of such minimal gestural information seems to be a controlled rather than automatic process.

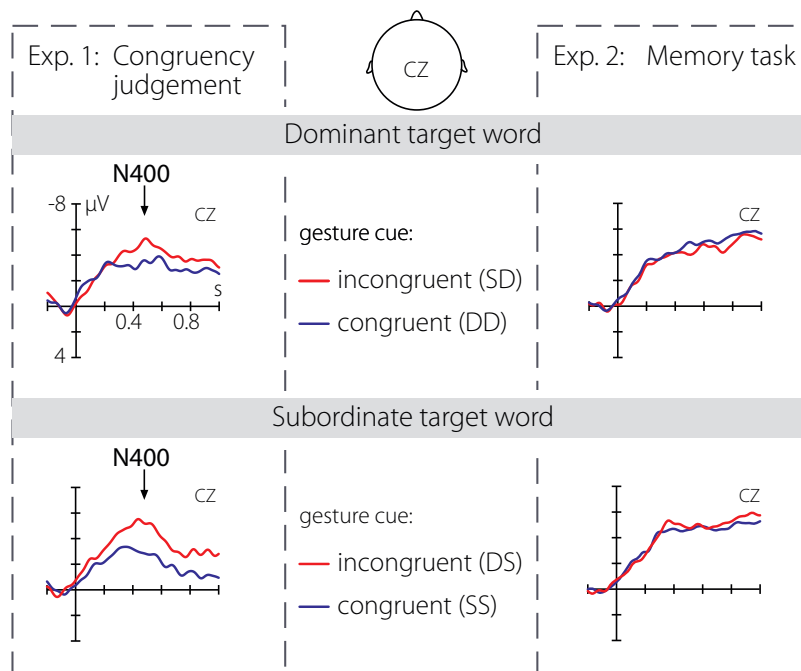


Figure 2.1.16 ERPs for gesture target word congruency obtained at the target words for Experiments 1 (left plots) and 2 (right plots).

2.1.17

Comprehending prehending: Neural correlates of processing verbs with motor stems

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The interaction between language and action systems has become an increasingly interesting topic of discussion in cognitive neuroscience. Several recent studies have shown that the processing of action verbs elicits activation in the cerebral motor system in a somatotopic manner. In this fMRI study, we investigated (1) whether or not a distinction between the processing of motor-related vs. abstract verbs could be seen in the motor areas of the brain, and (2) whether morphologically complex verbs, which have an abstract meaning but a motor-related stem elicit activations that are more similar to simple motor verbs or to abstract verbs.

Participants were presented visually with verbs and pseudoverbs and asked to make a lexical decision task. Verbs were presented in the infinitive form, and belonged to one of four conditions: Motor (i.e. greifen, to grasp); Abstract (i.e. denken, to think), Complex Motor Stem (i.e. begreifen, to comprehend), or Complex Abstract Stem (i.e. bedenken, to comprehend). The analysis was based on direct comparison between Motor vs. Abstract verbs and Complex Motor Stem vs. Complex Abstract Stem items.

The results show that activation elicited by the comprehension of verbs with motor meanings differs fundamentally from that elicited by the processing of verbs with abstract meanings. This difference is characterized by increased levels of activation for motor verbs in left sensorimotor cortex (precentral gyrus and postcentral gyrus) as well as secondary somatosensory cortex - areas related to movement preparation and perception. Secondly, regarding the neural correlates of the processing of morphologically complex verbs with abstract meanings but having stems with motor vs. abstract meanings, while residual effects of motor stem meaning might have been expected, we found no evidence for this in our data. Processing of morphologically complex verbs built on motor stems showed no differences in the involvement of the motor system when compared to processing of complex verbs with abstract stems. Complex verbs built on motor stems did show an increased activation compared to complex verbs with abstract stems in right posterior temporal cortex. This result might reflect involvement of right temporal cortex in the comprehension of metaphoric or figurative language.

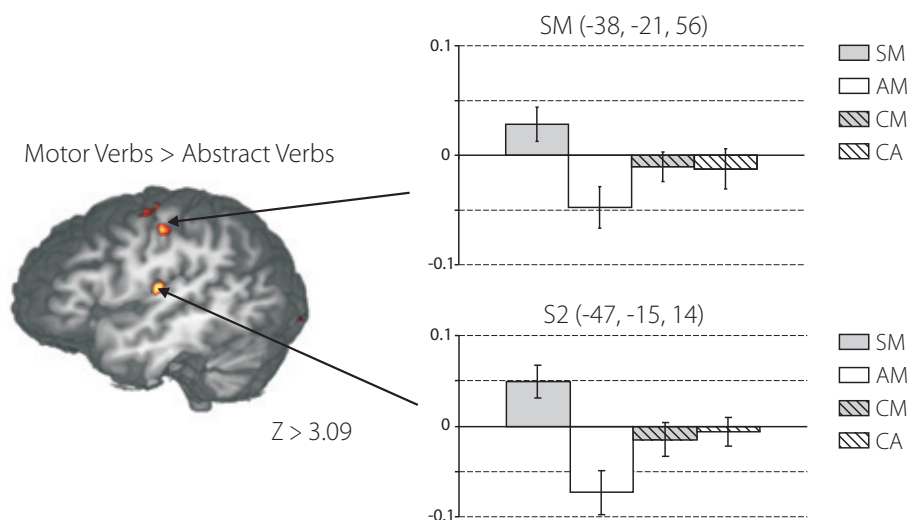


Figure 2.1.17 Area shows a greater activation for simple motor verbs than simple abstract verbs. In addition, the significant interaction between morphological complexity and verb stem meaning is shown in terms of percent signal change for the sensory motor (SM) cortex and for the secondary sensory (S2) cortex. Abbreviation to the right refer to: SM = simple motor verbs, AM = abstract motor verbs, CM = complex motor verbs, CA = complex abstract verbs.

Cognitive priming in sung and instrumental music: Activation of inferior frontal cortex

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The present study investigates the neural correlates for the processing of musical syntax-like structures using a paradigm based on an expectancy violation derived by the introduction of a musically unrelated (i.e. unexpected) event to an established musical context. Previous studies implicated the inferior frontal cortex in musical structure processing. However – due to the strong musical manipulations involved – activations may have in fact indicated sensory deviance detection or repetition priming. The present study investigated the neural correlates of musical structure processing using subtle musical violations in a musical priming paradigm (see Fig. 2.1.18.1).

Instrumental and sung sequences ended on related and less-related musical targets. The material controlled sensory priming components, and differences in target processing required listeners to employ their knowledge about musical structures. Participants were scanned with functional Magnetic Resonance Imaging (fMRI) while performing speeded phoneme and timbre identification judgments on the targets. Behavioural results acquired in the scanner replicated the facilitation effect of related over less-related targets. The blood oxygen level-dependent (BOLD) signal linked to target processing revealed activation of right inferior frontal areas (i.e. inferior frontal gyrus, frontal operculum, anterior insula) that was stronger for less-related than for related targets, and this was independent of the material carrying the musical structures (see Fig. 2.1.18.2).

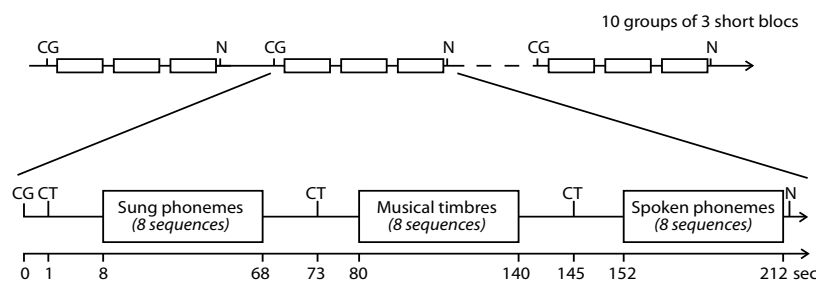


Figure 2.1.18.1 Schematic presentation of the time course of the experimental session: 10 groups of 3 short blocks (containing 8 sequences of either timbre sequences, sung or spoken phoneme sequences) were separated by rest periods (bordered by N and CG). CG (Cue Group) is the cue indicating the group's position (i.e. first, second ...). CT (Cue Targets) indicates the presentation of the two target types: Timbre A and Timbre B for the timbre identification task, di and du (sung or spoken) for the phoneme identification task. N represents the noise bursts indicating the end of the third short block and the beginning of the rest period. The bottom part of the figure displays the construction of one group with approximate timing (for detailed timing information, see Methods).

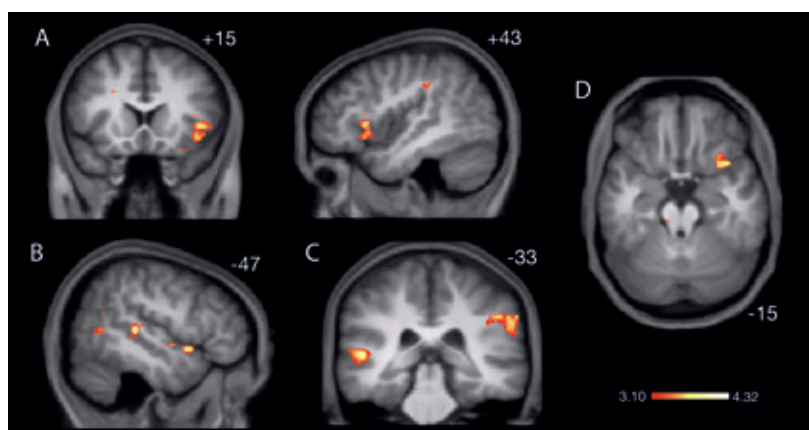


Figure 2.1.18.2 Group image showing significant differences in BOLD signal ($P < 0.001$; $z > 3.09$) of less-related over related targets. (A) inferior frontal activation (frontal operculum, anterior insula), (B) activation in left anterior STG, STS and posterior MTG, (C) activation in left STS and right SMG and (D) right orbital gyrus activation. Activations are superimposed on the averaged T1-weighted anatomical images of all participants.

2.1.19 From air oscillations to music and speech: Functional magnetic resonance imaging evidence for fine-tuned neural networks in audition

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Music and speech have high informational and emotional value for human beings. However, the degree of functional specialization of the cortical and subcortical areas in encoding music and speech sounds is still controversial. We investigated the functional specialization of the human auditory system in processing music and speech using functional magnetic resonance imaging. Subjects were presented with saxophone sounds and pseudo-words /ba:ba/ with comparable acoustical content. The experimental paradigm is illustrated in Fig. 2.1.19.1.

Our data show that areas encoding music and speech sounds differ in the temporal and frontal lobes (see Fig. 2.1.19.2 A & B). Moreover, slight variations in sound pitch and duration activated thalamic structures differentially (see Fig. 2.1.19.2 C & D).

Our data reveal the existence of a functional specialization of the human brain in accurately representing sound information at both cortical and subcortical areas. They

indicate that not only the sound category (speech/music) but also the sound parameter (pitch/duration) can be selectively encoded.

Experimental paradigm

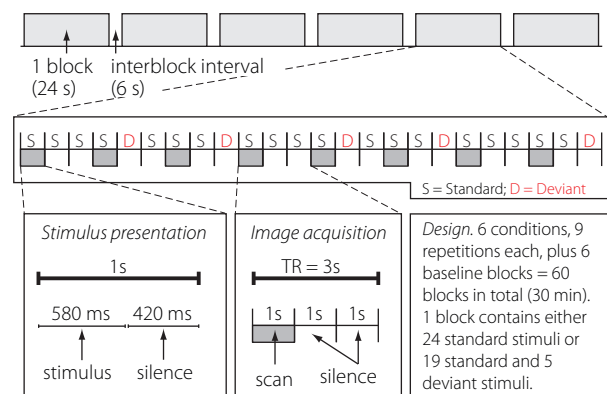


Figure 2.1.19.1 Schematic illustration of the experimental paradigm

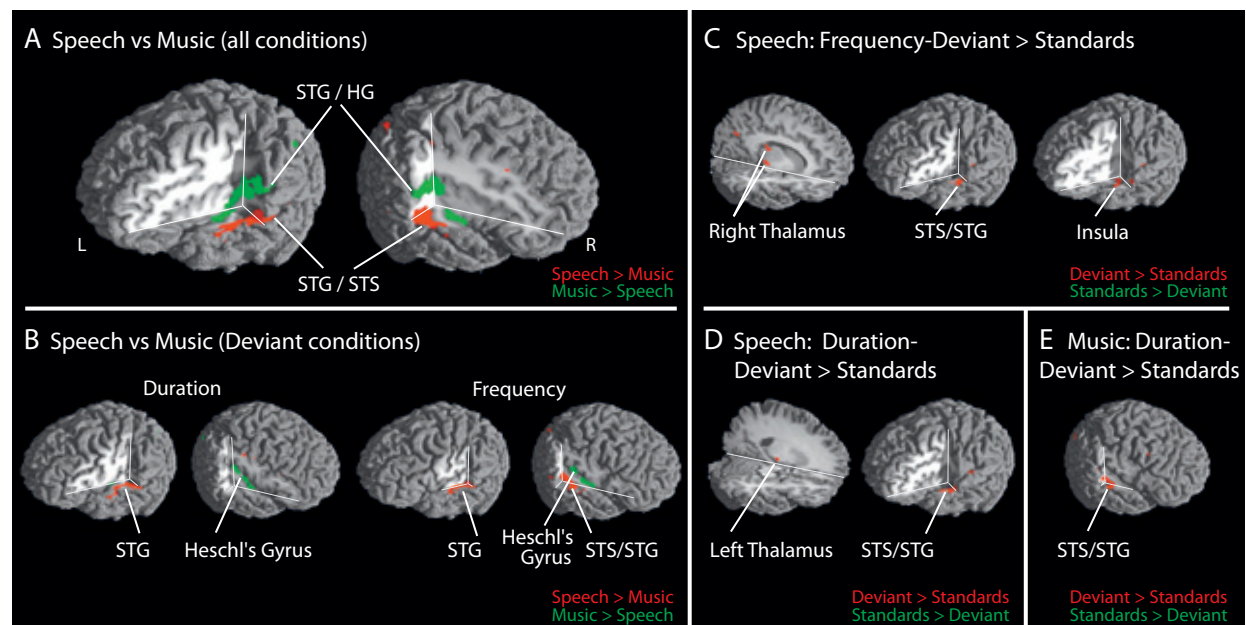


Figure 2.1.19.2 Significant foci of activity in speech versus music contrast (all conditions included) (A), speech versus music deviant contrasts (B), deviant versus standard contrast for speech (C, D), and deviant versus standard for music (E). a, b, Red illustrates stronger activation for speech than music sounds, and green illustrates stronger activity for music than speech sounds. C - E, Red illustrates stronger activation for deviant than standard sounds, and green illustrates stronger activity for standard than deviant sounds.

Brain networks of music perception – Influence of cultural context and phrase structure

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The current study used functional magnetic resonance imaging (fMRI) to investigate the neural basis of musical phrase boundary processing during the perception of music from native and non-native cultures. German musicians performed a cultural categorization task while listening to phrased Western (native) and Chinese (non-native) musical excerpts as well as modified versions of these, where the impression of phrasing was reduced by removing the phrase boundary marking pause (henceforth called “unphrased”). Bilateral planum temporale was found to be associated with an increased difficulty of identifying phrase boundaries in unphrased Western melodies. A network involving frontal and parietal regions showed increased activation for the phrased condition with the orbital part of left inferior frontal gyrus

presumably reflecting working memory aspects of the temporal integration between phrases, and the middle frontal gyrus and intraparietal sulcus probably reflecting attention processes. Areas more active in the culturally familiar, native (Western) condition included, in addition to the left planum temporale and right ventro-medial pre-frontal cortex, mainly the bilateral motor regions. These latter results are interpreted in light of sensorimotor integration. Regions with increased signal for the unfamiliar, non-native music style (Chinese) included a right lateralized network of angular gyrus and the middle frontal gyrus, possibly reflecting higher demands on attention systems, and the right posterior insula suggesting higher loads on basic auditory processing.

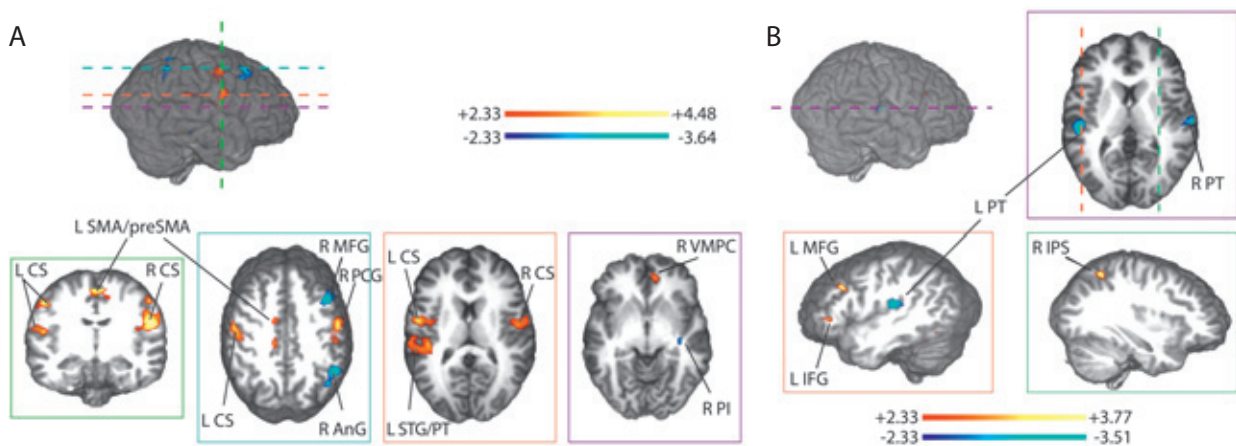


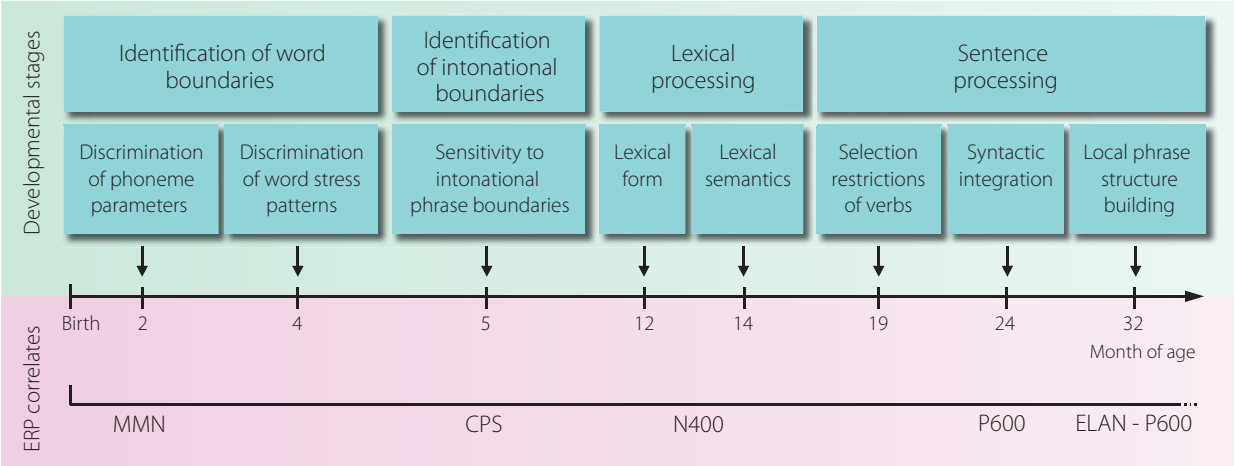
Figure 2.1.20 (A) Differences between Chinese and Western music and (B) phrased and unphrased music. Colour scales denote z values : red - Chinese/phrased, blue- Western/unphrased. R - right, L - left, MFG - middle frontal gyrus, AnG - angular gyrus/inferior parietal lobule, PI - posterior insula, PFG - medial part of precentral gyrus/foot area, CS - central sulcus, posterior bank of precentral gyrus in mouth and hand regions, PT - planum temporale, HeG - Heschl's gyrus, STG - superior temporal gyrus, VMPC - ventral medial prefrontal cortex (superior rostral gyrus), IPS - intraparietal sulcus, IFG - inferior frontal gyrus, orbital part (BA 47).

2.2

Neurocognition of Language Development

Based on the research of the past two years, we have updated our schema describing the major developmental stages and the neurophysiological markers of phonological, lexical and syntactic processes (see Fig. below). For the phonological domain, we demonstrated in a cross-linguistic ERP study on word stress that infants provide language-specific responses to stress patterns by the age of 4 and 5 months (2.2.1). In a longitudinal study, we found that the infants' ability to discriminate native from non-native stress patterns at this early age predicts their language performance at the age of 2;6 years (2.2.2). Prosodic information at the sentence level is relevant for language acquisition as each intonational phrase boundary is a syntactic phrase boundary in language. Here we report that 5-month-old infants already demonstrate a particular ERP component reflecting the processing of intonational phrase boundaries (2.2.3). The neural network underlying these processes of prosodic information has a right hemispheric dominance in adults. By means of optical imaging using near infrared spectroscopy, NIRS (2.2.4), a similar right hemispheric dominance was shown in 4-year-old children (2.2.4).

The development of word comprehension between 12 and 19 months is correlated with early word production (2.2.5), and can be used successfully to predict language skills later in life (2.2.6). We also investigated lexical-semantic processing in children diagnosed with specific language impairment at the age of ten years (2.2.7). The acquisition of syntactic regularities seems to become established between 24 and 32 months, as children reveal an adult-like ELAN-P600 pattern at the age of 32 months but only a positivity at the age of 24 months (2.2.8). In order to identify the neural network underlying semantic and syntactic processing in 5- and 6-year-old children, an fMRI experiment was conducted. The data suggest that the neural network has not yet fully matured in these children, as the activations observed for semantic and syntactic processing were less specialized than in adults (2.2.9).



2.2.1 Language-specific brain responses in German and French infants

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In German, primary stress in disyllabic words is most often located on the first syllable, e.g. pápa/daddy, whereas in French it is located on the second syllable, e.g. papá/daddy. Using a cross-linguistic study, we investigated whether early experience with German or French stress patterns differentially affects the brain responses of 4- and 5-month-old infants. The ERPs obtained in an oddball study with the pseudowords bába and babá showed a different pattern for the two language groups (Fig. 2.2.1). German infants demonstrated an infant-specific positive mismatch response (MMR) when the deviant stimulus

had the stress on the second syllable, but no MMR when the stress was on the first syllable. For French infants, we observed the reverse pattern with a positive MMR when the stress was on the first syllable, but no MMR when the stress was on the second syllable. That is, both groups reacted strongly to the stress pattern that was not only deviant in the experimental setting but moreover in the respective group's native language. Thus, by four months of age, language-specific memory representations for prosodic word forms are established in the infant brain.

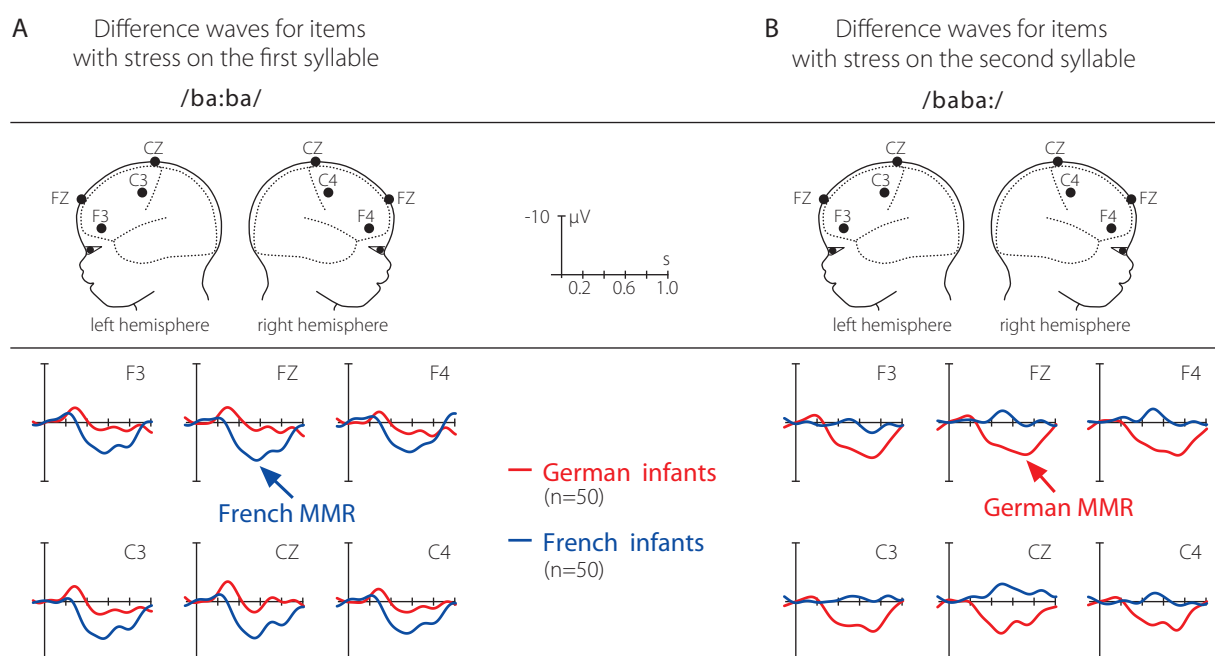


Figure 2.2.1 Difference waves (deviant minus standard) for the two language groups (German/French) (A) for items with stress on the first syllable and (B) for items with stress on the second syllable. Data were filtered by 0.3-15 Hz.

2.2.2 Word stress processing in infancy and language performance later on

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Familiarity with native language prosody is assumed to facilitate infant's entrance into language by aiding word form acquisition and inducing sensitivity to syntactic structure. In a longitudinal study we investigated whether the early processing of native and non-native language

word stress patterns is related to a child's language skills later on. ERP data of 4- and 5-month-old infants were retrospectively grouped according to the children's performance in a language test at 2;6 years. Children with better language skills (high performers) displayed a nega-

tive mismatch response (MMR) when processing the native language stress pattern *bába* as infrequent deviant stimulus. Children with poorer language skills (low performers) did not show this mature response. Both groups displayed an infant-specific positive MMR when the non-native language stress pattern /*baba:/* was the infrequent deviant stimulus. This less mature response was

enhanced and prolonged in high performers as compared to low performers (Fig. 2.2.2). The results suggest that memory structures for word stress patterns were differently established in infants with different language skills at 2;6 years. This supports the notion that the early acquisition of word prosody plays an important role in children's further language development.

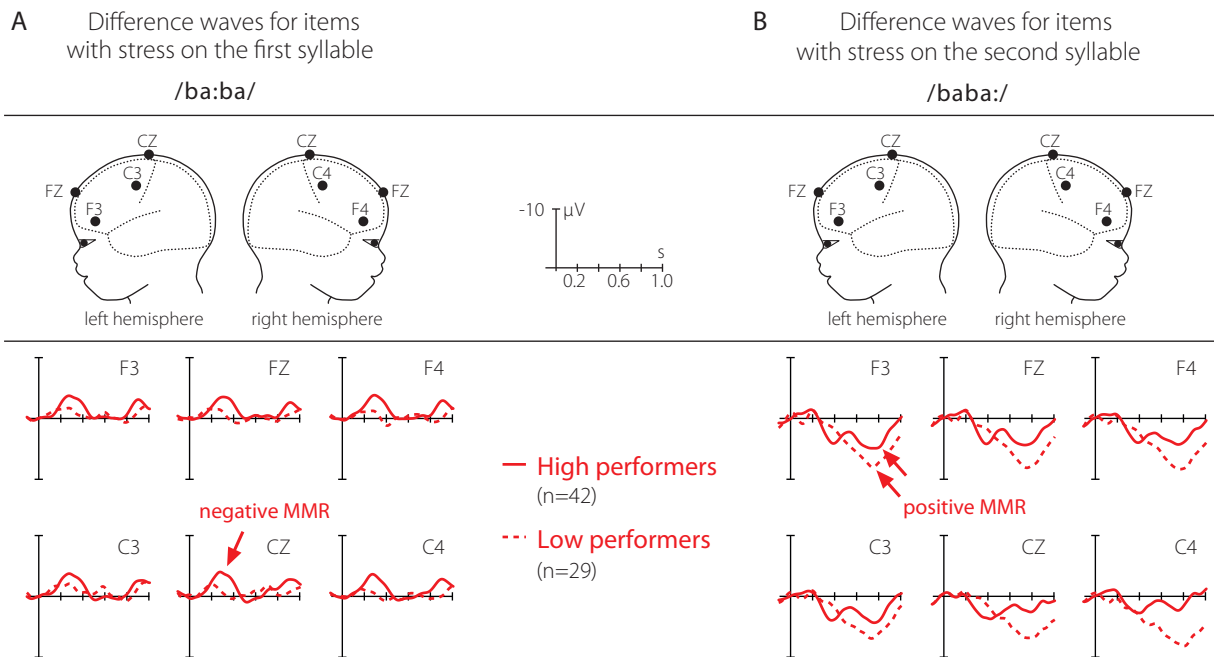


Figure 2.2.2 Difference waves (deviant minus standard) of the post-hoc defined groups (High performers/Low performers) (A) for items with stress on the first syllable and (B) for items with stress on the second syllable. When evaluating the positive MMR data were filtered by 0.3-15 Hz. To detect the negative MMR a 1-15 Hz filter was applied.

5-month-olds perceive phrase structure in language and music: Two ERP studies

2.2.3

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In language acquisition, the perception of prosodic cues (e.g. intonational sentence contour) strongly aids the segmentation of the incoming speech stream into lexical and syntactic units. In the present study we investigated the ability of 5-month-old infants to process phrase structure information in language and music. In adult ERP studies involving language processing tasks, the so called Closure Positive Shift (CPS) is observed in response to the processing of intonational phrase (IPh) boundaries (Steinhauer, Alter, & Friederici, 1999, *Nat Neurosci*, 2, 191-196). In music perception, studies report differential ERP effects in relation to musical phrase (MPH) boundaries depending on a subject's musical expertise.

We presented simple infant-directed sentences and melodies in phrased and unphrased versions to infants and adults. The sentence material comprised sentences with a sentence-internal IPh boundary and sentences without an IPh boundary. Similarly, melodies that were otherwise identical either contained two MPHs divided by a pause, or consisted of one MPH without a pause.

For sentence processing (A in Fig. 2.2.3), the ERP results show a positive shift in response to the IPh boundaries in adults as well as in 5-month-old infants, although at a delayed latency in infants. For music perception (B in Fig. 2.2.3), the adult data (nonmusicians and low-level nonprofessionals) show a negativity in response to

MPH boundaries as has already been reported for non-musicians (Neuhaus, Knösche, Friederici, 2006, *J Cogn Neurosci*, 18, 472-493). In contrast, the infant data reveal a positive shift that resembles the music CPS observed for professional musicians (Neuhaus et al., 2006, *J Cogn Neurosci*, 18, 472-493).

Our results extend the recent finding by Pannekamp et al. (Pannekamp, Weber, & Friederici, 2006, *Neuroreport*, 17, 675-678) that 8-month-old infants are able to detect

sentence-level prosodic cues. Furthermore, the observation of ERP responses to musical phrasing support behavioural studies showing that infants are able to process phrase structure in music relatively early (Jusczyk, & Krumhansl, 1993, *J Exp Psychol Hum Percept Perform*, 19, 627-640). Our results suggest that at an age when infants heavily rely on prosodic information for language learning, they are able to extract structuring information from music, much as adults with formal musical training do.

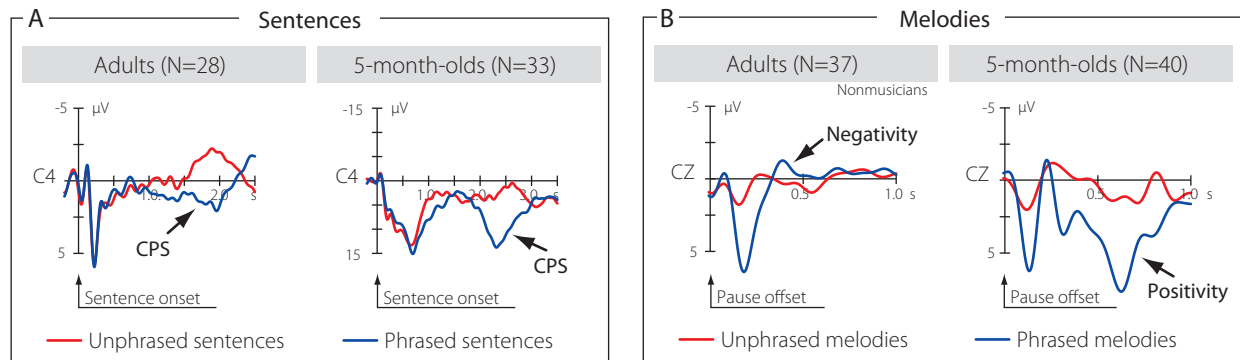


Figure 2.2.3 Grand average ERPs (A) for sentence and (B) music perception in adults and 5-month-olds.

2.2.4 The processing of prosody: Evidence of interhemispheric specialization at the age of four

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Beyond its multiple functions in language comprehension and emotional shaping, prosodic cues play a pivotal role in children's amazingly rapid acquisition of language. However, cortical correlates of prosodic processing are largely controversial, even in adults, and functional imaging data in children are sparse. Here, we used an approach

which allowed us to experimentally determine the brain activations correlating to the perception and processing of sentence prosody during childhood. In 4-year-olds, we measured focal brain activation using near-infrared spectroscopy to normally spoken sentences containing phonological, syntactic, semantic and prosodic informa-

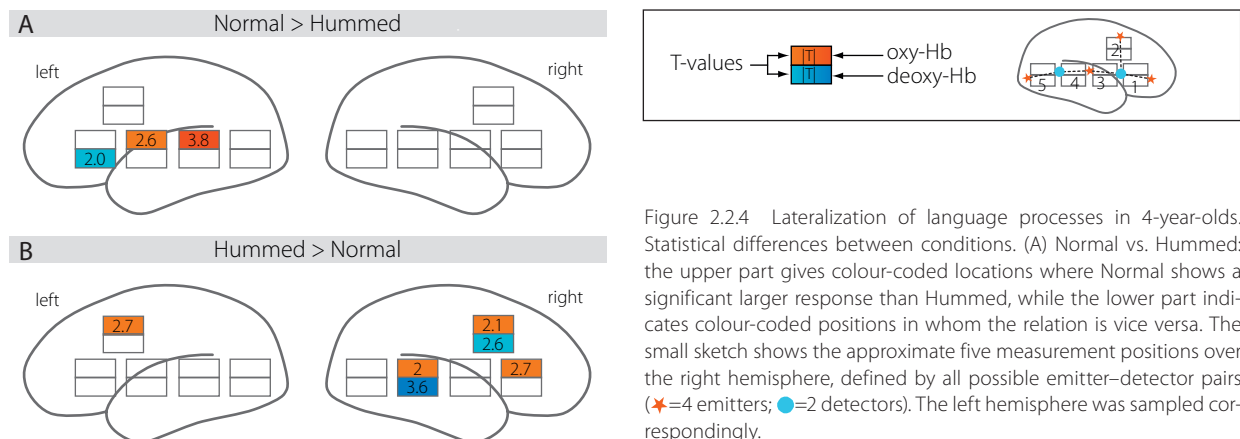


Figure 2.2.4 Lateralization of language processes in 4-year-olds. Statistical differences between conditions. (A) Normal vs. Hummed: the upper part gives colour-coded locations where Normal shows a significant larger response than Hummed, while the lower part indicates colour-coded positions in whom the relation is vice versa. The small sketch shows the approximate five measurement positions over the right hemisphere, defined by all possible emitter-detector pairs (★=4 emitters; ●=2 detectors). The left hemisphere was sampled correspondingly.

tion and to hummed sentences only containing prosodic information. Processing prosody in isolation elicits a larger right fronto-temporal activation whereas a larger left hemispheric activation is elicited by the perception of normal language with full linguistic content (Fig. 2.2.4). Hypothesized by the dual-pathway-model (Friederici, & Alter, 2004, *Brain Lang*, 89, 267-276) the present data provide experimental evidence that in children specific language processes rely on interhemispheric specialization

with a left hemispheric dominance for processing segmental information (i.e. phonological forms signalling syntactic and semantic information) and a right hemispheric dominance for processing suprasegmental (i.e. prosodic) information. Generally in accordance with the imaging data reported in adults, our findings support the notion that interhemispheric specialization is a continuous process during the development of language.

Maturing brain mechanisms and developing behavioural language skills

2.2.5

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The ERPs acquired in a picture-word study in children at 12 months (Friedrich, & Friederici, 2005, *J Cogn Neurosci*, 17, 1785-1802) were analyzed according to the children's word production at that age, as rated by parents in a standardized questionnaire. Latency differences in early ERP components indicated an auditory sensory processing advantage for infants with particularly early word production. In these infants, moreover, semantic inte-

gration mechanisms indexed by the N400 were already functional at 12 months. In slower developing children, semantic integration mechanisms were not yet mature (Fig. 2.2.5). This result indicates the relevance of semantic integration mechanisms for early word acquisition and their possible relation to the qualitative shift from slow to fast word learning, which at the earliest has been observed at 13 months.

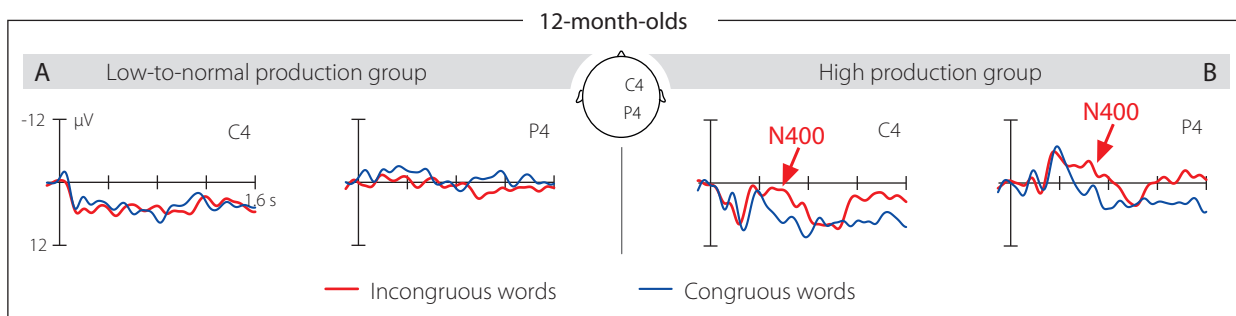


Figure 2.2.5 The ERPs for congruous and incongruous words in 12-month-old infants (A) of the group with low-to-normal word production and (B) of the group with high word production. Solid lines represent the ERP for congruous words and dotted lines the ERP for incongruous words.

Early word processing and later language performance

2.2.6

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ERP data of 19-month-old children obtained in a picture-word study (Friedrich, & Friederici, 2004, *J Cogn Neurosci*, 16, 1465-1477; Friedrich, & Friederici, 2005, *J Cogn Neurosci*, 17, 1785-1802) were retrospectively grouped according to the children's verbal language skills at 2;6 years. In children with poorer language skills at 2;6 years, the word form priming effect was stronger and more

prolonged in its duration than in children with better language skills at that age. This suggests that children who develop language more slowly find it more difficult to adequately process word forms that are unexpected in picture contexts. In addition, the ERP of children who acquired language more quickly displayed responses that indicate their sensitivity to the phonotactic regularities of

German. Such neural markers of phonotactic knowledge were not present in children with slower language development. Moreover, children with better language skills at 2;6 years displayed the ERP correlate of semantic integration mechanisms (N400) at 19 months, whereas children

with poor language skills at 2;6 did not. The results imply that variability in language development at 2;6 years has precursors in ERP correlates of word processing at 19 months.

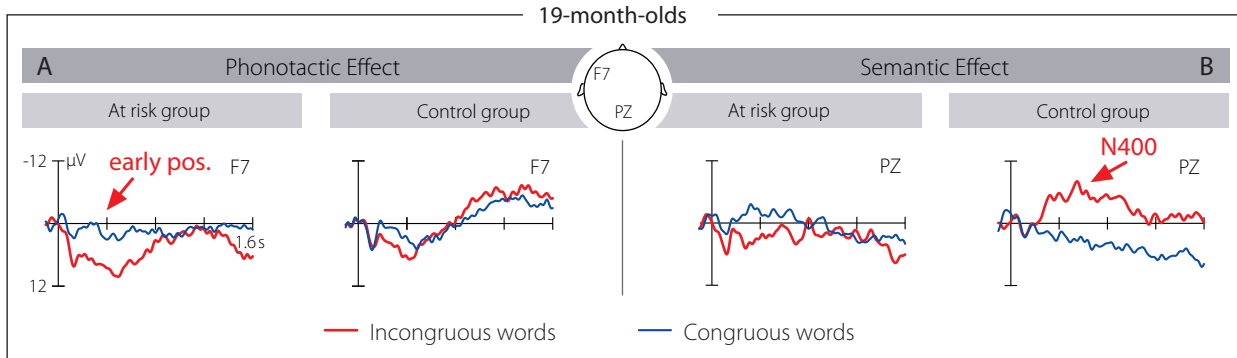


Figure 2.2.6 (A) The phonotactic familiarity effect and (B) the N400 semantic integration effect (right column) in the post-hoc defined subgroups of 19-month-old children with different later language development. At risk group: children with poor later language skills ($n = 18$), Control group: children with age-adequate later language skills ($n = 22$).

2.2.7 Lexical-semantic processing in children with specific language impairment

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Children with specific language impairment (SLI) have been shown to have deficits in the processing of phonological, syntactic and/ or semantic information. In the present study, event-related brain potentials were used to compare lexical-semantic processing abilities in children with SLI with those of control children.

The study included 16 children with SLI and 16 control children who were pair-wise matched on age, sex and nonverbal intelligence (12 boys, mean age = 9;7, $SD = 1;9$). Children with SLI were required to have language comprehension and/ or production abilities of at least 1.5 standard deviations below the mean as well as a dis-

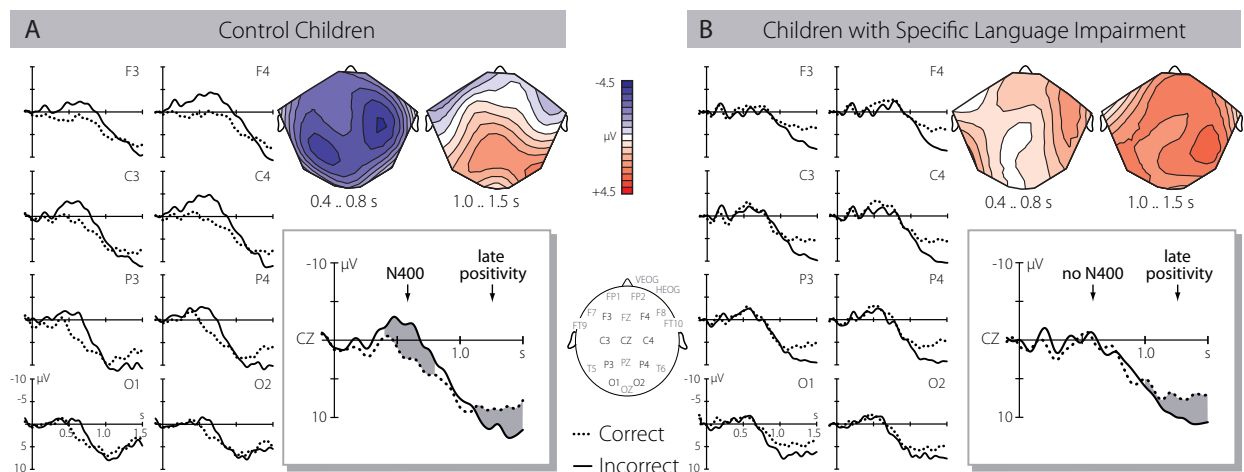


Figure 2.2.7 Grand average ERPs of (A) the control children and (B) the language impaired children. The semantically incorrect condition (solid line) is plotted against the correct condition (dotted line). The axis of the ordinates indicates the onset of the critical word (past participle). Negative voltage is plotted upwards. The pictures of the enlarged electrode Cz contain gray hatched sections referring to effects which revealed statistical significance.

crepancy of at least one standard deviation between nonverbal intelligence and language ability. All children were German-speaking monolinguals, without any hearing impairment or reported neurological disorder and had a nonverbal intelligence within the normal range.

Four sentence types were presented. All were in the passive voice and comprised a noun, an auxiliary and a past participle. Of interest here is the contrast between the semantically correct and incorrect conditions i.e. *Das Brot wurde gegessen/The bread was eaten* versus *Der Vulkan wurde gegessen/The volcano was eaten*. As is clear in these examples, the sentence-final verb in the semantic violation condition is incompatible with the subject-noun phrase.

Two distinct effects for the semantically incorrect sentences were observed in the ERPs of the control children, namely a broadly distributed N400 (0.4-0.8 s) followed by a late positivity (1.0-1.5 s, see Fig. 2.2.7). By contrast, in the

ERPs for the children with SLI, no N400 effect (difference between responses to semantically incorrect and correct condition) was observed. This lack of an N400 effect reflects similar N400 components in response to both conditions. The absence of the N400 effect suggests weaker lexical-semantic representations of the verb meaning in these children suggesting a similar degree of effort is required for the processing of the lexical-semantic content of the sentences regardless of whether the verb is readily integrated into the preceding sentential context or not. Interestingly, children with SLI showed a late and broadly distributed positivity whereas the same positivity in the control children was restricted to the central electrodes. This late positivity response is thought to reflect processes of sentential judgment and the differences in the distribution of the late positivity between the two groups of children may provide further evidence for more effortful sentential processing by the children with SLI.

Syntactic ERP components in 24-month-old children

2.2.8

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The processing of phrase structure violations in adults is associated with two ERP components: an early left anterior negativity (ELAN) and a late positivity (P600) (Hahne,

Eckstein, & Friederici, 2004, *J Cogn Neurosci*, 16, 1302-1318; Oberecker, Friedrich, & Friederici, 2005, *J Cogn Neurosci*, 17, 1667-1678). The ELAN reflects highly automatic sen-

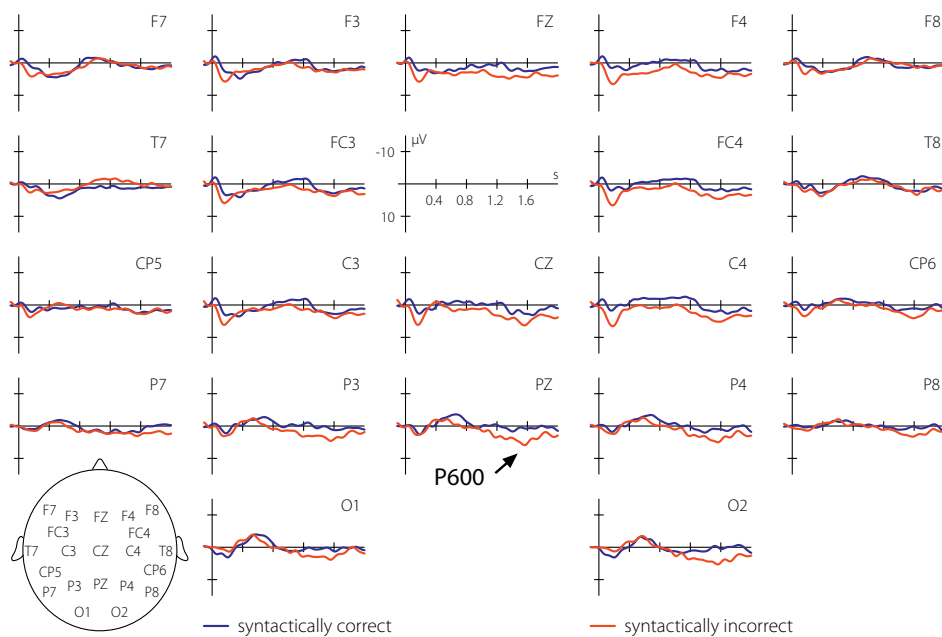


Figure 2.2.8 Grand-average ERPs of 39 24-month-olds for the critical word in the syntactic violation versus correct condition. The violation condition (red line) is plotted against the correct condition (blue line). The vertical line indicates the onset of the critical word; negative voltage is plotted upwards.

tence parsing, and the P600 reflects later and more controlled processes of syntactic integration processes. In a former study, we found that an adult-like ERP-pattern was also present in 32.5-month-old children (Oberecker, Friedrich, & Friederici, 2005, *J Cogn Neurosci*, 17, 1667-1678). In the present study we investigated the processing of phrase-structure information in 24-month-old children. The children passively listened to short active sentences that were either syntactically correct (e.g. *Der Löwe brüllt/The lion roars*) or contained a phrase-structure violation (e.g. *Der Löwe im brüllt/The lion in the roars*).

Furthermore, sentences containing a full prepositional phrase were included as filler sentences (e.g. *Der Löwe im Zoo brüllt/The lion in the zoo roars*). Each condition (correct, incorrect, and filler) contained 60 sentences. All sentences were spoken by a trained female speaker. The ERP results of the 24-month-old children displayed a late positivity for the processing of the syntactic violation condition. The findings of the present study indicate that the ability to detect syntactic errors in the form of phrase structure violations is present very early in childhood.

2.2.9 The functional neuroanatomy of language comprehension and its development

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The functional neuroanatomy of language in the adult brain separates semantic and syntactic processes in the superior temporal gyrus (STG) and inferior frontal gyrus (IFG). In order to investigate whether a similar specialization is present in the developing brain, semantic and syntactic aspects of sentence processing were investigated in 5 to 6-year-old children and in adults using functional magnetic resonance imaging (fMRI). Our findings indicate that the semantic and syntactic processes have not fully matured in the language network of children aged 6 years. At this developmental stage, the neural substrates for language comprehension processes are less special-

ized than in the mature brain. Moreover, both semantic and syntactic processes demand a higher involvement of the IFG at this age than in adulthood (see Fig. 2.2.9). These data are not only in line with findings from on-line behavioural studies demonstrating that syntactic processes only start to gain their independence from semantic processes after the age of 5 years (Friederici, 1983, *Linguistics*, 21, 717-739), but also with ERP results indicating that ERP patterns for syntactic processes in syntactically complex sentences are not yet identical to adults in 6-year-olds (Hahne, Eckstein, & Friederici, 2004, *J Cogn Neurosci*, 16, 1302-1318).

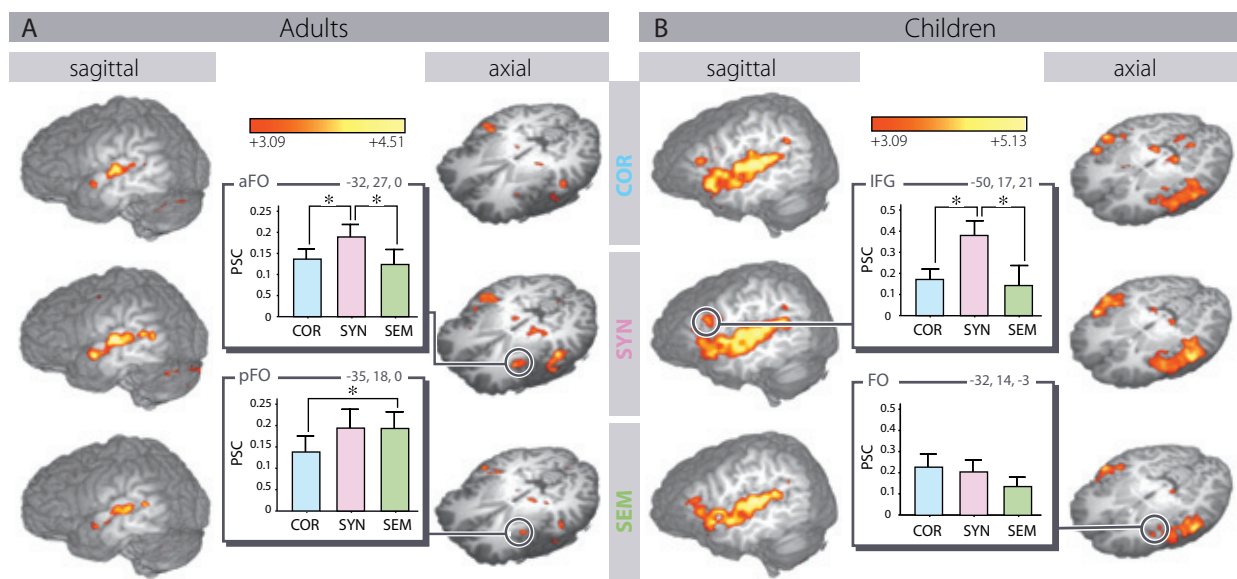


Figure 2.2.9 Activation maps of (A) adults and (B) children for the processing of correct (COR), syntactically incorrect (SYN), and semantically incongruous (SEM) sentences against resting baseline. Bar graphs illustrate BOLD percent signal change (PSC) in selected brain areas (aFO, pFO = anterior, posterior frontal operculum, IFG = inferior frontal gyrus).

Furthermore, the timing of recruitment of language-related brain activation was examined focusing on the temporal dynamics of the BOLD response in IFG and STG. Children's blood oxygenation level dependent (BOLD) responses showed overall longer latencies when compared to adults. Moreover, a temporal primacy of right over left hemispheric activation was found for children. While in adults, inferior frontal activation showed peak latencies close to superior temporal activation, children's IFC activation peaked much later than STC activation.

These latency differences between children and adults in the functional BOLD response during language comprehension are in line with our current understanding of the maturational changes in language-related brain areas and the structural connections between them. The data also support the view that developmental changes evolve from higher processing costs in the developing brain to faster and more automatic language processing in the mature brain.

Congresses, Workshops, and Symposia

- 2006** ■ Kotz, S. A., & Pell, M. D. (May). *Understanding emotions in speech: Neural and cross-cultural evidence*. Symposium. 3rd International Conference on Speech Prosody, Dresden University of Technology, Germany.
- Gunter, T. C., & Holle, H. (July). *Neurocognition of gesture processing*. Workshop. Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.
- Kotz, S. A., & Weniger, D. (July). *Prosody and faces as multi-faceted means of emotional expression*. Symposium. INS/SVNP/GNP Mid-Year Meeting, University of Zurich, Switzerland.
- 2007** ■ Gunter, T. C., & Lausberg, H. (June). *The neurocognition of gesture*. Symposium. 3rd Illinois State Genealogical Society's (ISGS) Conference, Northwestern University, Evanston, USA.
- Anwander, A. (August). *Fiber tracking I + II*. Symposium. 2nd International Summer School in Biomedical Engineering, Ilmenau University of Technology, Germany.
- Anwander, A. (August). *Modelling and analysis*. Symposium. 2nd International Summer School in Biomedical Engineering, Ilmenau University of Technology, Germany.
- Anwander, A. (August). *Visualization and software demonstration*. Symposium. 2nd International Summer School in Biomedical Engineering, Ilmenau University of Technology, Germany.
- Friederici, A. D. (August). *13th European Conference on Developmental Psychology (ECDP)*. Conference (Member of the Scientific Committee). Friedrich Schiller University Jena, Germany.

Appointment

- 2006** ■ Kotz, Sonja A. *W2 Minerva Professorship funded by the Max Planck Society*. Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.

Degrees

Habilitations

- 2006** ■ Kotz, S. A. *The role of the basal ganglia in auditory language processing: Evidence from ERP lesion and functional neuroimaging*. Faculty of Biology, Pharmacy and Psychology, University of Leipzig, Germany.

PhD Theses

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- Eckstein, K. *Interaktion von Syntax und Prosodie beim Sprachverstehen: Untersuchungen anhand ereigniskorrelierter Hirnpotentiale [Event-related potential studies on the interaction of syntax and prosody in speech comprehension]*. University of Leipzig, Germany.
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- Hofmann, J. *Phonological, morphological, and semantic aspects of grammatical gender processing in German*. Saarland University, Saarbrücken, Germany. ■
- Nan, Y. *Music phrase structure perception: The neural basis, the effects of acculturation and musicality*. University of Leipzig, Germany. ■
- Paulmann, S. *Electrophysiological evidence on the processing of emotional prosody: Insights from healthy and patient populations*. University of Potsdam, Germany. ■
- Sivonen, P. *Event-related brain activation in speech perception: From sensory to cognitive processes*. University of Leipzig, Germany. ■
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- Cleveland, A. *Joint attention during the first year*. University of Leipzig, Germany. ■ **2007**
- Dietrich, S. *Vom Brüllen zum Wort – MRT-Studien zur kognitiven Verarbeitung emotionaler Vokalisationen [From bursts to words – fMRI investigations of cognitive processing of emotional vocalizations]*. Eberhard Karls University Tübingen, Germany. ■
- Holle, H. *The comprehension of co-speech iconic gestures: Behavioral, electrophysiological and neuroimaging studies*. University of Leipzig, Germany. ■
- Lueck, M. *Die Verarbeitung morphologisch komplexer Wörter bei Kindern im Schulalter: Neurophysiologische Korrelate der Entwicklung [The processing of morphologically complex words in school-aged children: Neurophysiological correlates of development]*. University of Potsdam, Germany. ■
- Oberecker, R. *Grammatikverarbeitung im Kindesalter: EKP-Studien zum auditorischen Satzverstehen [The processing of grammar in preschool children: ERP studies on auditory sentence comprehension]*. University of Potsdam, Germany. ■
- Sabisch, B. *Mechanism of auditory sentence comprehension in children with specific language impairment and children with developmental dyslexia: A neurophysiological investigation*. University of Leipzig, Germany. ■
- Schmidt-Kassow, M. *What's beat got to do with it? The influence of meter on syntactic processing: ERP evidence from healthy and patient populations*. University of Potsdam, Germany. ■

Awards

- Kanske, P. *Werner Straub Award*. Department of Psychology, Dresden University of Technology, Germany. ■ **2006**
- Bangert, M. *Scientific Award 2007*. German Association for Music Physiology and Musicians' Medicine (DGfMM). ■ **2007**
- Kaden, E., Knösche, T. R., & Anwender, A. *2nd Place Poster Award*. Joint Annual Meeting ISMRM-ESMRMB, Berlin, Germany. ■
- Kotz, S. A. *Five year award "Excellence Support for Women in Neuroscience"*. Max Planck Society. ■
- Paulmann, S. *Post-Doc Scholarship*. German Academic Exchange Service (DAAD). ■

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Figure 2.1.6

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Figure 2.1.7

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Figure 2.1.8

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Figure 2.2.2

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Figure 2.2.4

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Figure 2.2.7

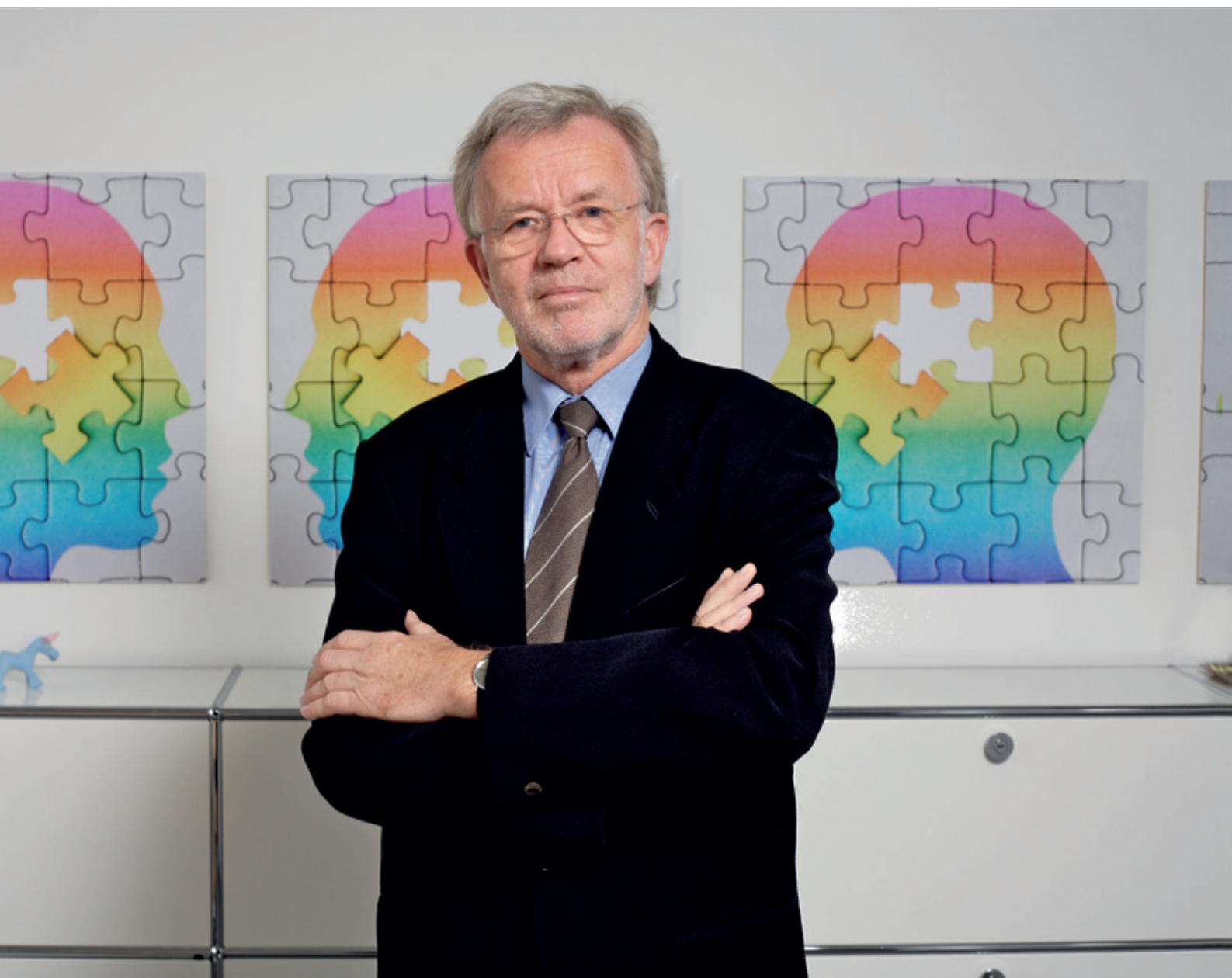
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Sabisch, B., Hahne, A., Glass, E., Suchodoletz, V. W., & Friederici, A. D. (2006). Lexical-Semantic Processes in Children with Specific Language Impairment. *NeuroReport*, 17(14), 1511-1514.

Figure 2.2.8

Oberecker, R., & Friederici, A. D. (2006). Syntactic event-related potential components in 24-month-olds' sentence comprehension. *NeuroReport*, 17(10), 1017-1021.

Figure 2.2.9

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Prof. Dr. Wolfgang Prinz
Director

3

Cognition and Action

Department of Psychology

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

Our research programme has two dimensions to it. On one hand we adopt a functional stance on cognition. Here we view cognitive functions in the service of action and study their role for action planning and execution. On the other hand we adopt this cognitive stance on action. Here we view action in the service of cognition, and study its impact on cognitive operations. Accordingly two major research perspectives are combined in most of our projects. One goes from perception to action and studies the cognitive underpinnings of action and task control. The other goes from action to perception and studies the action-related underpinnings of action understanding and intention reading.

Further theoretical intuition that has recently had increasing impact on our research is derived from the notion that the functional machinery for cognition-action-coupling may play an important role not only for action control and action perception within individuals, but also for interaction and communication across individuals. In a stronger version of this notion, one may even claim that that machinery has mainly evolved for the sake of supporting a variety of sub-symbolic, embodied forms of interaction and communication across individuals such as imitation, joint action, and task sharing.

The following overview of our projects starts with individual performance and concludes with inter-individual interaction. Projects at the individual level are concerned with (3.1) relationships between goals and movements; (3.2) representational underpinnings of tool use; and (3.3) cross talk between concurrent action and perception. At the inter-individual level, projects address (3.4) the interplay between cognition and action in early infancy; (3.5) mechanisms of observation/executions matching; and (3.6) functional foundations of task sharing and joint action.

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3.1 Goals and Movements

3.1.1 Intention-based and stimulus-based action: Functions and neurophysiology

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Humans either carry out actions to produce effects in the environment (intention-based) or to accommodate environmental demands (stimulus-based). Previous studies suggest that these two types of action are controlled by different neural structures, with the medial wall of the premotor cortex being involved in intention-based action and parietal and lateral premotor areas being involved in stimulus-based action (Waszak, Wascher, Keller, Koch, Aschersleben, Rosenbaum, et al., 2005, *Exp Brain Res*, 162, 346-356; Keller et al., 2006).

To investigate in more detail the neurophysiological underpinnings of intention-based and stimulus-based actions, Müller et al. (in press) asked subjects to make left or right key presses at the midpoint between adjacent items in evenly-timed sequences of visual stimuli. Under the stimulus-based condition, subjects reacted to the previous stimulus with the appropriate key press. Under the goal-based condition, each of the subjects' actions determined the position of the subsequent stimulus. Using functional magnetic resonance imaging (fMRI), Müller et al. showed that the preSMA (supplementary motor area) contributes to both internally and externally selected actions. By contrast, the RCZ (rostral cingulate zone) was more active in internally selected actions. This suggests that the RCZ is involved in the self-induced selection of actions (WHAT-component), whereas the preSMA is linked to the self-induced timing of an action (WHEN-component).

In a follow-up study, Müller, Brass, Prinz, & Waszak required subjects to perform one of two actions at one of two points in time. In this study, the authors distinguished between subjects freely choosing between the two possible actions and the two possible points in time, and actions and points in time being indicated by a stimulus. In other words, WHAT and/or WHEN-decisions were either intention-based or stimulus-based. The results confirm that the RCZ is involved in the internal decision as to which movement to perform (Fig. 3.1.1 A). Moreover, they suggest that an area in the left superior frontal gy-

rus (SFG) at the border between Brodmann area (BA) 6 and BA 8 is in charge of the decision when to perform an action (Fig. 3.1.1 B), whereas preSMA and SMA are implicated in the initiation of an action.

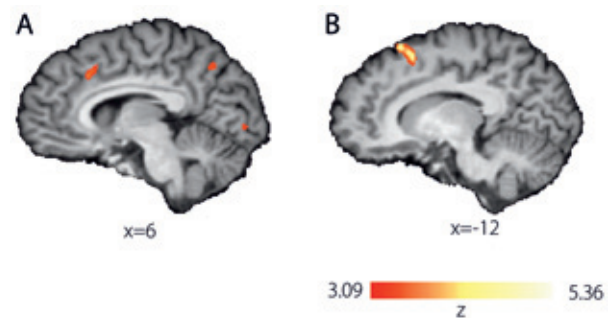


Figure 3.1.1 In this study by Müller et al., the RCZ was active when subjects had to select one of two possible actions on their own (panel A). By contrast, the SFG at the border between BA 6 and BA 8 was active when the subjects were required to decide at which of two possible points in time to perform an action (panel B).

However, despite the vast knowledge about the neurophysiological underpinnings of stimulus-based and intention-based actions, only little is known about the functional differences between the two types of action. Herwig et al. (in press) addressed this issue. They showed that action-effect learning only takes place if the actions are performed in an intention-based way. They suggest that this is because, in the stimulus-based mode, subjects pass on control to the stimuli: actions are selected with respect to their antecedents. In the intention-based mode, by contrast, actions are guided by the ideomotor principle, i.e. they are selected with respect to their consequences. It is only in this case that action and effect are associated.

Intention-based action modulates deviance processing in the brain

3.1.2

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Intention-based actions are performed to achieve goals in the environment. However, the effect of an action does not always come out as expected, indicating a major perturbation of the agent-environment interaction. Waszak & Herwig (in press) investigated how performing an intention-based action associated with an auditory effect influences deviance processing in the brain. In the first part of their experiment, an association was established between two actions (left/right key press) and two tones (high/low pitch). In the second part subjects performed key presses, freely choosing between left and right. The actions triggered randomly one of two tones (the same tones used in the first part). One tone, the standard, was presented very often; the other one, the deviant, only

rarely. Deviant tones elicited a smaller P3a when the action that triggered stimulus presentation was associated with the deviant tone than when it was associated with the standard tone (see Fig. 3.1.2). The P3a is considered to reflect an orienting response towards events that are unexpected in the given stimulus context. The findings suggest that the context with which incoming information is compared in order to detect deviant stimuli is determined by the effects humans anticipate their actions to have.

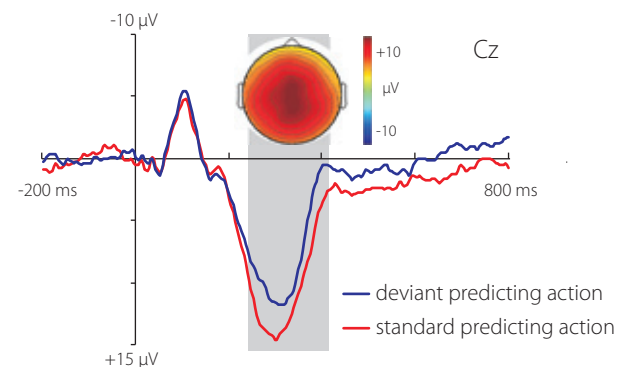


Figure 3.1.2 Grand mean ERP waveforms for deviant stimuli for actions associated with the standard and with the deviant tone (standard predicting and deviant predicting, respectively). The P3a is smaller when the action that triggered stimulus presentation was associated with (and, thus, predicted) the deviant tone. The ordinate indicates the stimulus-onset (which coincides with movement-onset). The inset shows the scalp topography for the P3a at 300 ms.

Physical targets as action goals

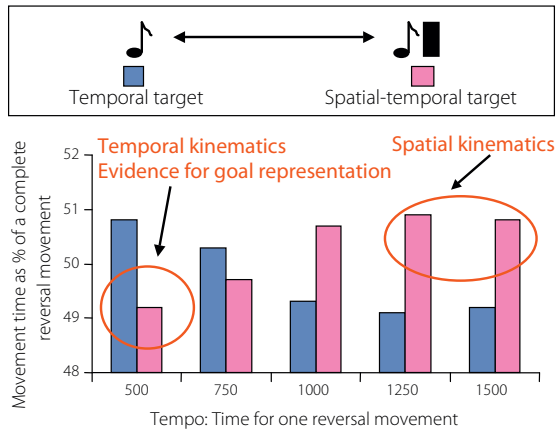
3.1.3

Rieger, M.¹

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An action goal can be either to produce an effect (change the environment) or to be at a physical target (change the situation of the individual in the environment). So far mainly action effects have been investigated with respect to their role as action goals. However, when interacting with the environment, one often has to make movements to certain locations at certain times (targets) – for example when catching a ball. Targets can be spatial (endpoint of a movement, e.g. to a light switch) or temporal (rhythm in dancing). Traditionally it is assumed that movement kinematics reflect physical properties (e.g. position and time) of movement targets. However, targets may also evoke intentional goals like “to be in a certain position at a given time”. Therefore, kinematics may be viewed not as reactions to stimuli, but rather as the means to at-

tain intended goals. In Rieger (2007) participants performed continuous reversal movements. The experiments showed that kinematics towards temporal and spatial targets differ from kinematics away from those targets. Further, kinematics are different for movements to temporal (relatively short movement times, high and late peak velocity) and spatial (relatively long movement times, early peak velocity) targets. In order to test whether the way in which targets are represented influences kinematics (goal representation hypothesis), participants were presented with combinations of temporal and spatial targets. Not only the physical features of the targets, but also how they were represented as goals had an influence on kinematics. For example, fast movements to a spatial-temporal target showed a more pronounced temporal kinematic



pattern than movements to a temporal target alone (see Fig. 3.1.3). Thus, the results show that how targets are represented as movement goals is important for movement execution.

Figure 3.1.3 The upper part of the figure illustrates one of the experimental conditions. Participants made continuous reversal movements between a temporal and a spatial-temporal target. The lower part shows movement time as a percentage of a complete reversal movement. Most importantly, at the fastest movement tempo, movements to spatial-temporal targets show a more pronounced temporal kinematic pattern than movements to temporal targets (evidence for the goal-representation hypothesis).

3.1.4 Movements and goals in animated objects

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It is well established that even simple geometric shapes elicit the attribution of complex internal states when moving in a contingent manner. That is, animated shapes are reliably described as having internal states such as intentions and beliefs when they show life-like movements. In recent studies, participants were presented with two triangles that move across a computer monitor according to one of three conditions: random movement, simple interaction, and interaction implying complex mental states (Theory of Mind, ToM). Participants verbally described the displays indicating that they supported the validity of the three types of animations. In a series of experiments, we investigated whether there are differences in the perception of these animations depending on whether or not they elicit mental state attribution that we can find also in oculomotor indica-

tors. Specifically, we investigated whether there are differences in visual fixation patterns for adults watching the different types of animations. We presented twelve video clips on an eye tracker monitor to each participant (Tobii 1750; corneal-reflection system, see Fig. 3.1.4.1 and 3.1.4.2). The clips fit into the three categories ToM, goal-directed and random animation. After having watched each clip, the participants described what happened in the clip. The intentionality scores replicated previous findings. The analyses of the eye-tracking data showed that there were significant differences in the average frequencies of fixations between the different categories. Participants made the most fixations while watching random animations and the least while watching ToM animations, with the frequency of fixations in goal-directed animations lying in-between. In another experiment, we

manipulated the processing of the intermediate goal-directed category by showing either random or ToM-clips beforehand. The same goal-directed clip was differentially interpreted depending on the preceding category of animation, indicating that the participants' expectation influenced their perception. Overall, the results of the experiments show that differences in the interpretation of animations concur with differences in the fixation patterns.



Figure 3.1.4.1 Experimental setting

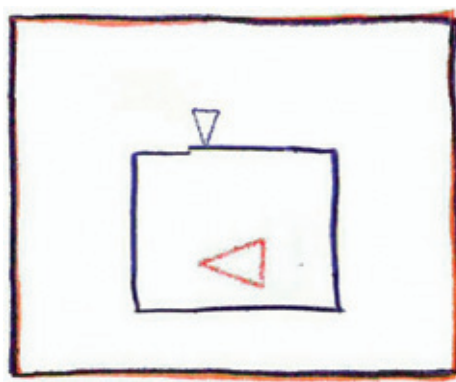


Figure 3.1.4.2 Example of stimulus material

3.2

Tool Transformations

Planning tool-use actions

3.2.1

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When humans plan to execute a tool-use action, they can only specify the bodily movement parameters by taking into account the external target or goal of the tool-use action and the target-to-movement mapping implemented by the tool. In this study, the movement precuing method was used to investigate how people prepare for actions made with tools. More specifically, we asked whether people would be able to specify the spatial target and the target-to-movement mapping of the tool-use action independently of each other, and to what degree they would be able to prepare these components in advance. In the experimental task employed, target locations had to be reached with a lever. Participants had to switch between different target-movement mappings, that were realized by different pivotal points of the lever (see Fig. 3.2.1). In three experiments, either the target or the target-to-movement mapping (either compatible or incompatible) of the action was precued. Results indicate that participants benefit from partial advance information about the target-to-movement mapping, whereas no significant effects were found for precuing the spatial target of the action. These results occurred regardless of

whether the target-to-movement mapping was compatible or incompatible, and provide evidence for the notion that the target-to-movement mapping of a tool-use action is part of its cognitive representation. Two further experiments confirmed that this pattern of results is not influenced by the saliency or the distality of the action goal.

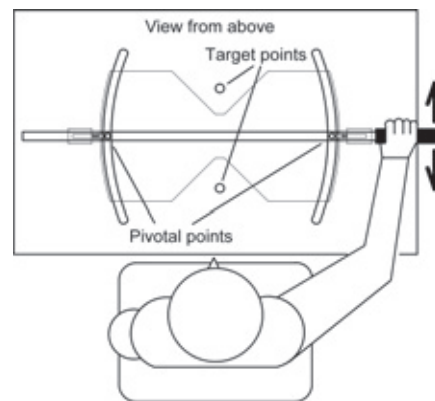


Figure 3.2.1 Illustration of the lever apparatus. In each trial a pivotal point and a target location were indicated by lights and the participant had to move the handle of a lever in the appropriate direction to touch this target location, taking into account the active pivotal point.

Transformation rules in tool-use

3.2.2

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This project aims to explore how humans represent and apply compatible and incompatible transformation rules that are incorporated in mechanical tools. In task-switching paradigms, action rules are typically provided as explicit and arbitrary mapping rules between task elements. In contrast to that, tool-associated transformation rules that define the association between a bodily movement and the associated effect at the distal end of the tool are embodied in the tool structure and therefore do not have to be defined explicitly. The question is whether these rules nevertheless obtain an action-relevant representation that is abstract in the sense that it is not bound

to a specific tool-surface. A second question is whether movement-effect associations in tool-use resemble the arbitrary associations that are the result of explicit rule application. Following the rationale of task-switching paradigms, we developed a tool-switching paradigm in which participants switched between tools that implement either a compatible movement-effect relationship (nippers and tweezers) or an incompatible one (clothespin and clip). With this paradigm, it is possible to dissociate rule repetition benefits and rule switch costs from the repetition of tool surface characteristics (Fig. 3.2.2).

The results show that for compatible as well as for incompatible tool-use actions, there is a benefit for abstract rule repetitions in comparison to rule switches. For the compatible transformation rule, this effect is independent from movement repetitions/switches. For the incompatible transformation rule, however, the benefit of rule repetition is present only for movement repetitions. These results are specific for tool stimuli. In a control experiment with geometric stimuli indicating compatible or incompatible rule application, the rule repetition benefit depends on movement repetitions to both rule types. Furthermore, the dependency of the rule repetition benefit on movement repetitions is much stronger for geometric stimuli than for tool stimuli. These results suggest

that movement-effect associations in tool use are more easily established in the course of action planning than are those from arbitrarily defined action rules. Recently, we have applied the tool-switching paradigm in an fMRI study in order to explore the neural correlates of switching between tool-associated transformation rules.

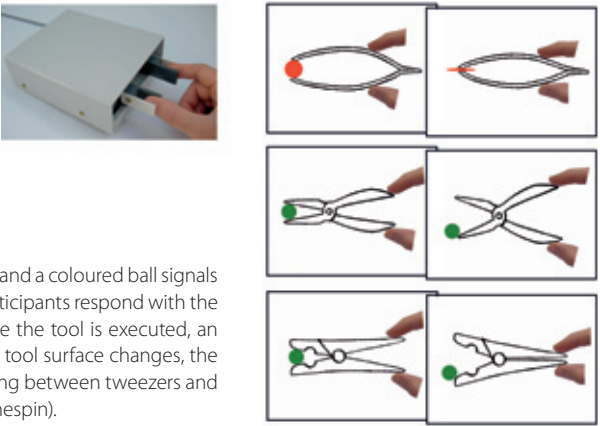


Figure 3.2.2 The basic task: In each trial, a tool picture appears on the screen, and a coloured ball signals whether the tool has to be opened or closed (illustrated on the left side). Participants respond with the response device depicted above. If the correct finger movement to handle the tool is executed, an effect picture is presented (pictures on the right side). In trials in which the tool surface changes, the tool-associated transformation rule can either remain the same (e.g. switching between tweezers and nippers), or can also change (e.g. switching between tweezers and the clothespin).

3.2.3 Internal models in bimanual tool use

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Recent studies about unimanual tool use have shown that humans have an abstract internal model of the tool-specific mapping between external effect and associated bodily movement, which is accessed in the process of action planning. This project addresses the question how such internal models are represented in bimanual tool use, where the mapping may depend on the part of the tool that is operated and the effector used (e.g. two oars operated by the left and right arm moving in opposite directions in order to generate the same boat movement). We conducted three experiments to investigate whether participants have a higher-order representation of a tool, with associated representations of effector-specific mappings at a subordinate level, or whether participants have more specific internal models tailored to the current effector situation. In our paradigm participants touched target locations with a two-jointed lever, using either the left or the right hand (see Fig. 3.2.3). In the first and second condition, the joint of the lever was constant, and switching between hands was associated with switching the target-to-movement mapping. In the third and fourth condition, switching between hands was associated with switching the joint, but the target-to-movement mapping remained constant. Results indicate superior performance of participants in the condi-

tion with constant target-to-movement mapping. This finding suggests that participants construct flexible internal representations of a tool in situations where the target-to-movement mapping depends on the part of the tool that is operated.

Trial $n-1$	Trial n
Joint constant / Mapping switched	
A1	
A2	
Joint switched / Mapping constant	
B1	
B2	

Figure 3.2.3 Illustration of the four experimental groups (A1-B2) in the bimanual lever task. In each trial, one handle of the lever and one target position light up. Participants have to move the lever with the correct hand in the correct direction to hit the target.

Unimanual coordination with regular and transformed feedback

3.2.4

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Coordination of unimanual movements with events in extracorporeal space is essential for many everyday tasks. But how exactly do we coordinate our hand movements with external stimuli? Two alternative hypotheses can be drawn from bimanual research. Coordination could take place either between the stimulus and the actual movement or between the stimulus and the visual effect of the movement. To test these hypotheses we used a circling paradigm that required participants to coordinate hand movements with a clockwise circling stimulus. We dissociated the participants' hand movements from their visual effects by means of transformed feedback. Additionally, we confronted participants with in-phase and anti-phase instructions to manipulate task difficulty and we varied stimulus-effect-relation (symmetric/parallel). In three experiments with different spatial arrangements of stimulus and visual movement effect (see Fig. 3.2.4), we investigated how different the spatial relations between stimulus and effect influence coordination performance. Results show that participants' performance is more accurate if the stimulus and the visual effect form a simple pattern. Participants show different coordina-

tion strategies depending on the design of the visual display. Thus, external effects of movements are important for their coordination with events in the environment. However, our results also indicate that participants integrate proprioceptive feedback, especially in more difficult tasks. We conclude that, in order to achieve optimal performance, participants use both visual and proprioceptive information to coordinate their hand movements with external events.

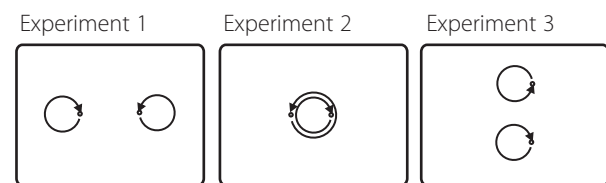


Figure 3.2.4 Illustration of the visual displays of the experiments. Stimuli and movement effects were presented next to each other (Experiment 1), inside each other (Experiment 2), or on top of each other (Experiment 3).

Interference between language and tool-use actions

3.2.5

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Recent studies on language comprehension suggest that we understand linguistic descriptions of actions by mentally simulating these actions. Evidence is provided by the action-sentence compatibility effect (ACE), which shows that sensibility judgements for sentences are faster when the direction of action described in the sentence matches the direction of action required to respond. Since research on spatial compatibility effects indicates that reactions are facilitated by feature correspondence of stimulus and intended action effect, we aimed at investigating whether the ACE refers to the direction of the action, or to the direction of the action effect.

In two experiments, action was dissociated from action effect in the ACE by means of tool-like transformations between action and action effect. Participants were re-

quired to judge the sensibility of auditorily presented sentences by moving a rod either toward or away from their body. To shift the rod, subjects had to move a covered handle either in the same direction in which they wanted to move the rod (regular action-effect relation), or in the opposite direction (transformed action-effect relation) (see Fig. 3.2.5). In the transformed condition, the direction of action described in the sentence was compatible with either the direction of the arm movement or with the direction of the action effect. In Experiment 1, a continuous effect was used – the rod running from the middle position to the near or far response position. In Experiment 2, this continuous effect was compared with a discrete effect where moving the handle turned on a light at one of the response positions. In addition,

the experiments differed in their designs concerning the interindividual or intraindividual variation of response location and transformation.

In the first experiment, results revealed an effect-related ACE, whereas the ACE was movement-related in the second experiment. Subsequent experiments aim at examining the conditions that determine whether the ACE is movement-related or effect-related.



Figure 3.2.5 Illustration of the response tool with (left) regular and (right) transformed action-effect relation.

3.3 Concurrent Action and Perception

3.3.1 Interference between concurrent action and perception

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³ Institute for Occupational Physiology at the University of Dortmund, Germany

Assuming that perception and action rely on common codes, interference should arise when both occur at the same time. Despite the frequency of concurrent action and perception in everyday life and its importance in professional applications, as for example micro-surgery, research has long ignored the specific influence of overlapping features. According to a common coding view, however, these overlapping features would compete for common codes for action and perception and thereby lead to interference.

The paradigm depicted in Fig. 3.3.1 was developed to address these specific interference effects in more detail. In the paradigm participants produced hand movements in certain directions while observing a dot moving on a screen for later perceptual report. The hand movements were performed with a stylus on a graphics tablet. This allowed for the movement trajectories to be analysed. For the perceptual judgment participants were asked to stop a rotating line when it matched the dot motion seen earlier.

In contrast to earlier paradigms (e.g. Hamilton, Wolpert, & Frith, 2004, *Curr Biology*, 14, 493-498; Schubö, Aschersleben, & Prinz, 2001, *Psychol Res*, 65, 145-157; Schubö, Prinz, & Aschersleben, 2004, *Psychol Res*, 68, 208-215), it was possible to measure the effects of action on perception and perception on action at the same time. A mutual contrast effect was found (Zwicker, 2007), i.e. the produced

movements veered away from the perceived directions. Similarly, perceived directions were repulsed from the produced directions. This mutual interference effect was what had been expected based on the assumption of common codes for action and perception. Additional experiments confirmed that this contrast effect does not depend on eye movements (Zwicker, 2007) or memory processes (Zwicker, Grosjean, & Prinz, 2007) and therefore represents a true concurrent action-perception interference effect.

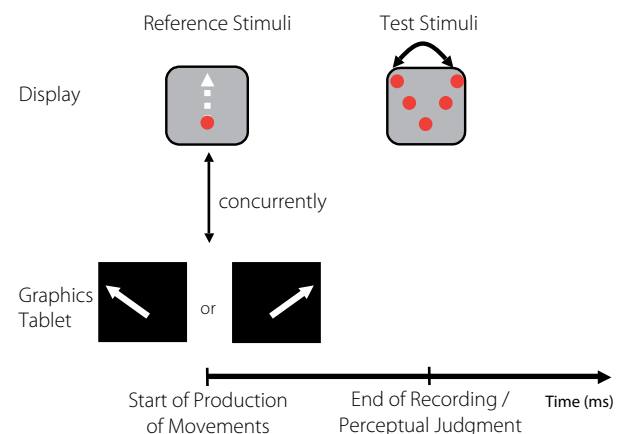


Figure 3.3.1 Trial events in the concurrent action perception paradigm.

Automatic keypress activation in skilled typewriting

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It was previously shown that one of the mechanisms contributing to the high performance levels in people skilled in using the ten-finger system for typing is that fingers are automatically activated when seeing a letter. Based on these results, it was investigated in the first series of experiments whether letters have an influence on actions in their role as action effects in typing (i.e. they usually appear on the screen after a keypress) (Rieger, 2007). Participants who type using the ten-finger system, and participants who do hunt-and-peck typing both responded to coloured squares, either on a keyboard or on an external response device. Subsequently, participants were presented response-corresponding or non-corresponding letters. In Experiment 1, evidence for action activation by anticipated action-effects was found. In Experiment 2, evidence that actions can activate the corresponding action-effects was obtained, but only when participants responded on a keyboard and only in the first half of the experimental trials. Effects were only present in participants who type using the ten-finger-system. Thus, results provided evidence for bidirectional action-effect associations in ten-finger-system typists. Functionally, anticipating visual action-effects is important for action selection in expert typists. Visual action-effects also play a role in performance monitoring, but only in an appropriate context. Thus, the functional use of existing action-effect associations is flexible and not automatic.

In another series of experiments, it was investigated whether the automatic activation of fingers in people using the ten-finger-system includes activation of movement direction and/or activation of movement end-position, and whether a special representation for the letters from the home-row of the keyboard exists. In the experiments participants reacted to the colour of coloured let-

ters. In different conditions they were required to a) press a key, b) move up and press a key, or c) move down and press a key. Reactions occurred either on a computer keyboard or on an external response device. The pattern of congruence effects indicated that movement direction and movement end-position are automatically activated when people who usually use the ten-finger-system see a letter. There was also evidence for a special representation of the letters from the home row. Multiple representations seem to be contributing to skilled performance. Previous results showed that seeing a letter automatically activates effector-dependent and spatial representations in people skilled in using the ten-finger system for typing. In a further series of experiments, spatial representations were investigated in more detail. In the experiments the spatial position (key-congruence) and name (name-congruence) of keys on a keyboard were dissociated. Participants responded with crossed hands to the colour of coloured letters on a keyboard. In Experiment 1 the keys were without names, in Experiment 2 the keys were renamed (see Fig. 3.3.2). This resulted in effector-congruent, incongruent, and different key/name congruent conditions. An effect of effector-congruence was always found. In Experiment 1 participants showed facilitation in the key-congruent/name-neutral condition. In Experiment 2 participants showed interference in the key-congruent/name-incongruent condition. No effect was obtained in the key-incongruent/name-congruent condition. Thus, key names are neither sufficient nor necessary for the activation of spatial representations in skilled typing. However, key-names are processed, and if they do not match the keys they disturb the development of spatial representations.

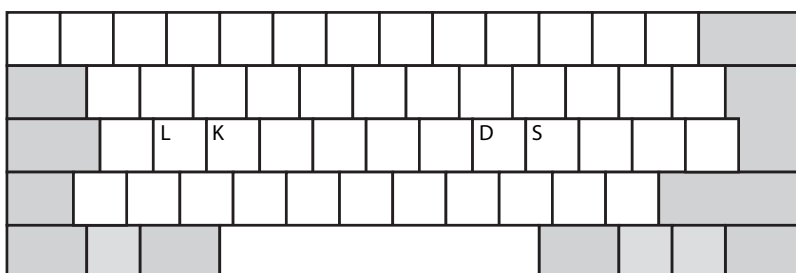


Figure 3.3.2 Illustration of the keyboard participants responded on in Experiment 2 of the third series of experiments. Four of the keys were renamed with respect to their usual names. All other keys were blank.

3.3.3 Neural correlates of error detection in performing musicians

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This project is part of a cooperation between the Department of Psychology and the Independent Junior Research Group “Neurocognition of Music” with the aim to investigate the neural correlates of error processing. Playing a musical instrument is a highly demanding task requiring planning and execution of fast and complex movements. In addition, the constant and precise monitoring of one’s own actions and their effects is necessary to achieve successful performance. This study investigated neurophysiological correlates of error detection in performing musicians. In an action condition, twelve pianists were blindfolded and asked to play fast sequences bimanually on a digital piano while the electroencephalogram (EEG) was recorded. At random positions in the performance, we manipulated the auditory feedback by lowering the pitch of a pressed key by one semitone (sounding as if the pianist made a mistake by pressing the wrong key). In a perception condition, pianists listened to

the same type of stimuli, which were recorded prior to the experiment. Again, the pitch of random tones was lowered by one semitone. Event-related potentials (ERPs) for pitch manipulations as well as for self-made errors were computed and compared to those of correct tones. Results showed that feedback manipulations in the action condition elicited a potential around 200 ms after the onset of the keypress (strongly reminiscent to the “feedback error-related negativity”), followed by a positive deflection (Fig. 3.3.3). Results of manipulated tones in the perception condition showed similar results, but a slightly decreased negativity. This suggests that the error detection mechanism is enhanced by action-related expectations in the action condition. ERPs of performance errors showed that electric brain responses differed between correct and erroneous performance already 100 ms before the onset of a wrong keypress (Fig. 3.3.3). This implies that not all error-related mechanisms rely on auditory feedback, and that errors can be neurally detected prior to the completion of an erroneous movement. One possible account for this finding is that this difference in the ERPs reflects the output of an internal forward model, detecting a discrepancy between the predicted result of a planned movement and the movement goal.

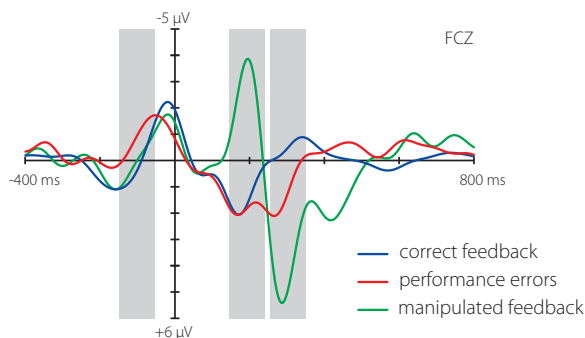


Figure 3.3.3 ERPs for correct feedback, performance errors, and manipulated feedback at electrode FCZ in the action condition. The y-axis indicates the onset of the keypress.

3.3.4 Action-effect associations in experienced musicians

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Previous studies have shown that experienced pianists have acquired integrated action-effect (A-E) associations between piano sounds and the corresponding actions on a keyboard. In Drost, Rieger, & Prinz (2007) we were interested in the question how specific those associations are. Does the perception of any musical sound or only the perception of sounds from the learned instrument have an influence on actions in trained musicians? We investigated whether A-E associations are specific for the

learned instrument in pianists and guitarists. A-E associations were examined by testing whether the perception of a “potential” action-effect has an influence on actions. Participants played chords on their instrument in response to visual stimuli, while they were presented task-irrelevant auditory distractors (congruent or incongruent) in varying instrument timbres (see Fig. 3.3.4). Pianists exhibited an interference effect with timbres of their own instrument category (keyboard instruments: piano



and organ). Guitarists showed an interference effect only with guitar timbre. Thus, the perception of learned action effects consisting of the timbre of one's own instrument leads to activation of corresponding actions. Categorical knowledge about how an instrument is played is also involved in action activation.

Figure 3.3.4 Illustration of the logic of the experimental setup. Participants played chords on their instrument in response to visual stimuli, while they were presented task-irrelevant auditory distractors (congruent or incongruent) in varying instrument timbres (piano, organ, guitar, flute, voice).

Tapping on one's skin: The role of feedback in movement timing

3.3.5

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Precise movement timing is fundamental to most human skills, whether they underlie actions performed alone or in concert with others. In both cases action goes along with concurrent perception. Two basic types of afferent feedback can be available to the actor. Normally there is tactile and proprioceptive feedback generated by the moving effector(s); e.g. the feet when dancing. In addition, 'receptive' feedback is often generated when one's own or another's effector(s) impact upon the body; e.g. feeling one hand make contact with the other hand while clapping in time with music or feeling a partner's body impact upon one's own body when dancing. This project is concerned with the role of such receptive feedback in rhythmic coordination.

In one recent experiment, people synchronized their movements with an auditory pacing signal (clicks separated by 500 ms) while tapping with the right index finger on different regions of their own and others' bodies. Two body regions that vary in sensitivity were targeted: (1) the palmar surface of the left index fingertip (which is high in mechanoreceptor density) vs. (2) the less sensitive volar surface of the forearm (see the top two panels of Fig. 3.3.5.1). Synchronization accuracy was assessed by recording finger movements using an Optotrak motion capture system and then analysing tap contact times.

The results indicate that body region sensitivity affects movement timing accuracy (see Fig. 3.3.5.2). When tapping on one's own body, timing is more variable for the fingertip than for the forearm. This may be because receptive feedback is attenuated most strongly when the

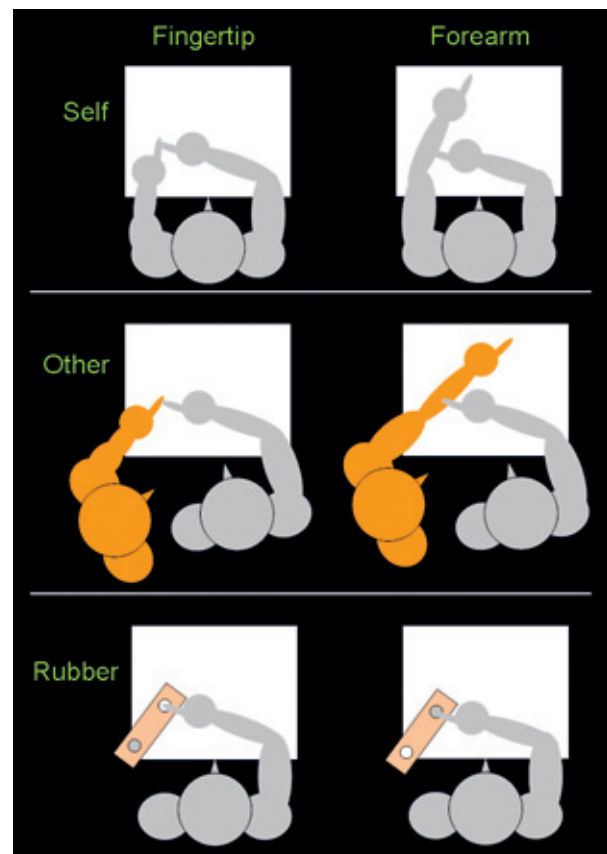


Figure 3.3.5.1 Six 'body tapping' conditions. The top panel illustrates 'self' conditions where participants tapped on their own finger and forearm. The middle panel illustrates conditions where participants tapped at the equivalent locations on another's body. The bottom panel shows conditions where participants tapped on circular rubber surfaces that were similar in firmness to an average finger or forearm.

actor anticipates (via an internal 'forward model') the stimulation of the more sensitive body region. Somewhat remarkably, similar effects of body region sensitivity occur when tapping on another person's body. This is not due to the difference in firmness of the fingertip and the forearm, as analogous effects are not observed when participants tap on rubber surfaces that match the firmness of these body regions (see the bottom panel of Fig. 3.3.5.1 and the rightmost bars in Fig. 3.3.5.2). It may be the case that individuals simulate their co-actors' receptive feedback when required to coordinate movements in social contexts involving body contact.

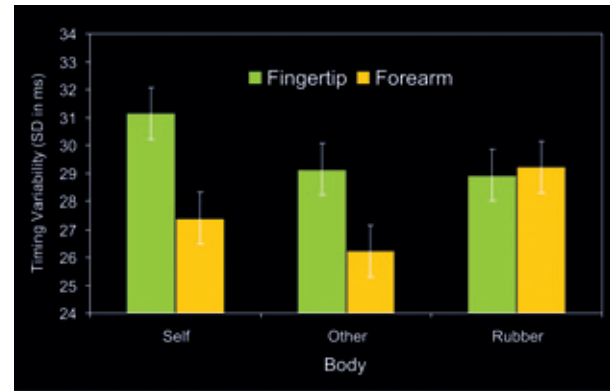


Figure 3.3.5.2 Movement timing variability (the standard deviation of asynchronies between tap contact times and pacing signal clicks) while tapping on fingertips and forearms belonging to the three different types of body: self, other, and rubber.

3.4 Perception and Action in Infancy

3.4.1 Understanding goal-directed actions

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One aim of the research on the early development of perception and action is to study the development of infants' understanding of actions performed by others. The understanding of a goal-directed but uncompleted reach-

ing action was investigated in six- and nine-month-olds. Infants saw the video of an actor's uncompleted reaching movement towards one of two objects. Subsequently, an expected and an unexpected final state of the reaching

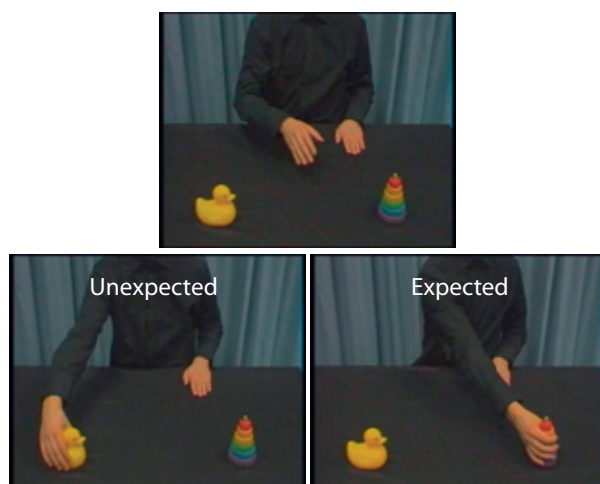


Figure 3.4.1.1 Arrangement of stimulus displays. The upper middle display shows the final position of the actor's reaching movement. The two lower displays show the unexpected and the expected final state as it was presented after the presentation of the reaching movement on the upper monitor had ended.

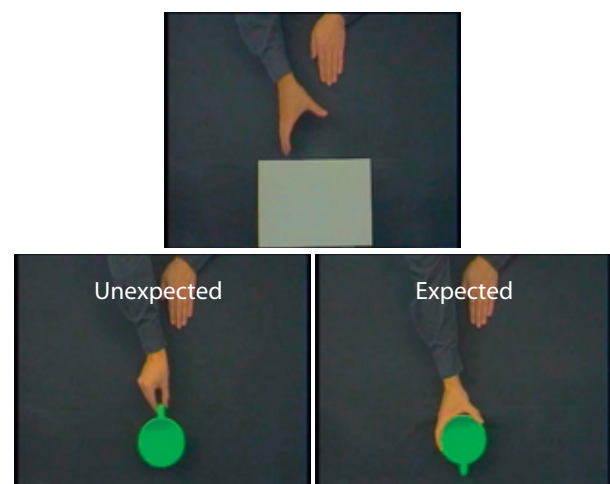


Figure 3.4.1.2 Arrangement of stimulus displays in the follow-up study. The upper middle display shows the final position of the actor's grasping movement. The two lower displays show the unexpected and the expected final state as it was presented after the presentation of the grasping movement on the upper monitor had ended.

movement were presented simultaneously. Additionally, in order to test whether the perspective from which the demonstrated action is viewed is of importance for its interpretation, the action was either presented from an allocentric perspective (i.e. the perspective from which one perceives other people acting) or from an egocentric perspective (i.e. the same perspective from which one sees one's own hands). Both six- and nine-month-olds looked longer at the unexpected final state, but only if the scene was presented from an allocentric perspective and not if it was presented from an egocentric perspective. These findings show that six-month-olds are able to infer the goal of an uncompleted human action, but only when the action was presented from an allocentric perspective and not from an egocentric perspective (Daum, Prinz, & Aschersleben, in press).

In a follow-up study, we tested whether six- and nine-month-olds are able to encode the goal of a human grasping action towards objects of different sizes. Infants saw an actor grasping with either large or small hand aperture size towards an occluded object. Then, an expected and an unexpected final state of this grasping movement were presented simultaneously. Results showed that six- and nine-month-olds looked longer at the unexpected than at the expected final state, and that this discrimination was not due to effects of geometrical familiarity or novelty. These findings provide evidence that infants are able to encode the goal of a grasping action from the aperture size of an actor's hand during the grasp. This ability seems to be independent of infants' competence to anticipatorily adjust the aperture size of their hands to an object as this ability starts at nine months of age.

Interplay between action perception and action production

3.4.2

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Based on the assumption that even young infants have an abstract representation of actions and that this representation is used by both the perceptual and the motor system, various conclusions can be drawn concerning the relation between infants' abilities to interpret other people's actions, and their abilities to actively perform the same actions. In the literature, there is disagreement concerning the direction of this relation. In order to directly compare infants' abilities of action understanding and performance, the interplay of action perception and production was investigated in six-month-olds. Infants

received two versions of a means-end task. In the perception version, infants were shown an actor performing a means-end action with either an expected or an unexpected outcome. In the production version, infants had to pull a cloth to receive a toy placed on the cloth. Results showed that in the perception task, infants distinguished between the expected and the unexpected outcome. This discrimination was independent of their performance in the production task, as both infants who succeeded in the production task and infants who failed in this task discriminated between the two final states.

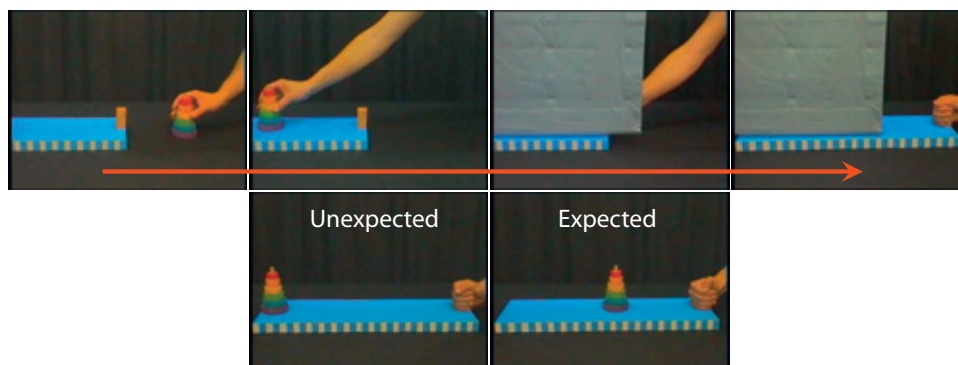


Figure 3.4.2 Stimulus displays from the means-end task. Upper panel: An actor's hand put a wooden tower on the far end of the board. The actor then grasped the handle of the board, the scene was covered with a curtain and the actor pulled the board towards himself. Lower panel: Unexpected final state (left panel) and expected final state (right panel).

3.4.3 Perception and imitation of peers

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In research on infants' perception and imitation of others, adults are mostly used as models. Everyday experience with infants, however, suggests that older children and infants at the same age are of high interest as well. In this study, we investigated infants' perception of different age groups by measuring heart rate and looking time. Infants were shown videos and static images of differently aged actors (same-age, three-and-a-half-year-olds, adults). Results indicated that infants at the age of twelve months, but not younger, showed decreased heart rates and increased looking times during the observation of older children acting. No differentiation was found when static images of the actors were presented. These findings indicate that by twelve months of age, infants exhibit a preference for older children and that this preference is based on the way the models act and not on their visual appearance.

The preference for different age groups was further investigated using an imitation paradigm. The similarity between infant participants and peer models and the competence provided by adult models might both evoke imitative behaviour. However, studies comparing adult and peer imitation are rare and provide mixed results. This study explored whether the age of a demonstrator influenced imitation performance of fourteen-month-olds when presented with a non-familiar or a familiar action. Results showed that the older the model was, the more often a non-familiar action was imitated, suggesting that in this domain infants rely on the adult demonstrator who is presumably perceived as the most competent. In contrast, a familiar action was most frequently imitated from a peer model, indicating that the similarity of the infant participant and the model facilitated imitation of familiar actions.



Figure 3.4.3.1 Stimulus displays from the peer perception study: Same-aged infant, three-and-a-half-year-old child, and adult (from left to right).

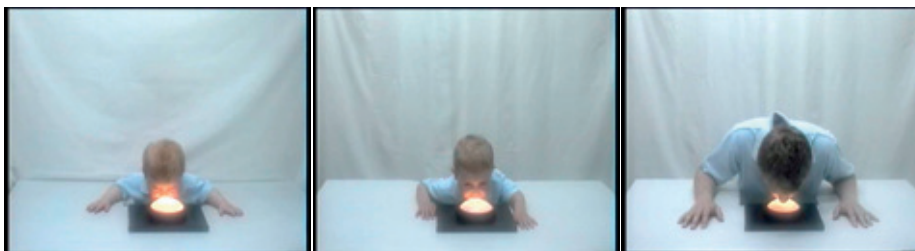


Figure 3.4.3.2 Stimulus displays from the peer imitation study: Same-aged infant, three-and-a-half-year-old child, and adult (from left to right).

Observation/Execution Matching

Activation of action rules in action observation

3.5.1

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Visually perceiving an action may activate corresponding motor programmes. Such automatic motor activation can occur both for high-level (i.e. the goal of an action) and low-level aspects of an action (i.e. the specific effector with which it is executed). We used a tool-use action paradigm to experimentally dissociate priming effects for observing the target, the movement or the target-to-movement-mapping of a tool-use action. In three experiments, participants took turns in acting, observing the tool-use action of another person in trial n-1, and executing one in trial n. Trial transitions from n-1 to n were manipulated in four conditions with either a) mapping repeated, movement and target changed, or b) target repeated, movement and mapping changed, or c) movement repeated, target and mapping changed, or d) all components repeated. Results indicate priming effects

for repeating the target-to-movement mapping (i.e. the action rule) of a tool-use action and suggest that a rather abstract action schema is activated during action observation.

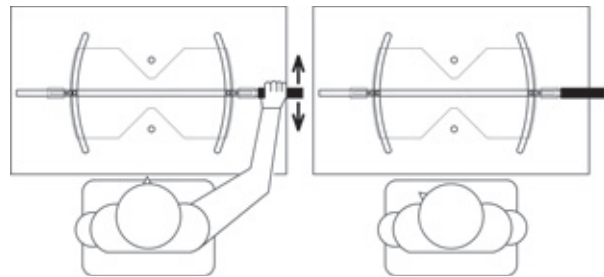


Figure 3.5.1 Experimental setup of the study. Two participants take turns in acting (see Figure 3.2.1 for an explanation of the lever apparatus). The model participant (left side) is being observed by the participant on the right.

Dynamic representation of occluded action

3.5.2

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This project addresses functional relationships between action perception and action simulation. More specifically we examine the time course of action simulation, using a paradigm in which observers watch an action that is partially occluded. We study the interaction between perceptual mechanisms (that take care of representing the action before and after occlusion) and simulation mechanisms (that take care of action representation during occlusion). How should we understand the transition between perception and simulation? Does simulation just carry on old processes – or initiate new ones? Does it use old representations, or does it create novel ones?

The experimental paradigm requires observers to watch a partially occluded action in which a human hand transports an object from one place to the other. The task is to judge the time of reappearance of the transporting hand from behind the occluder. Pilot studies indicated that a substantial positive time error is obtained in this task: The



Figure 3.5.2 A manual transport action as seen from the observer's perspective. The action consists of grasping the mug on the left hand side, transporting it to the right hand side and placing it there. The transport phase of the action is partially occluded.

continuation of the action after occlusion is perceived to happen just in time when the point of reappearance of the transporting hand is actually shifted ahead (by 20–100 msec). This time error seems to reflect a signature of action simulation during occlusion. In a series of experiments we studied how the error depends on factors like occluder width, movement speed, etc. (Prinz & Rapinett, in press). Altogether, our findings suggest that the operations that carry out the simulation during occlusion rely

on generating an entirely novel action rather than just continuing the initial movement. Simulation thus seems to start something new, rather than carrying on something old that perception has begun with. This is what we call the RESTART hypothesis.

3.5.3 Predicting point-light actions in real-time

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There is convincing evidence for a mirror system in humans which simulates actions of conspecifics. One possible purpose of such a simulation system is to support action prediction in real-time. Our goal was to study whether the prediction of actions involves a real-time simulation process (Graf et al., 2007). We motion-captured a set of human actions and rendered them as point-light action sequences. Observers perceived brief videos of these actions, followed by an occluder and a static test posture. We independently varied the occluder time and the movement gap (i.e. time between the end of the action and the test posture). Observers were required to judge whether the test stimulus depicted a continuation of the action in the same depth orientation. Prediction perfor-

mance was best when occluder time and movement gap corresponded, i.e. when the test posture was a continuation of the sequence that matched the occluder duration (Experiments 1, 2, and 4, see Fig. 3.5.3). This pattern of results was destroyed when the sequences and test images were flipped around the horizontal axis (Experiment 3). Overall, our findings suggest that action prediction involves a simulation process that operates in real-time. This process can break down under conditions of action viewing of which observers have little experience.

At least two research strategies seem helpful to decide whether the motor system is involved in real-time prediction. First, functional MRI may help to disentangle perceptual and motor aspects in prediction tasks (see project description by Stadler et al.). Second, dual task paradigms can be used to investigate whether and to what extent the real-time pattern may be modulated by semantic and motor-related influences (see project description by Springer et al.).

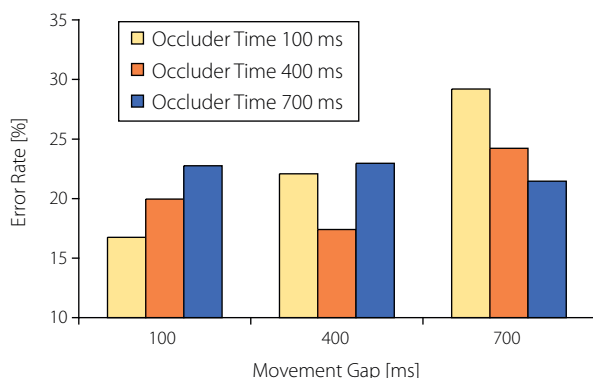


Figure 3.5.3 Error rates for the different movement gaps and occluder times (Graf et al., 2007, Experiment 2). In accordance with the real-time prediction hypothesis, performance is best when occluder time and movement gap correspond. For instance, error rate was lowest when the occluder was on the screen for 100 ms, and the test posture was extrapolated 100 ms into the future.

Semantic and motor interference in action simulation

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² International School of Advanced Studies, Cognitive Neuroscience Sector, Trieste, Italy

Experimental evidence suggests that humans simulate actions observed in other people. For instance, observing an action activates similar cortical regions as producing that same action (e.g. Buccino, Lui, Canessa, Patteri, Lagravinese, Benuzzi et al., 2004, *J Cognitive Neurosci*, 16, 114-126). In turn, the premotor cortex has been framed as a 'mirror system' that allows one to adapt one's own actions to the actions of con-specifics. Our present study aimed at further exploring the mechanisms underlying action simulation. We assume simulation to be a predictive process that operates in real-time and crucially depends on semantic action representations.

We presented a sequence of point-light figures performing one out of nine familiar actions (see Fig. 3.5.4) that was occluded by a blank screen after some time. Participants then saw a static posture and were asked to indicate whether the posture was a continuation of the action or had been rotated in depth. The duration of the occluding blank (i.e. 200, 400, or 700 ms) and the movement gap (i.e. the number of frames between the

end of the action and the static test posture) varied independently. During the occluding blank we presented single verbs for 200 ms describing the nine actions presented (i.e. bowling). Thus, the verbs were either congruent or incongruent to the action. If simulation drew on semantic mechanisms, we expected congruent (relative to incongruent) verbs to facilitate the real-time prediction pattern (i.e. according to Graf et al., 2007 best performance is expected when occluder time and movement gap correspond to each other). Taken together, our data support the idea that action semantics influence the real-time prediction of action.

Further experiments are designed to clarify the precise nature of this influence: First, we want to investigate the time course and the neural correlates of action prediction using EEG. Second, using a new set of point-light stimuli we study the impact of the observer's motor-activity on prediction performance in order to further differentiate between semantic and non-semantic functions in action simulation.

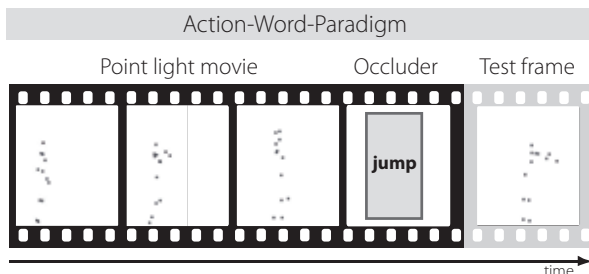


Figure 3.5.4 Each trial presented a point-light action sequence that was then occluded by a blank. During the blank, a verb was presented that was either congruent or incongruent to the action. Then participants saw a static posture and made a yes/no decision whether the posture was a continuation of the action or not. The paradigm was adapted from Graf et al. (2007).

Neural correlates of simulation during action prediction

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Brain imaging studies have shown that, during action observation, the premotor cortex builds a functional network with parietal areas related to sensory-motor mapping and with perceptual regions associated with biological motion or form. The aim of this project was to study which perceptual and motor regions are involved in simulation processes that are assumed to internally model a transiently occluded action (as suggested by be-

havioural studies described in projects by Rapinett and Prinz, by Graf, and by Springer et al.). Our participants saw video-clips in which a woman performed sequences of every-day actions in a natural environment, which were then repeatedly occluded (see Fig. 3.5.5 A). In a prediction task participants judged whether an action was continued with coherent or incoherent timing after occlusion. When contrasting the simulation phase (during which

the action was occluded) with the mere perception of an action, activity increased in a network that has previously been associated with action simulation. However, this network did not selectively respond to phases of transient action occlusion only, but was also active in an action-observation condition and a memory condition. As the absence of these effects in a passive viewing condition suggests, the activation of this network presupposes that the action is actively attended. A selective effect for the simulation phase in the pre-

diction task was found in the rostral part of the dorsal premotor cortex (pre-PMd) of the left hemisphere (see Fig. 3.5.5 B). This region presumably reflects the internal modelling of transiently occluded actions, including the mental generation of new action sequences on the basis of previous perceptions and procedural knowledge. Prediction predominantly concerned visuo-spatial relations between body parts (e.g. the hand) and object details (e.g. the handle of a watering pot), which is reflected in the left dorsal localization of this effect.

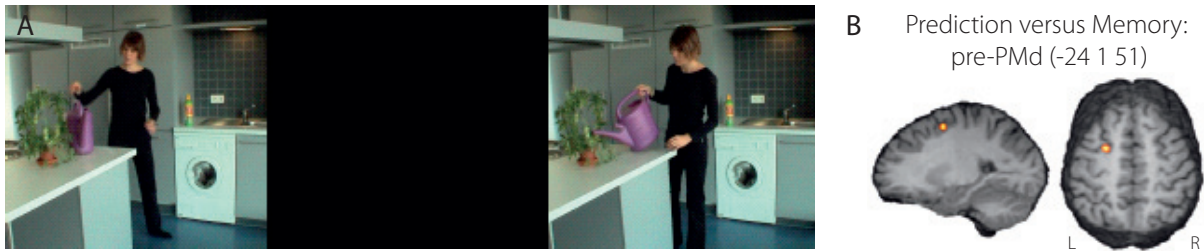


Figure 3.5.5 A Example of a video-clip being occluded for one second.

Figure 3.5.5 B Group-averaged z-maps ($n = 18$) time-locked to occlusion show the selective activation in the action prediction task as compared to the action memorization task.

3.5.6 Temporal awareness of self- and other-generated actions

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Awareness of actions is partly based on the intentions accompanying them. Thus, the awareness of self-generated and other-generated actions should differ to the extent the access to own and others' intentions differs. However, we recently showed that the estimated onset times of actions are similar for self-generated and other-generated actions, but different from similar movements executed by a machine or rubber hand (Wohlschläger, Haggard, Gesierich, & Prinz, 2003, *Psychol Sci*, 14, 586-591). Further investigations showed that the similarity in the awareness of self-generated and other-generated actions (button presses in our experiments) critically depends on the presence of a distal action effect (typically a beep following the button press after 250 ms). Actions with a distal effect lead to a shift of the estimated onset time towards the effect (Haggard, Aschersleben, Gehrke, & Prinz, 2002, *Action, binding and awareness*, In Prinz & Hommel (Eds.), *Common mechanisms in perception and action: Attention and Performance*, Vol. XIX, pp. 266-285. Oxford: Oxford University Press). If the action is void of

any distal effect, the temporal awareness of self-generated and other-generated actions is no longer similar, and self-generated actions are estimated to happen earlier than those of others (Wohlschläger, Engbert, & Haggard, 2003, *Conscious Cogn*, 12, 708-716).

We call this phenomenon temporal binding. In another series of experiments that controlled the intentional attributions and expectations of the effect, we could identify three additive components of temporal binding. As described above, temporal binding depends on the occurrence of an effect. However, temporal binding also occurs when an effect that is expected (due to the history of movement-effect contingencies) does not actually occur. We call this main component of temporal binding operant binding. Nevertheless, temporal binding is stronger if the expected effect does actually occur, but the increase is small and similar to the binding that occurs for purely passive movements followed by an effect. We call this component perceptual binding. Finally, temporal binding can be increased further if, in addition to

being expected, the effect was also intended. We call this last component of temporal binding intentional binding (Engbert & Wohlschläger, 2007).

Temporal binding refers to a temporal attraction in the perceived times of actions and effects. So far, the measures we used were only indirect, using judgements of the perceived time of actions or their effects. A more direct method is the estimation of the time interval between a voluntary action and its subsequent effect. Estimates were obtained for intervals bounded by different kinds of actions and effects: The actions were either performed by the participants themselves or by the experimenter. The effects, in turn, were movements either applied to the body of the participant or the experimenter.

The data showed that interval estimation is a valid method for exploring action awareness. Intentional binding is stronger for self-generated compared to observed actions, indicating that private information about the action contributes to action awareness. In contrast, tempo-

ral binding did not depend on whether a somatic effect was applied to the participant's or another person's body. Third, for self-generated actions, distal events gave rise to a stronger intentional binding than proximal somatic effects. This indicates that temporal binding especially links actions with their distal effects (Engbert, Wohlschläger, & Haggard, in press; Engbert, Wohlschläger, Thomas, & Haggard, in press).

Our results are consistent with the view that (1) intentions are attributed to others but not to machines; (2) that we attribute intentions to ourselves in the same way as we do to others; and (3) that (2) is only true or possible if the content of the intention can be shared between Me and You, i.e. if the intention is about a distal effect. Finally, temporal binding parallels operant learning in many aspects, and thus one important role of temporal binding can be considered to be the conscious back side of a coin labelled operant learning.

Motor resonance to other versus self

3.5.7

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Modern theories of social cognition propose that another's action is mapped onto a motor representation for the same action in the observer. Thus, others' and one's own

actions are represented in the same format. This, however, raises the problem of action attribution: How do we know who has performed a certain action if we represent others'

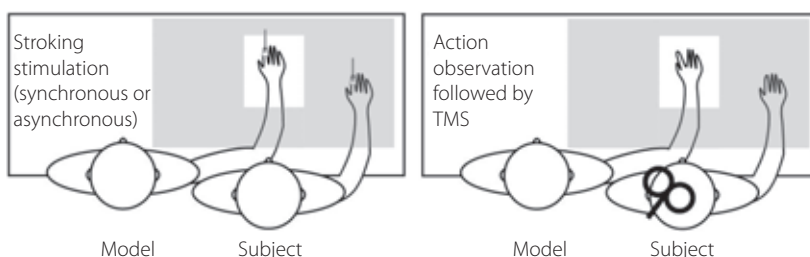


Fig. 3.5.7.1 The subject sat resting his or her right arm on a table. The arm was hidden under a surface, which could appear either as a mirror or as transparent glass, according to computer-controlled illumination under the surface. An experimenter's right arm was positioned in front of the subject's midline. The illumination was controlled so that the subject could either see this arm or not. Tactile stimulation was applied simultaneously to the subject's and the experimenter's index finger by two identical paintbrushes mounted on computer-controlled motors. In the synchronous condition, the two paintbrushes stroked the subject and the experimenter with identical onset times, directions, speeds, and durations. In the asynchronous condition, the two paintbrushes moved with different onset times, directions, speeds, and durations. Synchronous stroking induced the illusion that the experimenter's hand was part of the subject's own body. Once the illusion was established, the experimenter's index finger made unpredictable abduction movements. On some trials, the subject received a TMS pulse over the motor cortex shortly after observing the experimenter's action so that it could be probed how observation of action influenced cortical excitability.

actions in the same way as our own? Researchers have proposed a 'Who'-system that shall enable perceptual identification of self and other, perhaps on the basis of non-overlapping cortical activations simultaneous with activation of the mirror neuron system.

Consistent with the idea of a "Who"-system, we find evidence for the idea of social differentiation, not equivalence, within the motor system. By using an established illusion to manipulate the sense of body ownership (the 'Rubber Hand Illusion') for a hand that in fact belonged to another person (cf. Fig. 3.5.7.1), it was found that the human motor system distinguishes the agent of an observed action. When participants clearly attrib-

uted an observed hand action to another person, a strong motor resonance effect was found. That is, motor-evoked potentials to single transcranial magnetic pulses recorded from participants' hand muscles showed a significant increase when participants passively watched another's hand making an action compared to when the hand was at rest (cf. Fig. 3.5.7.2). However, when they thought they were looking at their own hand (because the illusion was effective), an effect in the reverse direction emerged. Thus, entrainment of the motor system by observing actions critically depends on the attribution of the observed action. In further studies, we will investigate to what extent this sensorimotor-based social differentiation is involved in conscious distinctions between self and other.

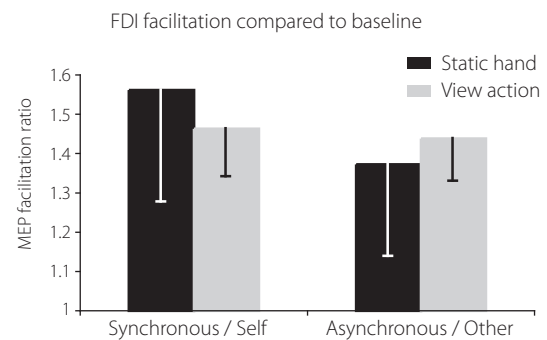


Figure 3.5.7.2 Mean (+SE) cortical motor excitability of First Dorsal Interosseus (FDI) following action observation, or while viewing a static hand, in each ownership condition.

3.6 Task Sharing and Joint Action

3.6.1 Musical ensemble synchronization

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Ensemble musicians are able to coordinate their actions with remarkable precision. Previous research has identified three core cognitive processes that may assist them in doing so. One is 'prioritized' integrative attending, which involves dividing attention between one's own actions (high priority) and those of others (lower priority) while monitoring the overall, integrated ensemble sound (Keller & Burnham, 2005, *Music Percept*, 22, 629-661). The second process is auditory imagery; more specifically, anticipating one's own sounds (Keller & Koch, 2006b, 2007) and the sounds produced by other performers (Keller, Knoblich, & Repp, 2007). The third process is adaptive timing, i.e. adjusting the timing of one's movements in order to maintain synchrony in the face of tempo changes and other, often unpredictable, events.



Figure 3.6.1.1 Stages in measuring body sway coordination in piano duos: (1) Pianists' body movements and sounds are recorded (for two pieces); (2) One-dimensional information about anterior-posterior body sway is extracted from normalized movement data; (3) The difference in body positions across time is estimated by cross-recurrence analysis with a moving window; (4) Coordination is quantified by averaging the differences within this window for the two pieces (the linear relation provides evidence that the method is reliable).

The relationship between adaptive timing and ensemble coordination was investigated in a recent study in which performance on a simple finger-tapping task was used to predict the ability of pianists to synchronize with one another while playing duets.

First, the body movements of seven pairs of pianists were recorded using a motion capture system while they performed the duets. Analyses of these movements revealed that body sway was more strongly correlated in some pairs of pianists than in others (see Fig. 3.6.1.1). These differences between pairs were both reliable (constant across contrasting musical pieces) and valid (correlated with measures based on the degree of asynchrony between sounds). Then, several months later in the finger-tapping task, the same pianists tapped (alone) in time with a computer-controlled auditory pacing signal that contained varying amounts of tempo change. The speed and completeness of adaptation to the tempo changes were estimated to yield an adaptive timing index for each pianist.

An analysis comparing body sway coordination and adaptive timing indices revealed that highly coordinated pairs included individuals with high adaptive timing

indices (see Fig. 3.6.1.2). This finding suggests that basic timing mechanisms may be fairly direct determinants of the complex coordination patterns that arise in real musical contexts. The ultimate goal of this project is to understand how these basic mechanisms interact with higher-level processes such as prioritized integrative attending and anticipatory auditory imagery in shaping the quality of ensemble coordination.

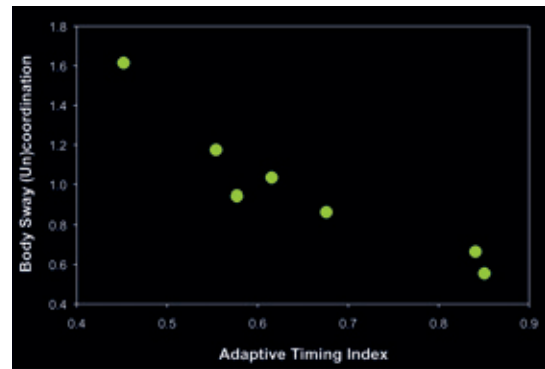


Figure 3.6.1.2 Scatter plot showing the relationship between adaptive timing (high values indicate strong adaptation) and body sway coordination (low values represent good coordination).

Task sharing in beat synchronization

3.6.2

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Previous research has revealed a wealth of insights into the psychological mechanisms underlying sensorimotor synchronization with computer-controlled sequences. However, little is known about the influence of other human actors on one's own performance in musical con-

texts involving joint action. We investigated this issue by examining the timing of finger taps produced by a single actor versus taps produced alternately by two coactors while synchronizing with computer-controlled auditory sequences. Pairs of musically trained participants tapped

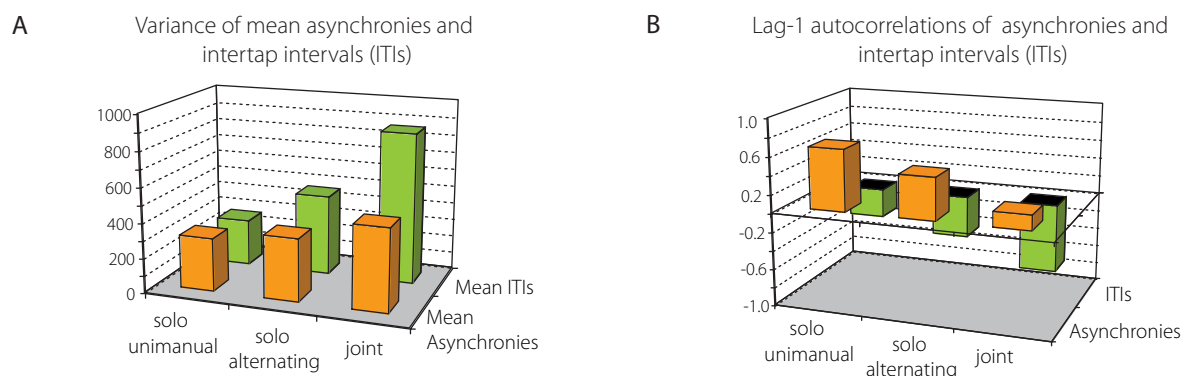


Figure 3.6.2 Variance (A) and lag-1 autocorrelations (B) for asynchronies (orange) and inter-tap intervals (ITIs; green) in solo unimanual, solo alternating, and joint conditions.

(Note that the solo unimanual condition involved tapping alone with the beat using the right hand, while the solo alternating condition involved tapping with the beat using the right and left hands in alternation.)

the beat of musical or isochronous tone sequences either on their own (solo) or alternating with the other person (joint). Taps triggered percussion sounds, making the task a rudimentary form of ensemble performance.

Participants' tap timing became more variable when tapping in alternation with a partner than when tapping alone (see Fig. 3.6.2 A). This increase in variability may be due partly to mutual error correction; specifically, compensatory adjustments to tap timing made by an indi-

vidual in response to their partner's timing error on the preceding beat. Such mutual error correction would give rise to an increase in the interdependence between adjacent taps, and this was in fact observed, as indicated by more negative lag-1 autocorrelations under joint than solo conditions (see Fig. 3.6.2 B). Mutual error correction may be an automatic process that serves to make the multiple performers in an ensemble sound as one.

3.6.3 Joint compatibility in a face-name interference task

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Common coding theory claims that perceived events and planned actions share a common representational domain. There is evidence that these representations may be shared between self and others. Investigating task sharing is one way of studying real-time social interactions. In this paradigm two or more individuals take care of a certain aspect of a common task with no interpersonal coordination being required. The task is administered under different social contexts: (1) individual (each subject performs their task set individually), and (2) shared (the full task is divided up among two subjects sitting next to each other). This paradigm enables us to investigate whether representation of each individual is limited to the action knowledge of one's own task set or whether the other's share is taken into account as well.

A face-name interference task was employed, in which subjects were required to perform naming responses to a coloured diamond (one's own name vs. the name of a friend). The relevant stimulus (diamond) was superimposed on the task's irrelevant (but socially relevant) stimulus, a picture of one's own face, a friend's face, or a neutral face (for an example, see Fig. 3.6.3).

When the task was distributed among two friends (each person responding with his/her own name), a compatibility effect was observed in the joint condition, but not in the individual condition. Investigating the underlying mechanisms, the effect was found to be primarily based on the compatibility between face and identity of the responding person, rather than on the compatibility between face and naming response. Thus, these results clearly suggest that it might be important to differentiate which response dimension was responsible for the joint compatibility effect in previous studies.



Figure 3.6.3 Example of (relevant) diamond stimulus superimposed on (socially relevant) stimulus of neutral face.

3.6.4 Bimanual coordination within and across individuals

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A bimanual aiming paradigm was used to investigate task sharing. The task was divided between two subjects, each responding with one hand. Targets were illumi-

nated red dots and were presented at the left and right side of a white rectangular response pad. There were two possible amplitudes resulting in four potential mappings:

near-near, near-far, far-near, far-far. The targets served as both cue and go-signal. In the unimanual condition there were no significant differences between right and left hand performance in both reaction time and movement time. In contrast the results of the joint condition showed an advantage for the right hand in reaction time but a disadvantage in movement time compared to the performance of the left hand (see Fig. 3.6.4). One explanation may be that having a reference point in space (co-acting partner) in the joint condition might lead to a stronger activation of the related hemisphere. Motor preparation processes are known to be located in the

right hemisphere of the brain which might result in faster RT for the right sitting subject while the left hemisphere is responsible for motor control leading to shorter MT for the left sitting subject. Further studies are necessary to investigate this hypothesis.

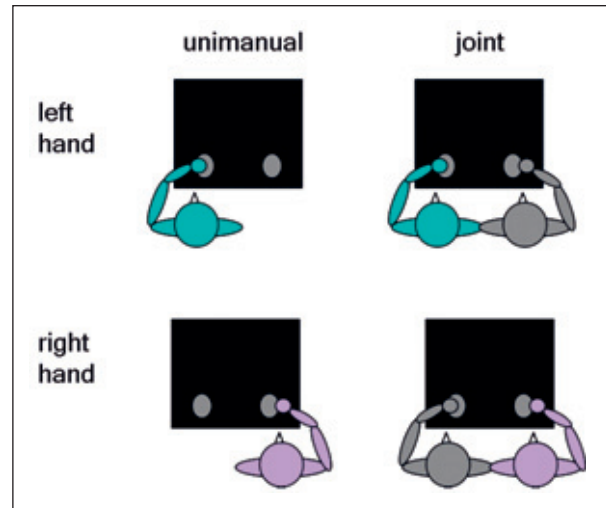


Figure 3.6.4 Two conditions in a fixed order were conducted: 1) unimanual condition (one subject using his left or right hand) 2) joint condition (two subjects working together; one using his left the other one his right hand). In the joint condition subjects were instructed to act as if they are doing the task alone. Task and movements in both conditions are exactly the same, except that two subjects are acting alongside each other.

Shared task representations in coacting individuals: Inferences from CNV and LRP

3.6.5

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The underlying mechanisms of co-representation in task sharing will be examined by using electroencephalogram (EEG). In contrast to reaction time experiments, event-related potentials provide information about internal processes in the respective non-acting person while the other agent is performing his/her share of the task. The contingent negative variation (CNV) and the preparation-related lateralized readiness potential (LRP) are used as measures of relative activation of the subject's motor cortices. The typical S1-S2-design with S1 being the preparative/informative stimulus and S2 the imperative stimulus will be ap-

plied. Studies on action observation and action prediction using EEG suggested that similar neural mechanisms are involved in monitoring one's own actions and the actions of others (e.g. van Schie, Mars, Coles, & Bekkering, 2004, *Nat Neurosci*, 7, 549-554; Kilner, Vargas, Duval, Blakemore, & Sirigu, 2004, *Nat Neurosci*, 7, 1299-1301). Thus, it is tempting to speculate that not only in observing another's action, but also in task sharing, the other's action is represented in a functionally equivalent way as one's own.

Congresses, Workshops, and Symposia

- 2006** ■ Graf, M., Rapinett, G., Schubotz, R. I., & Prinz, W. (February). *Embodied Simulation*. Symposium. Kloster Irsee, Germany.
- Gade, M., & Lepper, M. (March). *“Geregeltes” kognitives System – Welche Art der Information kann wie genutzt werden? [The representation of rules in our cognitive system: What kind of information can be used?]*. Symposium. 48th Meeting of Experimentally Working Psychologists (TeaP), Johannes Gutenberg University Mainz, Germany.
- Koester, D., & Friedrich, C. K. (March). *Prozesse des Sprachverstehens [Processes of language comprehension]*. Symposium. 48th Meeting of Experimentally Working Psychologists (TeaP), Johannes Gutenberg University Mainz, Germany.
- Rieger, M., & Kunde, W. (March). *Handlungsziele in der Bewegungssteuerung [Action goals in movement control]*. Symposium. 48th Meeting of Experimentally Working Psychologists (TeaP), Johannes Gutenberg University Mainz, Germany.
- Weigelt, M. (March). *Perceptual-cognitive mechanisms of action control*. Symposium. 9th Tübingen Perception Conference, Max Planck Institute for Biological Cybernetics, Tübingen, Germany.
- Wohlschläger, A., Engbert, K., & Haggard, P. (March). *Intentions, Binding, and Causality*. Workshop. University College London, United Kingdom.
- Prinz, W. (July). *Free will vs. determinism?* Euroscience Open Forum (ESOF) 2006, Munich, Germany.
- Hollaender, A. (August). *Task Sharing and Joint Action*. Workshop. Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.
- 2007** ■ Springer, A., & Volz, K. G. (January). *Finding culturally (in)dependent levels of self-representation: The case of emotions*. Workshop. Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.
- Koester, D. (March). *Sprachproduktion [Speech production]*. Symposium. 49th Meeting of Experimentally Working Psychologists (TeaP), University of Trier, Germany.
- Rieger, M., & Massen, C. (March). *Werkzeugtransformationen [Tool transformations]*. Symposium. 49th Meeting of Experimentally Working Psychologists (TeaP), University of Trier, Germany.
- Daum, M. M., & Elsner, B. (August). *Eyes, hearts, and brains: Using psychophysiological measures to explore infants' cognitive development*. Symposium. 13th European Conference on Developmental Psychology (ECDP), Friedrich Schiller University Jena, Germany.
- Volz, K. G., & Springer, A. (September). *Dissociating Levels of Emotional Self-Representation*. Workshop. Max Planck Institute for Neurological Research, Cologne, Germany.
- Holländer, A., & Daum, M. M. (November). *Action and Perception*. Workshop. Max Planck Institute for Human Cognitive and Brain Sciences.

Appointments

- Hauf, Petra. *Professor of Psychology*. St. Francis Xavier University, Antigonish, Canada. ■ 2006
- Hohenberger, Annette. *Assistant Professor*. Middle East Technical University (MECA), Ankara, Turkey. ■
- Knoblich, Günther. *Professor of Psychology*. University of Birmingham, United Kingdom. ■ 2007
- Stenneken, Prisca. *Professor of Clinical Linguistics*. University of Bielefeld, Germany. ■

Degrees

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PhD Theses

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- Körner, J. *Identification of factors contributing to driver workload: Searching in lists while driving*. Ludwig Maximilians University Munich, Germany. ■
- Stadler, W. *The context of events modulates attention: A study of EEG correlates of anticipation and attention*. University of Salzburg, Austria. ■
- Sänger, J. *ERP-correlates of action preparation*. Ludwig Maximilians University Munich, Germany. ■ 2007
- Zwicker, J. *Specific interference effects between temporally overlapping action and perception*. University of Leipzig, Germany. ■

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- Weigelt, M. *Nachwuchspreis 2006 [Advancement Award]*. DVS-Kommission Sportspiele.
- 2007** ■ Weigelt, M. *Reinhard-Daug's-Förderpreis für den wissenschaftlichen Nachwuchs der dvs-Sektion Sportmotorik [Reinhard-Daug's-Price for young scientists of the dvs sport motorics section]*. Deutsche Vereinigung für Sportwissenschaft.

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- Daum, M. M., Rauch, J., & Wilkening, F. (in press). Intuitive physics: Naïve concepts about the ball's inertia in professional football players. In P. Andersson, P. Ayton, & C. Schmidt (Eds.), *Myths and facts about football: The economics and psychology of the world's greatest sport*. Newcastle upon Tyne: Cambridge Scholar Press.
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Figure 3.4.1.1

Daum, M. M., Prinz, W., & Aschersleben, G. (in press). Encoding the goal of an object-directed but uncompleted reaching action in 6- and 9-month-old infants. *Developmental Science*.

Figure 3.5.3

Graf, M., Reitzner, B., Corves, C., Casile, A., Giese, M., & Prinz, W. (2007). Predicting point-light actions in real-time. *NeuroImage*, 36, T22-T32.

Figure 3.5.7.1

Schütz-Bosbach, S., Mancini, B., Aglioti, S. M., & Haggard, P. (2006). Self and other in the human motor system. *Current Biology*, 16, 1830-1834.



Prof. Dr. Robert Turner
Director

4 Mapping Brain Structures Using MRI Techniques

Department of Neurophysics

In recent years, physics has played a major role in the rapid advance of cognitive neuroscience. The most widely used methods of mapping brain function, using magnetic resonance imaging (fMRI), were developed in the early 1990s by USA-based physicists working at labs in Boston, Minneapolis, Murray Hill and Washington. Methods for interpreting measurements of magnetic fields generated by brain activity (MEG) have also seen major recent improvement in the hands of physicists. The physics of electromagnetic fields, nuclear spins, and the biophysics of blood and brain tissue have thus been combined to provide non-invasive methods that can resolve brain activity within a millimetre in space, or milliseconds in time. These methods allow the exploration of profound neuropsychological questions regarding the organization of human brain function, and even the relationship between mind and brain. With a much improved understanding of normal brain function, it is hoped that far more empirically based treatments for a wide range of neurological and psychiatric conditions can be developed.

For this reason, the Department of Neurophysics was established at the Max Planck Institute for Human Cognitive and Brain Sciences in Leipzig. In order to push forward the frontiers of neuroimaging techniques, it is necessary to integrate the efforts of physicists skilled in MRI technique development, neuroanatomists, image analysts, engineers and neuropsychologists. This department has excellent access to a state-of-the-art high field MRI scanner suitable for human use, working at 7T, more than double the field strength of the most powerful clinical MRI scanners used today. Researchers can also use the other facilities of the Institute, including an MEG scanner and two 3T MRI scanners.

The most urgent challenge is to answer the question: What next can MRI methods teach us regarding the structure and function of the human brain?

Because of MRI's remarkable safety record, MRI techniques can be easily explored with volunteer human subjects. High field strength allows the use of very high spatial resolution, so that details of structures less than a millimetre in size can be distinguished. The organization of the brain's white matter, consisting of the major long nerve fibres connecting different brain regions, can also be investigated with much greater accuracy. Changes in MRI image intensity caused by local brain activity can be measured with greater sensitivity and spatial precision.

Thus the potential exists for a richer and more detailed scientific understanding of the association of brain function with particular brain structures. Furthermore, the changes in brain structure, such as the thickness of grey matter, that are known to occur with repeated experience or practice, can be explored much more easily than at lower magnetic field strengths.

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Evaluation of the capability of a 3T MRI scanner for identifying the entire primary visual cortex in human subjects

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Much of the current work in the field of neuroscience is motivated by the quest to establish the correspondence between the functional organization of the neocortex and its cytoarchitectonic fields. The development of techniques which allow for the identification of cortical layers in the living cortex by MRI has made substantial progress in the recent years.

The visual cortex occupies nearly one third of the surface of the human cortex and is divided in several regions according to their structure and function. The primary area V1 is characterized by an easily identifiable (after dissection) anatomical landmark: the stria of Gennari. A few MRI studies were able to identify Gennari's stripe in vivo by its myelination pattern, exploiting the grey-white matter T1 contrast. Results were obtained at 1.5T as well as at 3T and 4.7T (Thomas, De Vita, Roberts, Turner, Yousry, & Ordidge, 2004, *Magn Reson Med*, 51, 1254-1264; Carmichael et al, 2006, *Neuroimage*, 32, 1176-1184). An in-plane resolution of at least 300 μm was needed, and was achieved by greatly sacrificing the slice resolution ($>1.5\text{mm}$) and orienting the slices such that partial volume effects were kept to a minimum. Only the portions of the stripe were visualized for which partial volume effects coming from tilted orientation of the stripe with respect to the slice were avoided. A complete characterization of the extent and boundaries of the area V1 is thus not possible or at best unreliable. Isotropic resolution is required for this aim. A whole-brain study at 1.5T with isotropic resolution of 0.61mm allowed for the occasional visualization of Gennari's stripe, but higher resolution is required for reliable characterization. We present a method which provides reliable 3D characterization of Gennari's stripe in vivo, using an affordable amount of measurement time at the widely available field strength of 3T.

All the measurements were performed on a 3T scanner (Siemens Trio), equipped with a 40mT/m gradient coil, an RF body coil operated in the transmit mode and a head phased array RF coil with 12 elements for signal detection. Images of six volunteers (four male and two female, mean age 32 years) were acquired. A volume perpendicular to the calcarine sulcus was investigated with high resolution; in addition, 3D images of the whole brain were acquired with a standard anatomical T1-weighted sequence (MP-RAGE). The high resolution investigation

of the visual area V1 was performed with a 3D magnetization-prepared turbo spin echo sequence, which was chosen according to following criteria: i) isotropic resolution; ii) high SNR per unit time; iii) good point spread function (PSF); iv) contrast weighted by T1 (inversion recovery preparation), T2 (echo time, turbo factor) and magnetization transfer (slab selective 180deg pulses). The repetition time, inversion time and turbo factor were optimized for signal, contrast and resolution (PSF properties). The original sequence was modified to output phase images in addition to the standard magnitude images. Two measurements with interleaved slab settings were combined to produce a contiguous volume. In order to check the quality of coregistration of the two interleaved sets of slabs, an identical fiducial slab (second slab group) was acquired every time. The TSE measurement parameters include: TR=2850 ms, TE=17 ms, TI=150 ms, flip=180, turbo factor=15, FOV=160x135x0.5 mm, matrix size 384x324, 10 slices/slab, 5+1 slabs (4+1 slabs, respectively). The highest nearly isotropic resolution (0.4x0.4x0.5mm) was chosen such that the SNR in the scans still allowed for a good coregistration with one average. An acceleration factor of 2 was crucial to keeping the total acquisition time per scan to 8 mins. Each saved scan consisted of a magnitude and a phase image in DICOM format. Between three and five sets of identical scans (two interleaves, 5+4 slabs) were acquired for each volunteer and averaged. 3D volumes, both magnitude and phase, were reconstructed and saved in Analyze format; the magnitude images were coregistered with the first scan of the series, and the magnitude, real and imaginary 3D data sets were resliced; all these operations were performed using MATLAB, based on functions from the SPM2 software package (SPM2, <http://www.fil.ion.ucl.ac.uk/spm>). In contrast to the averaging method which is commonly used, where only magnitude images are summed up, we use the resliced complex matrices for averaging. This ensures incoherent summation of the random noise and maximizes the gain in SNR especially for initial images with low SNR.

The dependence of the contrast between grey and white matter on the inversion time was investigated experimentally and modelled as a function of TR, T1, T2 and M0. The regular T1 relaxation times which characterize grey

(1500 ms) and white matter (1000 ms) at 3T, as well as the M0 ratio (80% vs 70%) were found to be inadequate for the description of the contrast behaviour. The effective T1 times were measured with the 3D TSE sequence, using the same parameters as for the high resolution study and varying the inversion time, and found to differ by roughly 50% from the values measured with a dedicated T1 mapping sequence. The effect is most probably due to magnetization transfer, as an additional investigation of the behaviour of the effective T1 relaxation times with the turbo factor and flip angle suggests. Using the relaxation times measured with the TSE sequence, the dependence of the grey-white matter contrast on TI can be very well described. The inversion time TI=150 ms was chosen as a compromise between contrast (quite flat between 150 and 350 ms) and signal (strongly decreasing).

An example of the in vivo visualization of the area V1 via its stria of Gennari is shown in Fig. 4.1. The stria of Gennari could be identified in all volunteers, irrespective of the sinuosity of their calcarine sulcus. Using the 3D data, slices perpendicular to the calcarine sulcus can be ob-

tained at every point along the sulcus. The stria can be visualized in the perpendicular sections and followed over several slices before a new reslicing becomes necessary. For a better visualization, a few consecutive slices can be summed up without introducing substantial blurring due to partial volume effects.

Besides optimization of the white-grey matter contrast with the magnetization-prepared TSE, coregistration, complex averaging and parallel imaging turn out to be very important in the detection of myelination patterns in vivo. Using complex averaging instead of summing only magnitude images leads to a significant increase in the final SNR, given the low SNR values of the magnetization-prepared images. The data quality is high enough to allow one to investigate the three-dimensional extension of Gennari's stripe. For an automatic segmentation, however, the endeavour will greatly benefit from measurements at higher field strength. In this respect 7T might be an optimal field value, providing increased SNR without prohibitive SAR limitations.

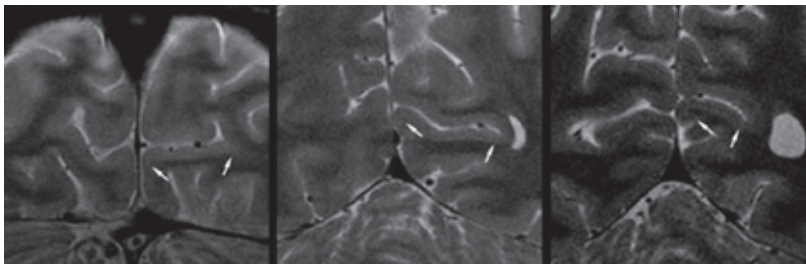


Figure 4.1 Coronal sections of TSE MRI scans of brains of three volunteers at 3T, spatial resolution $0.4 \times 0.4 \times 0.5 \text{ mm}^3$, showing Stria of Gennari within the calcarine sulcus.

4.2 Establishment of a 7T MRI scanner for human neuroanatomical and functional brain mapping studies

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It is clear from such studies as the one just described that the level of detail and image quality required to discriminate cortical areas non-invasively using MRI in human brain is barely achievable at the field strength of 3T. For such reasons, the Leipzig MPI decided to install an MRI scanner at the much higher field strength of 7T which is currently becoming well-supported by the major scanner manufacturers. While these scanners are still undergoing engineering optimization, early results from other labs are highly encouraging.

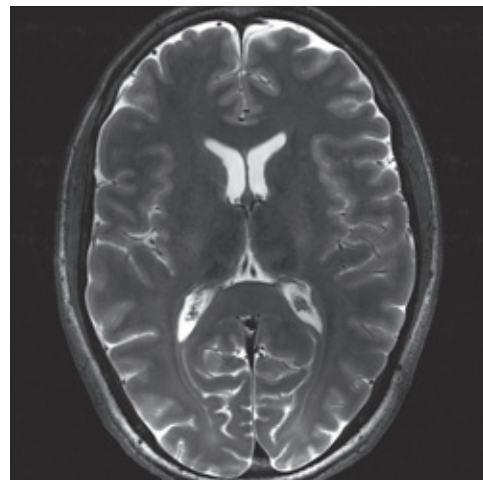


Figure 4.2 Transversal image acquired with a turbo spin-echo (TSE) sequence (TR = 5000 ms, TE = 78 ms, FOV $192 \times 192 \text{ mm}^2$, Matrix 1024×1024 , Slice thickness 2 mm) at 7T.

The scanner order included a powerful head-only gradient coil and 32-channel rf receiver capability. Multi-channel rf transmit equipment will be added over the next year, as it becomes available from the vendor.

A new building with an elliptical plan was completed in early 2007, and the magnet was installed on 29 March

2007. System preparation proceeded without incident, and the scanner was handed over to the Institute on 24 July, after passing an acceptance test supervised by Professor Turner and Professor Möller. A sample high resolution image of a human brain is shown here, which gives an indication of what is feasible.

Production, detection and modelling of radiofrequency electromagnetic fields used in MRI

4.3

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To make the best use of the powerful capabilities of a high field MRI scanner requires novel MRI techniques and novel hardware. Because the use of 7T MRI scanners for human studies is not yet widespread, there is a dearth of high performance radio frequency transmit and receive coils available from manufacturers. Indeed, considerable benefits can still be obtained from novel approaches to such hardware.

However, use of such high radiofrequencies (300 MHz) requires very careful attention to the safety of human subjects. At normal magnetic field strengths, MRI industry maintains routine and highly effective safety standards. Exposure to high steady magnetic fields has shown no harmful effects, on the basis of test results with hundreds

of human subjects in many laboratories across the world, and indeed there is no physical reason to anticipate such effects. But there is a safety issue at high magnetic field, for which the MRI industry has yet to develop standard procedures. The pulses of radio-frequency electromagnetic energy, intrinsic to the formation of MR images, can in principle heat the tissue. The careful safeguards set in place by MRI scanner manufacturers must be supplemented at high field strength by electromagnetic field calculations providing detailed limits to safe scanner operation. Such calculations can also guide strategies for the most efficient scanning techniques. The Department of Neurophysics thus includes expertise in radio-frequency modelling and hardware.

Radio frequency laboratory development

4.3.1

The main instruments used for magnetic resonance imaging (MRI) coil development, and multi-channel radio frequency (RF) transmit/receiver array design and investigation, comprise a network analyzer, a vector signal generator, a multi channel arbitrary waveform generator, a powerful oscilloscope, and a spectrum analyzer. Development of optimized MRI transmit and/or receive arrays (including single channel coil) entails: a) measurement and optimization of coil properties such as central frequency, Q factor, coupling, etc.; b) investigation of the stability of coil properties versus delivered power, temperature, scanner gradient switching, etc.; c) detailed investigation of multi-channel coil behaviour when RF pulses are combined; d) noise source investigation, including noise figure measurement of each stage; and e) RF shimming.

Thus the following technical capabilities are required: a) simultaneous multi-channel measurement of RF signals,

with high dynamic range and wide real-time bandwidth; b) arbitrary multi-channel RF signal generation, also with high dynamic range and wide real-time bandwidth; c) real-time simultaneous multi-tone (both single ended and differential) S parameter measurement; and d) vector signal design and analysis.

Instruments supplied by leading manufacturers appear at first glance to meet most of these requirements. However, preliminary tests of these devices showed that some required features are not included in the standard product delivery. For example, the network analyzer should have a) 16 channel phase-locked receivers with up to 15 MHz bandwidth; b) 8 channel high/low power S parameter measurement set-up, and c) four-tone simultaneous measurement to study the multi-channel coils using RF pulses. After direct negotiations with major manufacturers, one of them (R&S) offered a solution, taking the form of a collaboration contract between our laboratory and

R&S. Within this collaboration R&S will update hardware and software of the existing ZVT-8 network analyzer to the required specifications, and provide technical sup-

port for successful development of the software for the four tone measurement that will be done by our laboratory.

4.3.2 Radiofrequency coil design, optimization and safe operation at 7T

The goal of this project is to implement a robust and efficient strategy for optimized design of multichannel RF coil arrays at frequencies of 100, 200 and 300 MHz, in order to gain the best possible B1 homogeneity with simultaneous reduction of Specific Absorption Rate (SAR). To guarantee safe MRI scanning at 7T it is necessary to have excellent control of SAR. We have begun to investigate SAR dependence on head size and position, SAR effects of broken coil capacitances or cross element short circuits, and SAR dependence on indirect factors like coil temperature, or shock waves due to gradient switching, etc.

Before purchasing the equipment we analyzed commercially available solutions for computer aided RF system designs. Despite the fact that computer power and memory have increased significantly over the last few years, available 3D electromagnetic field simulation software packages still do not allow treatment of complete design problems that include complex RF circuits (power amplifier, RF cable, etc), and they are by no means optimal for coil tuning and impedance matching procedures. We have found that much faster and more reliable results can be obtained by performing a step by step combina-

tion of results from an RF circuit simulation (for example Agilent Advanced Design System) with data from a 3D electromagnetic field simulation software package. The 'S-Parameters' data output of such software constitutes the initial conditions for coil tuning and impedance matching that are performed by the RF circuit simulator. Then the tuned and matched RF circuit data becomes the source for accurate 3D simulation of the electrical and magnetic field profile of each coil. The data produced by the step that optimizes RF field uniformity ('B1 shimming'), which at present cannot be performed by available 3D simulators, become the source for B1 and SAR profile simulations as well as recalculation of the final circuit, offering very important information regarding the dependence of B1 and SAR on the power delivered by each RF channel. It should be noted that this recalculation of the final circuit provides information for coil decoupling, as required for transmit array excitation, which can be checked by measurement equipment. No visible difference between measured and simulated data is a guarantee for operational safety, since this demonstrates that the behaviour of the complete RF MRI scanner subsystem is properly understood.

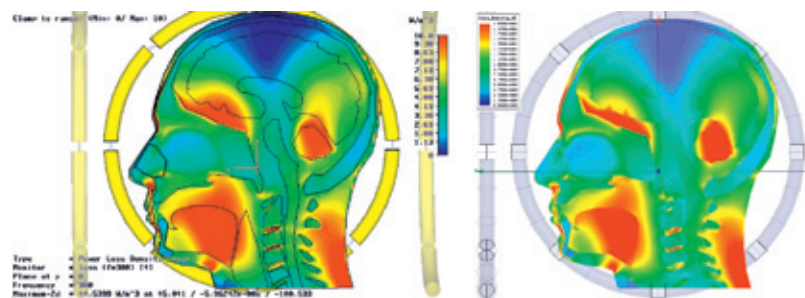


Figure 4.3.2 Simulated power loss density for ANSOFT head model. Left: time domain solution, right: frequency domain solution. Note differences in ventral brain areas and cerebellum.

4.3.3 Progress and problems in the 3D simulation of multichannel transmit/receive array properties

The advantages and limitations of different methods - the finite difference time domain (FDTD) and the finite-element method (FEM) - for electromagnetic analysis were investigated.

To obtain reliable 3D simulation results by any 3D solver requires a realistic body/head model. The 'Hugo' and

Ansoft human body models as well as the 'SAM' phantom model were used for our calculation. The SAM (standard anthropomorphic model) model, specified by and for IEEE/IEC/CENELEC standards, includes only two tissues: inner (homogeneous glycol-containing tissue-simulant liquid), and outer (material with skin-like properties). The

SAM model can be used for both (FDTD and FEM) solvers, and in most cases it gives an easy and fast simulation. Our results show that using the SAM (or scaled version of SAM) phantom is a good approach for initial coil design, and helps in evaluation of array performance for variations in loading (differences in head size and position inside the array). We developed a method for scaling the Hugo model geometrically for the FDTD solver, and we performed simulations for a set of scaled Hugo models with ratios 1.2 to 0.8. It is not clear, however, that a simple geometrical scaling provides a realistic representation of human heads with different sizes.

It is generally possible to scale a model as input to the Ansoft FEM solver. However, only the latest release of the solver is expected to perform such an operation with a human model without increased error during the model meshing stage. In addition, a more powerful workstation (with 64 GB memory and 8 processor cores) will be required to allow use of a high resolution human brain model.

Standard B1 shimming includes two steps – simulation of B1/SAR profiles, followed by tuning the amplitude and phase of each source in order to meet the goal.

Both CST and HFSS solvers perform the first step well, but neither solver offers built-in field optimization by variation of port source power and phase. This should be no

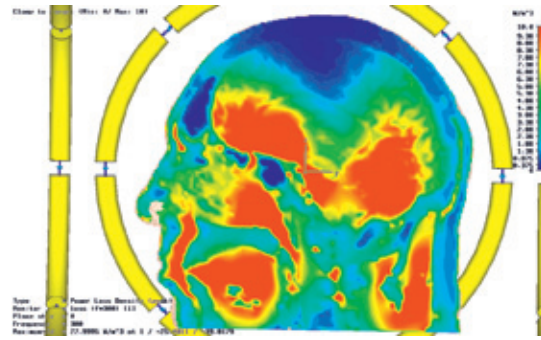


Figure 4.3.3 Use of Hugo model of human head in estimating rf specific absorption rate (SAR)

problem in principle, because such optimization could be done using third party software, for example Matlab scripts. However, lack of fast data export to a binary file, or directly to another application like Matlab, currently presents an insuperable problem, preventing use of third party software in conjunction with these solvers.

Another open question is the frequency dependence of tissue properties required for defining the Hugo model. When using the time domain solver, the existing default definition of constant tissue properties is not realistic if the simulation is performed over the rather wide frequency band necessary for multi nuclear magnetic resonance imaging experiments.

Simulation of the effect of tissue anisotropy on SAR and B1

4.3.4

Another of our research activities is to study the influence of tissue anisotropy on SAR and B1 values. To begin with we used a simple model - an anisotropic tissue insert, of various dimensions, that was placed inside a single tissue of cubic shape, or a SAM phantom with isotropic electromagnetic properties. Different types of tissue anisotropy were investigated – anisotropy only of electrical conductivity, only relative permittivity, and both electrical conductivity and relative permittivity. As a reference, we performed simulations of isotropic tissue inserts, whose electrical conductivity and relative permittivity were set to the maximum or minimum value of the corresponding anisotropic insert. The results for single coil excitation showed a significant influence of tissue anisotropy on SAR, but rather weak dependence of B1 maps for small inserts. As expected the effect is stronger if the tissue anisotropy axis is parallel to the electrical field. Unfortunately at present it is impossible to simulate a complex anisotropic object, such as the human brain, because with the CST software anisotropy cannot be locally defined, and with HFSS such a complex brain model cannot even be specified.

Once the problem of getting raw field data from both solvers has been solved, further analysis of the fields involved in RF array excitation can be performed.

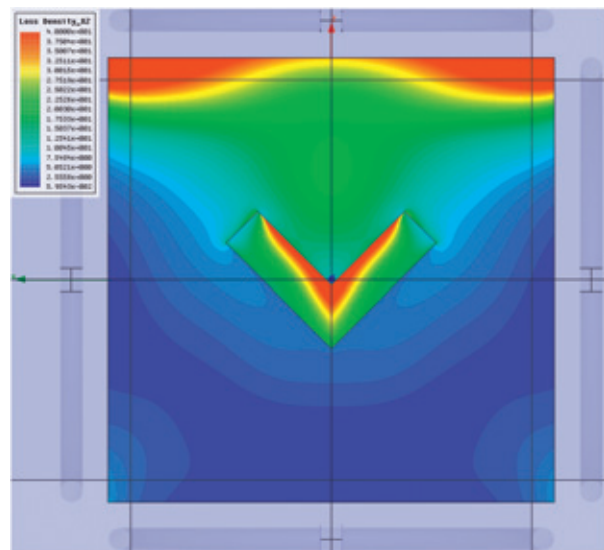


Figure 4.3.4 Modelled effects of anisotropy of conductivity and dielectric constant on rf power absorption.

4.3.5 Construction and testing of a realistic head phantom for assessment of radiofrequency power deposition in MRI

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One of the difficulties of getting high quality images in high-field MRI is the inhomogeneity of the RF field inside physiological samples. In addition since the RF field intensity distribution in a sample depends on the geometry and electrical properties of the coil-sample configuration, there is the possibility that, even if the overall power distribution may be weak, the power absorption of the tissue becomes locally excessive like you can see in our experimental and computational simulations (Fig. 4.3.5.1-3). Therefore, for safety reasons it is extremely important to establish some realistic experimental evaluation method for the measurement of the specific absorption rate (SAR), a value that is directly proportional to the temperature rise in the examined sample.

The SAR depends on the interaction of the electromagnetic radiation with the human tissue and it holds $SAR \propto E^2$. With our MRI scanner it is possible to measure the B1-Field distribution inside a sample. This can be converted computationally into the locally different strengths of the electric field, which lead us to the SAR and therefore give us some information about the temperature increase in certain regions in the head. Because a measurement at the living subject for the verification of simulated RF-field distributions inside the human head might be harmful to the patient, a realistic phantom is required. In general MRI phantoms play an important role in the calibration and design of MRI equipment. Many phantoms have already been constructed, either having realistic electrical properties like electrical permittivity and conductivity (Kato, Kuroda, Yoshimura, Yoshida, Hanamoto, Kawasaki

et al., 2005, Medical Physics, 32, 3199-3208), or having a shape close to the human anatomy (Shmueli, Thomas, & Ordidge, 2007, J Mag Res Imag, 26, 202-207).

We need a phantom that resembles the original in all of these aspects. This means that we want to implement various materials that represent the different kinds of tissues and also take into account the air spaces at the anatomically correct positions. Acquiring results more precise than our preliminary experimental simulations would help to better anticipate the effects of the electromagnetic radiation on the examined subject.

Other methods for a precise temperature mapping use the temperature dependence of various NMR parameters like the strong chemical shift dependence of TmDOTMA on temperature. We also want to use one of these methods to directly measure the temperature increase in our phantom.

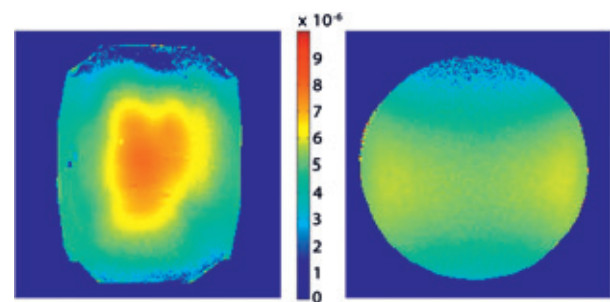


Figure 4.3.5.1 (left) Measured phase map of a phantom consisting of a conductive core and non conductive fluid around; (right) Phase map of a uniformly conductive phantom

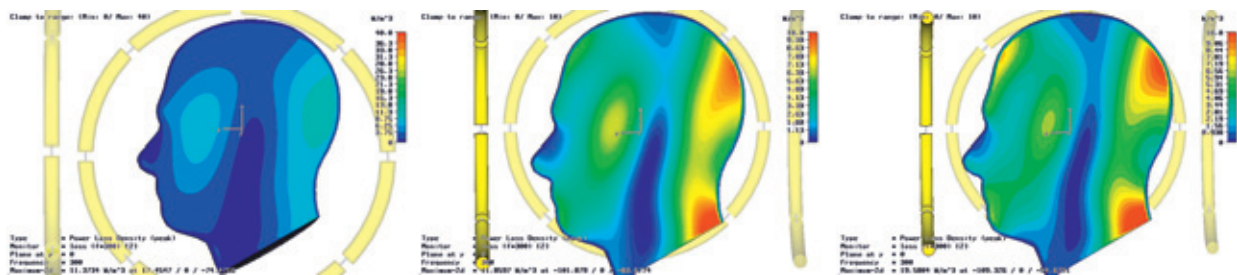


Figure 4.3.5.2 Simulated B1-Field maps of two-tissue head phantoms of different sizes; (left) small; (middle) normal; (right) large

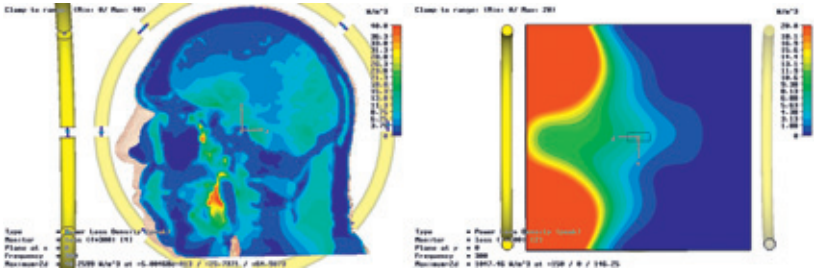


Figure 4.3.5.3 (left) Simulated B1-Field map of a realistic head phantom (HUGO); (right) simulated B1-Field map of a uniformly conductive cubic model

Evaluation of image statistical analysis tools

4.4

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A number of well-established software packages capable of performing functional imaging data analysis have been developed over the years. To date, many of these have originated from either the UK or USA. Statistical Parametric Mapping (SPM) for instance, a product of the Functional Imaging Laboratory in London, United Kingdom (<http://www.fil.ion.ucl.ac.uk/spm>), was first released in 1994, and has become increasingly popular across the neuroimaging community ever since. FSL (FMRIB’s Software Library - Oxford, United Kingdom (<http://www.fmrib.ox.ac.uk/fsl>)) has also been gaining recognition over the years, as have the AFNI, MEDx and FreeSurfer packages (all US-based), and BrainVoyager from the Netherlands. The Institute’s own in-house software, LIPSIA (Leipzig Image Processing and Statistical Inference), is perhaps less well-known, and so the aim of this study is to evaluate its merits, and to compare them with those of the other, more conventional packages.

We began by comparing the statistical approaches adopted in SPM, FSL and LIPSIA, using the visuo-auditory dataset acquired at Oxford and displayed on the FSL website (standard box-car design, visual: 30 s epochs, auditory: 45 s epochs, 21 slices, 180 timesteps, TR 3 s).

(Area: V1)	SPM 5	FSL 3.3	LIPSIA 1.3 <i>whitening</i>	LIPSIA 1.3 <i>coloring</i>
Max t-value	13.9	14.0	16.3	21.6
Coordinates of max t-value	4 -97 15	4 -97 18	7 -97 14	7 -97 14
Computational time (s)	46	70	7 <i>per contrast</i>	1

Table 4.4.1 Audiovisual paradigm. A further statistical comparison of the results obtained from these packages

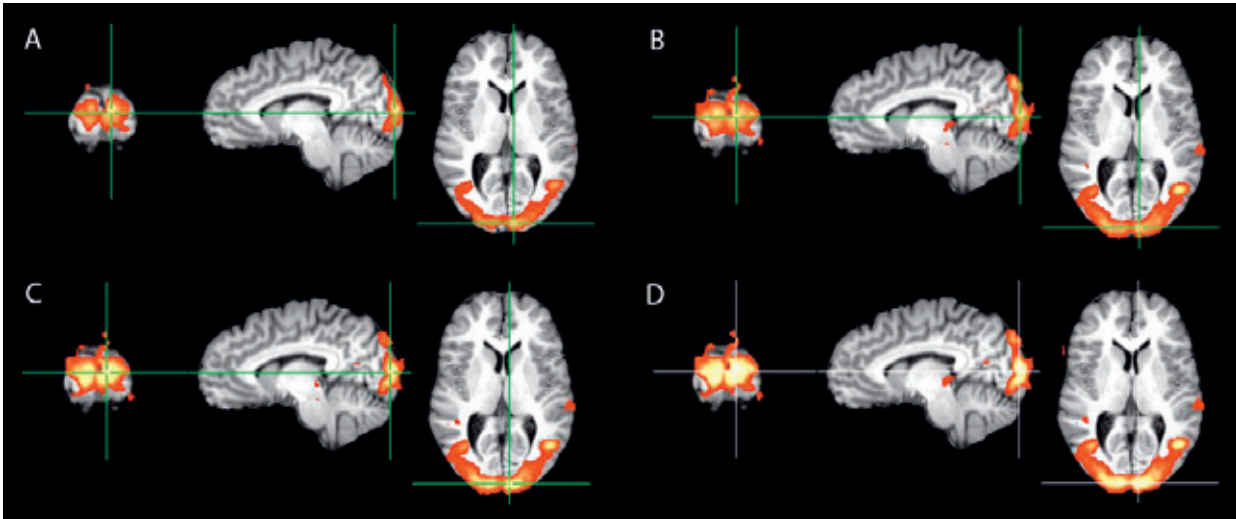


Figure 4.4.1 Audiovisual paradigm. Uncorrected t-maps obtained using (A) SPM 5, (B) FSL 3.3, (C) & (D) LIPSIA 1.3 (whitening) & (colouring)

We first pre-processed the dataset in FSL, and then statistically evaluated this preprocessed data in SPM, FSL and LIPSIA to compare the (uncorrected) t-values obtained by each (Fig. 4.4.1, Table 4.4.1).

Additionally we compared the results from a second data set, which used an event-related design with standard STROOP paradigm, acquired on our own 3 T Bruker system (Fig. 4.4.2, Table 4.4.2). From both sets of results, it is clearly evident that LIPSIA has the shortest computational time, and that all three packages produced similar (overlapping) activation sites.

(Area: Insula)	SPM 5	FSL 3.3	LIPSIA 1.3 <i>whitening</i>	LIPSIA 1.3 <i>colouring</i>
Max t-value	4.77	4.41	4.94	4.73
Coordinates of max t-value	-35 15 9	-35 15 9	-41 18 12	-38 15 9
Computational time (s)	210	1234	19 <i>per contrast</i>	8

Table 4.4.2 STROOP paradigm: A further statistical comparison of the results obtained from these packages

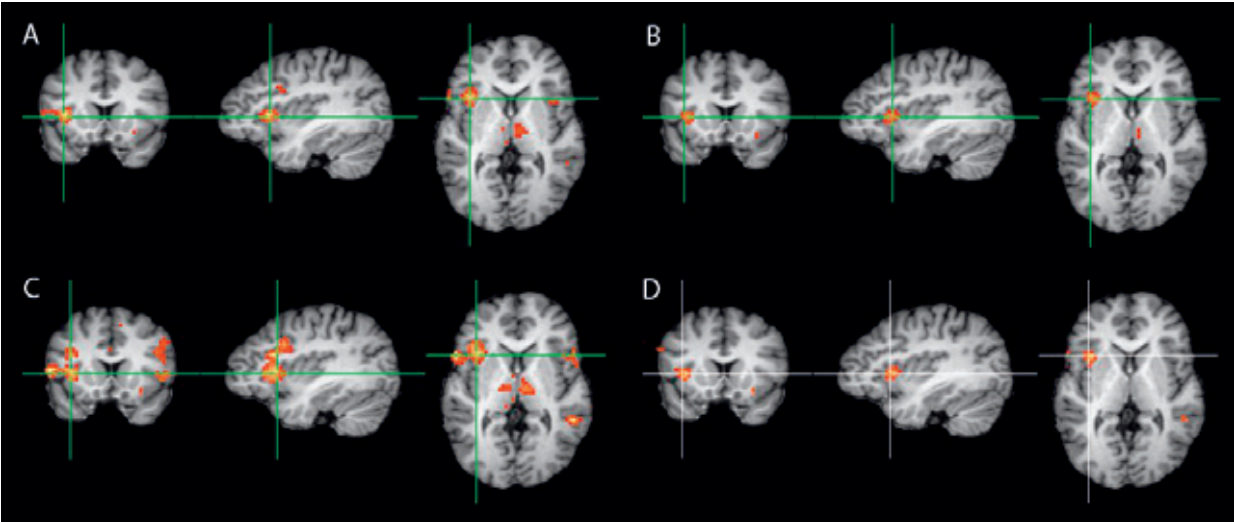


Figure 4.4.2 STROOP paradigm: Uncorrected t-maps obtained using (A) SPM 5, (B) FSL 3.3, (C) & (D) LIPSIA 1.3 (whitening) & (colouring)

4.5 Development of a deformable net for human cortical parcellation

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The extraction and reconstruction of the cerebral cortex surface based on magnetic resonance images of the brain has been a focus of research for many years. Since changes in neural activity are commonly localized in the neocortex, and a strong correlation between anatomy and function is a well accepted fact in neuroscience, there are several purposes which make an accurate segmentation of this part of the brain especially interesting. The widespread applications for surface representations of the cortex include non-voxel-based visualization techniques, inverse solutions for MEG or EEG signal localization, anatomical and morphometric studies, and the use of spherical or flat-map coordinate systems for fMRI or other analyses.

The identification of the cortical borders in three-dimensional images is in principle a problem of shape fitting, and has been intensively examined by the image analysis community. Starting with approaches using manual delineation in slices, up to algorithms extracting the inner, centre and outer cortical surface in one step, a huge number of diverse techniques has been developed over the years. The base for all of these was the fundamental work of Kaas, Witkin and Terzopoulos (1988, Intern J Comp Vision, 1, 321-331), which deals with deformable models. Such models describe the behaviour and interaction of objects based on partial differential equations (PDEs) expressing inner and outer forces as well as external constraints. These PDEs are then iteratively solved.

Initially deformable models were used for physical simulations and contour fitting. However one can model the behaviour of an object inside an image using the external constraints as an expression of local image information, it was quickly recognized that deformable models can be used for image segmentation and pattern recognition, and are thus applicable to a variety of computational problems. In general the techniques for brain surface reconstruction can be separated into two main branches of deformable models.

The first branch deals with parametric representation of the cortical surface, such as polygonal meshes, and solves the deformable model PDEs based on this parametric representation to give what are known as parametric deformable models (PDM). As a discrete, parametric representation of the developing surface is given, the spatial differentials in the PDEs can be approximated using differences while temporal differentials are transformed to iterative computation using small time steps. The main advantage of this method of solving deformable models is that it is intuitive and relatively easy to understand. Unfortunately PDMs are known to be computationally intensive especially when topology merging or avoiding of self-intersection are required. Although special data structures and algorithms help to reduce computation time, and although algorithms for topology correction in voxel space as well on polygonal representations can guarantee spherical topology, PDMs remain relatively time-consuming, which makes most widely available extraction tools (e.g. Freesurfer) inappropriate for high-resolution images.

A reasonable alternative to PDMs are the so-called geometric deformable models (GDMs). Best known example is the Level Set Method (LSM) introduced by Osher and Sethian in 1988. A propagating front (the developing surface) is represented as the zero level set of a function in space and solved over time or stationary. As the propagation of the front can be modelled by an intrinsic balloon-like force controlled by curvature as well as additional forces derived from image features the LSM is very flexible and can be applied to various types of images and even diffusion tensor imaging (DTI) data. Although the ability to change topology during development was one of the advantages of LSMs in general use in image analysis, this effect is unwanted in cases where the correct topology of the object (the cortex) is already known. Therefore topology preserving versions of the algorithm have been introduced by Han and co-workers in 2001 and extended by Ségonne and others to keep the spherical topology of the initialization unchanged until convergence at the demanded cortical surface. The LSM also

benefits from easy numerical implementation and quick computation times.

Based on earlier experiences in implementing a PDM related to the Freesurfer approach, our current work deals with a highly parallelized implementation of the Level Set Method using well-known speed-up techniques, such as the narrow band approach with Fast Marching Method for Reinitialization of the level set function, to reduce computation time as far as possible, and techniques such as the Gradient Vector Flow to provide precision and rapid convergence. This allows for construction of accurate representations of inner and outer cortical surfaces in only a few minutes, even for very high resolution image matrices.

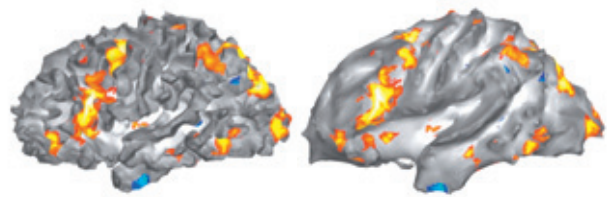


Figure 4.5 Reconstructed and inflated white matter surface with superimposed fMRI data

Once such surfaces have been determined, many further developments become possible. The improved spatial resolution of our projected 7T data can be used for more precise detection of morphometric variation across groups or within subject over time, using approaches well known from Thompson et al. Additionally, Yu (Yu, Grant, Qi, Han, Ségonne, Pienaar et. al., 2007, IEEE Trans Med Imag, 26, 582-597) recently reported a technique for analysing surface morphometry using spherical wavelets, which could provide further information about cortical structure and development.

Earlier cortical thickness measurements will be improved with the use of higher resolution data, and can be explored using novel analysis techniques such as small anatomical networks. Thickness can also serve as one of the variables used for local classification of cortical areas. Another interesting goal will be to use the reconstructed cortical surfaces to compute polar coordinates using an inflated version mapped to the sphere. These can then be used for surface-based fMRI studies which are known to provide increased statistical power (Fischl, Sereno, Tootell, & Dale, 1999, Human Brain Mapping, 8, 272-284).

4.6 MRI anatomical segmentation and connectivity of human amygdala

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The aim of the following study is to parcellate the amygdala in vivo, to distinguish non-invasively the nuclei of the amygdala, and to trace their connections to the rest of the brain, using different MRI techniques at 7T. This will employ the following techniques: Diffusion Tensor Imaging (DTI) mapping fibre directions to examine the

connectivity of different regions in the brain, diffusion-weighted imaging (DWI) producing images of biological tissues weighted with the local characteristics of water diffusion, and high resolution T1 and T2 weighted structural MRI. Previous histological work using cadaver brain has established the following structures.

Basolateral Complex	Cortical Complex	Centro Medial Complex
Lateral Nucleus - Dorsolateral - Ventrolateral - Medial	Bed Nucleus of Accessory Olfactory tract Nucleus of Lateral Olfactory Tract	Central Nucleus - Capsular Subdivision - Lateral and medial Subdivision - Intermediate Subdivision
Basolateral Nucleus - Rostral Magnocellular subdiv. - Caudal Intermediate - Parvicellular subdivision	Anterior and Posterior Cortical Nucleus	Centro Medial - Rostral - Central - Caudal
Accessory Basal Nucleus - Magnocellular Subdivision - Intermediate Subdivision - Parvicellular Subdivision	Peryamygdaloid Cortex - Peryamygdaloid Cortex - Medial Division - Sulcal division	Bed Nucleus of Stria Terminalis

Table 4.6 The amygdala is divided into three main areas, further subdivided into substructures

There is a final group of nuclei comprising the remaining amygdala areas: the anterior amygdala area, the amygdalo-hippocampal area (the most caudal of the amygdaloid nuclei, comprised of the medial and lateral subdivisions), and the intercalated nuclei, small groups of neurons found in clusters within the fibre bundles that separate the different amygdaloid nuclei. Based on the known connections of the amygdala an extended amygdala can be defined in which the centromedial amygdala is extended rostrally and medially, since the amygdala innervates the bed nucleus of stria terminalis and the caudodorsal regions of the substantia innominata (ventral pallidum). Furthermore, these two regions have similar efferent connections to the descending projections of the amygdala, and thus can be regarded as part of the amygdaloid complex. There is also a functionally based classification in which basolateral nuclei constitute the frontotemporal group, the centromedial nuclei form the autonomic group, and the cortical nuclei constitute the olfactory group.

Multiple afferent and efferent connections have been determined which join not just the main structures but

also specific substructures and subdivisions. Inputs can be classified into two major groups. The first set of inputs arise in cortical and thalamic structures, which supply information from sensory areas and memory system structures. These inputs can be divided into those that relay modality-specific sensory information, those that are polymodal, and those arising in the medial temporal lobe memory system. The second group of inputs are those arising in the hypothalamus or brain stem, connections of the amygdala with regions involved in behaviour and autonomic systems.

Afferent and efferent connections can both be clustered into sensory connections and polymodal connections. Inside the sensory complex are found olfactory inputs, arising from the main and accessory olfactory bulbs, as well as from the primary olfactory cortex, in this last case reciprocal with the cortical amygdaloid complex. For somatosensory inputs few projections arise directly from primary somatosensory areas, most afferents reach the amygdala via the dysgranular parietal insular cortex, via the pontine parabrachial nucleus and thalamic nuclei, the medial portion of the medial geniculate and the

posterior internuclear nucleus, this last nucleus involved in nociceptive information. Gustatory and visceral primary areas provide strong projections, and projections also arrive from posteromedial ventral thalamic nucleus and from the parabrachial nucleus. Auditory and visual information also reach the amygdala, from association areas rather than primary cortex. These pathways are particularly relevant during fear conditioning. For auditory information, area Te1 has no direct projections and the amygdala also has inputs arising from the thalamic medial geniculate nucleus. Visual cortical projections also originate from thalamic areas. Among polymodal input regions are found prefrontal cortex, the perirhinal and entorhinal cortex, parahippocampal cortex, hippocampus and ventrolateral medulla, all of them with reciprocal connections.

As a first step for amygdaloid nuclei segmentation we used diffusion data to provide a segmentation of amygdaloid nuclei, by means of a surprising apparent clustering of fibre directions. Diffusion Tensor Imaging is an MRI technique that measures the diffusion anisotropy of water molecules. We first extracted the amygdala from each subject's structural image, using the automatic segmentation tool in the software package Freesurfer. Each volume was then used as an individual mask to restrict the region of interest. Using VISTA software, every standard amygdala mask was superimposed on every individual

image containing the subject's fibre orientation information, and then these two images were also superimposed on maps colour-coded for vector orientation. This resulted in an amygdala shape for each individual, which could be observed to contain an apparent clustering of fibre orientations, indicated by grouping of voxels of different colours. For purposes of analysis and display, this grouping was manually accentuated using a subjective four-colour classification. We repeated this procedure with data from 5 subjects. We found four main structures consistently across subjects, forming a reasonable representation of the main amygdaloid nuclei: the basolateral complex, labelled in blue, the corticomedial complex in red, the cortico-rostral-ventral complex in green and the central-rostral complex labelled in pink (Fig. 4.6). These structures have a similarity to the probabilistic maps based on cytoarchitectonic data in which the corticomedial complex represents the superficial complex and the cortico-rostral-ventral complex represents the centromedial one. In all subjects we also found four smaller subdivisions. Adjacent to the basolateral complex we found a substructure (labelled in light blue), for the centromedial complex, a further substructure (labelled in orange), and similarly for the cortico-rostral-ventral complex (dark green) and the central-rostral complex (violet). These latter could possibly be identified as intercalated nuclei, which are small groups of neurons found in clusters within the fibre bundles that separate the different amygdaloid nuclei.

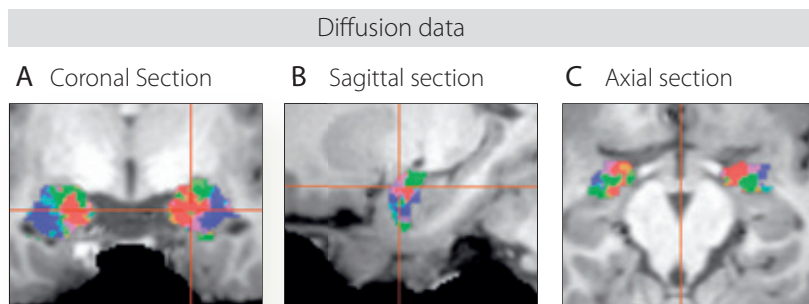


Figure 4.6 Diffusion data. The amygdala is divided into four different nuclei based on the direction of the principal eigenvector of the diffusivity tensor. (A) Coronal section of the human brain. (B) Sagittal section. (C) Axial section.

A unified approach for handling medical image data

4.7

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When working with different systems for generating, processing and analysing medical images, one problem arises immediately. There is a wide diversity of image data formats, and the available import and export features of any toolkit usually support only a subset of the needed formats. We describe an approach to design a unified and easily extensible interface for medical image data. Implemented in a function library, this interface can

be used efficiently to enable custom-built applications to read and write medical image data.

The Protocol-Data-Map

Unified access to diverse data formats implies a common access interface. Thus a data structure is required which provides a superset of all features of all data formats to be supported. Every medical image consists of image data, obtained in some specific modality, and metadata

related to this image data. This data pair will be discussed in the following.

The metadata which belong to an image usually describe its technical and administrative characteristics. They consist of some required information like image dimension and used data type, some common information such as the age of the subject or the date the image was taken, and some technical information regarding image acquisition such as field strength and MRI sequence used. These parameters are either in a header inside the image file or in a separate header file. The required and the common parameter are very useful to distinguish images. They, and with them the whole metadataset, can be used as a unique key to reference this image. In the following this parameter set will be called the protocol.

The actual data set of an N-dimensional image provides a value in a certain data type (float, byte, etc) for every pixel or voxel of the image. These data are usually stored binary in a one-dimensional array according to the following formula.

$$I = C_1 + C_2 S_1 + \dots + C_N \prod_{i=1}^{N-1} (S_i) \quad (4.7)$$

where $S_1, \dots, S_N$ describes the size of the image and $C_1, \dots, C_N$ is the N-dimensional vector pointing to the voxel whose value is stored at the index i in the one-dimensional array. The type of voxel data, the voxel representation, the number of dimensions (N) and the image size ($S_1, \dots, S_N$) need to be specified in the protocol for this image.

Some image file formats can only store two-dimensional images at most. In this case N-dimensional datasets are often stored by using stacks of two-dimensional images. The protocols of these images differ only in their coordinates (which need to be specified in this case). The system must recognize this and combine them into one N-dimensional dataset when reading. Conversely, the system must also be able to write N-dimensional data into a file format which does not support that many dimensions.

The pair of protocol and data set can be used as a universal interface to access image data. While the protocol offers all information required to interpret the data, the data set serves as a coordinate-based interface to the data for reading and writing. As the protocol by definition supports the superset of all features of all supported formats, it is assured that no information will be lost during a conversion. This loss can only occur when import-export filters of a particular tool set are used, because commonly at an intermediate stage of the conversion the data are stored in the native format of the tool set, which may not support all the needed features.

Multiple protocol-dataset pairs can efficiently be stored in an associative container where the protocol is the key which maps to the dataset. This enables the system to handle multiple datasets. A particular dataset can always be referenced by its protocol, and a list of the available datasets can be obtained by iterating through this protocol-dataset-map. Also, when reading multiple low-dimensional image files which are part of a high-dimensional image, they will all have the same protocol and will thus be automatically sorted into one high-dimensional dataset referenced by this protocol. This sorting is more robust and flexible than the sorting by filename traditionally used in common tool sets, which often has to rely only on filenames.

Reading and writing different file formats

To guarantee the flexibility of the system, the input from, and the output to, files is done via plug-ins which use the described protocol-dataset map as front end. These plug-ins are gathered at initialization and held in a map with the file suffixes they support as key. If available, they are also referenced by a regular expression to detect the supported format directly from that data.

The selection of the right plug-in is done in two ways. If a file format is directly requested, the corresponding plug-in is used. If the format is not selected explicitly, the system at first tries to get the suffix of the file requested for read or write and guesses the format. Many medical image formats exist in several different dialects or have optional extensions, which makes it necessary to finetune them. Thus every plug-in provides a set of additional parameters which can then be used by the client to modify their behaviour.

Implementation and Status

The algorithm has been implemented in C++, and is currently used as the FileIO module of the odin framework. Its development tree is available at <http://odin.sourceforge.net/>. In contrast with the import/export filters of common tool sets, it can smoothly be used separately for any other application on Linux, Irix, Solaris or Windows. Interface to the client is currently only available for C++ programmes which can simply use the inherent C++ interface and the data structures. These programmes set all parameters in the global parameter list (including plug-in specific parameters), execute a read, and gather their data from the protocol-dataset-map. Alternatively, they can store their data in this map and issue a write to the given file. Bindings to other languages, especially scripting languages, will be available soon via a swig (<http://www.swig.org>) based interface for the three primary interface objects (parameters, read/write and the protocol-dataset-map).

Perfusion imaging at a field strength of 7T

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Perfusion imaging using magnetically labelled water as an endogenous tracer is capable of measuring regional cerebral blood flow. Previous studies at a field strength of 3T were performed using continuous arterial spin labelling (CASL) for tagging the arterial blood. The implementation of two different RF coils for labelling and imaging enabled selective perfusion measurements of the left and right hemisphere, respectively. In Fig. 4.8 quantitative multi-slice perfusion maps of the right hemisphere are shown. For these experiments the labelling coil was placed over the right carotid artery of the subject (Annual Report 2001, Section 2.9.2; Annual Report 2002, Section 2.8.5). Furthermore, perfusion-based functional MRI (fMRI) was performed at 3T utilizing a two-coil CASL approach (Annual Report 2002, Section 2.8.6).

Because the signal-to-noise ratio (SNR) increases with field strength, perfusion measurements at 7T are expected to become more sensitive. This is especially relevant for white matter, where perfusion is two to three times lower than in gray matter. For MR angiography larger intrinsic magnetic field gradients in the vicinity of venous structures and elongated relaxation times at 7T result in a

higher spatial resolution and the possibility of visualizing blood flow dynamics in arterioles. Perfusion measurements using arterial spin labelling may benefit similarly.

At the 7T scanner PASL (pulsed arterial spin labelling) and CASL techniques are being implemented for tagging the arterial blood. For finding an optimized set of parameters for both labelling approaches a software package has been adapted, which was originally developed for simulating the process of the adiabatic inversion used in continuous arterial spin labelling (Annual Report 2003, Section 2.7.4). Acquisition of the perfusion-weighted signal can be realized by means of different pulse sequences. EPI (echo planar imaging) and GRASE (gradient- and spin-echo imaging, see below) are the most promising imaging techniques, and comparisons are taking place under different experimental conditions.

Perfusion-based fMRI at 7T is expected to benefit from higher contrast and better localization of the activated regions due to the increased signal of the capillary bed compared to larger veins. Therefore, fMRI experiments using PASL and CASL are also being performed using the 7T-scanner.

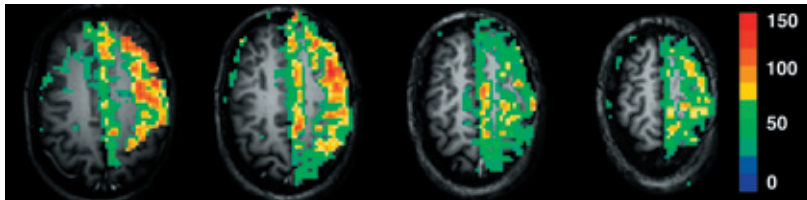


Figure 4.8 Quantitative perfusion maps (in ml/min/100 g) obtained by arterial spin labelling in a healthy subject at 3T.

Novel MRI sequence development at 7T: Parallel, zoomed, spiral

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The aims of this work are to test the current state of the art methods for neuroscientific applications implemented on Siemens MR scanners for operating at 7T, to optimize these methods, and to develop new methods for specific neuroscientific applications. At high field strength, there are five primary field-strength related effects which can diminish the image quality: susceptibility effects, T2* relaxation, T1 relaxation, specific absorp-

tion rate, and increased sensitivity to motion-related and physiological noise components. Each of these high-field related effects can be addressed using a different strategy (e.g. using reduced resolution, prolonged TR, multi-shot sequences, etc.) However, these conventional strategies have the disadvantage that most of them diminish, if not remove entirely, the advantages of operating at the higher field strength. On the other hand there are ap-

plications which will clearly benefit from the high field strength. These applications are in process of being identified, implemented and evaluated.

Three approaches have been identified with significant potential to improve image quality at high-field strength, and utilize at the same time the advantages of a high field strength such as increased SNR or increased spatial resolution and image contrast. These are parallel imaging, zoomed echo-planar imaging, and spiral imaging. Furthermore, arterial spin labeling (ASL) and perfusion territory mapping have been identified as applications which clearly benefit from high field strengths.

These projects can only be realized with a close and direct contact to the software and hardware experts from Siemens Medical Solutions in Erlangen. Dr. Heidemann has been assigned desk space within the Magnetic Resonance Applications Development Department at Siemens, working 75% of his time there, with the remaining time at the Leipzig MPI. In this way he has full access to the Siemens ClearCase archive (sequence and image reconstruction source code), and close contact to the sequence developers, to the ICE experts (image reconstruction group), and to the hardware development groups (gradient coils, RF coils, etc.). He is also able to implement rapidly newly developed sequence code on the 7T scanner in Leipzig.

4.9.1 Parallel imaging

Even though parallel imaging cannot completely solve the difficulties described above, this technique can greatly reduce their effects on image quality, see Fig. 4.9.1.

Here the effective inter-echo spacing can be reduced, which leads to significantly reduced off-resonance distortions. Furthermore, the shortened readout train allows a higher resolution compared to conventional imaging. In diffusion-weighted (DW) MRI, the use of parallel imaging enables a shorter echo time (TE), which directly translates into higher SNR. Thus the use of parallel imaging is mandatory for high-field applications.

The current implementation of parallel imaging has room for improvement. For instance, the long term stability of EPI time series typically used for fMRI can be improved. This can be realized, for example with an advanced pre-scan scheme using a different, more robust, sequence than EPI to acquire the calibration data (necessary for the parallel imaging reconstruction) in front of the actual accelerated EPI acquisition. Imaging protocols and parallel imaging reconstruction parameters have to be carefully adapted for higher field strength. For instance, the choice of imaging parameters (TE, BW, Resolution, etc.) in combination

with adoption of the parallel imaging parameters (kernel size, filter settings) can be used to improve the overall image quality of DW EPI (necessary for fibre tracking). There exist numerous methods for parallel imaging, which might outperform the current parallel imaging implementations on the Siemens scanner.

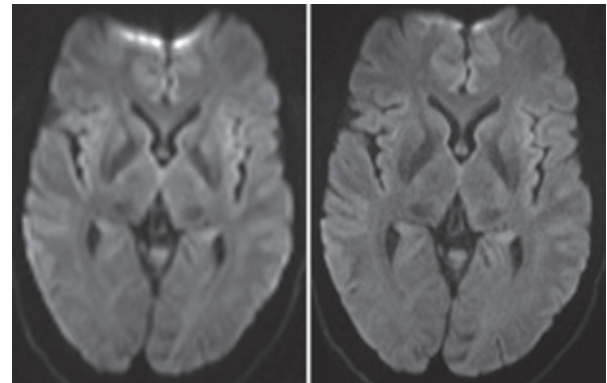


Figure 4.9.1 Diffusion-weighted EPI with $b=1000 \text{ s/mm}^2$ at 3T. The conventional image (left side) shows the typical EPI distortions in the frontal lobe. The use of parallel imaging reduces the distortions and can further be used to increase the resolution.

4.9.2 Zoomed EPI

The Siemens product EPI sequence can be equipped with the so-called zoomed functionality. The zoomed functionality allows one to acquire a reduced FOV without aliasing, even when the object to be imaged is larger than the desired FOV. This is achieved by the use of an asymmetric RF-pulse for outer-volume suppression (OVS). This method enables the acquisition of $T2^*$ weighted EPI series for BOLD fMRI at high field strength with a sub-millimetre resolution. Due to the shortened readout

train, susceptibility effects (mostly visible as distortions) are reduced. A combination of zoomed EPI with parallel imaging will further reduce the distortions, enabling high resolution fMRI examinations of the basal region and the frontal lobe.

The zoomed functionality can further be implemented in the DW-EPI sequence to enable high resolution DWI for tractography.

Spiral imaging

It has been shown that the spiral sequence offers several advantages compared to conventional Cartesian imaging sequences. The spiral sequence samples the k-space data very efficiently. The fast acquisition of the data and the robustness against flow effects are additional advantages. It has been shown in former experiments that the spiral sequence can outperform conventional EPI in terms of long term stability. Further, the sinusoidal gradient waveform is beneficial to reduce the mechanical resonances, i.e. acoustic noise and vibrations. Results obtained with a combination of spiral acquisitions with parallel imaging indicate that the behaviour of residual artifacts arising from the parallel image reconstruction are less degrading in spiral imaging than the respective artifacts in conventional EPI. As a consequence, higher acceleration factors appear to be feasible in spiral imaging. A basic spiral sequence (spiral in without trajectory correction) is being implemented quickly on the MR scanners as a starting point. The next steps are to test the sequence for trajectory errors and to compensate those errors, using for instance trajectory based reconstruction after the acquisition, or short correction gradient pulses during the acquisition.

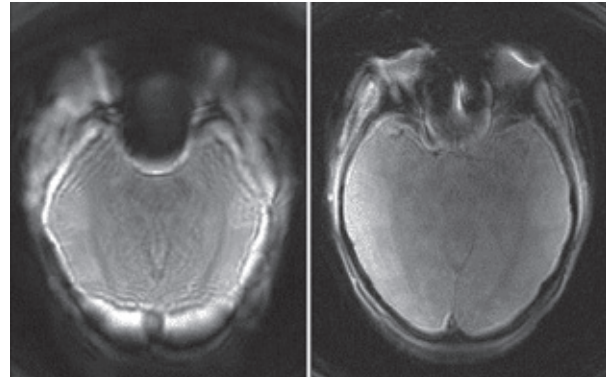


Figure 4.9.3 High resolution ($0.86 \times 0.86 \times 3.5 \text{ mm}^3$) T2* weighted single-shot spiral acquisitions at 3T, acquired with a 32 channel prototype head array. Especially in basal regions of the brain, the conventional single-shot spiral acquisition suffers from severe off-resonance artifacts (left side). The single-shot spiral GRAPPA acquisition with an acceleration factor of eight shows a significantly improved off-resonance behaviour (right side)

Implementation of GRAdient echo and Spin Echo (GRASE) sequences

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A serious problem for scanning at high magnetic fields is the relatively high SAR. This problem is especially severe for sequences that contain a high number of large 180° refocusing pulses, such as Turbo-spin-echo (TSE), which uses a train of up to 17 refocusing pulses per spin excitation. However, the TSE sequence has been shown to provide exceptionally good SNR and image quality, particularly at high static field (Carmichael et al, 2006, Neuroimage, 32, 1176-1184), in contrast with low flip-angle methods, which give progressively lower returns with increasing field strength. One way to circumvent the high SAR problem is to use the GRASE sequence as introduced by Dr. David Feinberg, which substitutes gradient refocusing pulses for a large fraction of the 180° pulses, to provide a kind of hybrid TSE/EPI sequence. Thus the SAR is substantially reduced, while with very careful sequence design it is possible to generate almost exactly the same image quality and SNR. With the help of Dr. David

Feinberg it was possible to arrange a contract between the Neurophysics Department and Dr. Matthias Günther, who worked as a research assistant with Dr. Feinberg during the development of the 3D version of the GRASE sequence. Dr. Günther is engaged in implementing various forms of the GRASE sequence on the 7 T scanner. One version under test is the 3D Turbo-GRASE ASL sequence can use single-shot acquisitions of whole brain to provide real time measurements of cerebral blood flow with good accuracy. This results from the beneficial effects of higher field not only on SNR but also on the ASL signal, due to its dependence on T1, which increases with field strength.

4.10.1 Development of 3D-GRASE-ASL

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Arterial Spin Labelling (ASL) techniques measure blood flow and perfusion without the use of external contrast agents. Instead the inflowing blood is typically labelled by inversion of its longitudinal magnetization in a slab of tissue located upstream from the acquisition region. The ASL sequence is alternated between this labelling phase and a control phase (where no inversion is applied), such that the difference between both images displays only signal from the inflowing blood. The FAIR alternative of this technique (Flow Alternating Inversion Recovery) is displayed in Fig. 4.10.1.1.

The 3D single-shot GRASE sequence is a suitable alternative to EPI for performing ASL measurements, due to its potential for less signal distortion and increased SNR. As such we are currently optimizing this technique for ASL

purposes on our 3T Siemens scanner. A Q2TIPS saturation pulse is applied in the sequence after the FAIR inversion pulse (Fig. 4.10.1.2), so as to limit the length of the bolus and thereby ensure the labelled blood has left the arterial system prior to measurement.

Some of the sequence parameters that were adopted into the GRASE readout train included a 64 x 64 x 26 matrix, 5/8 Fourier encoding, TE 18.58 ms, TR 3000 ms.

Our first aim of the study is to use the sequence to measure the T2 of blood as it circulates around the vasculature, by varying the inflow time, TI. At each TI, a series of ASL images of varying TE can be acquired to calculate the T2 of the blood. Additionally we also investigated varying diffusion weightings (b-values) to optimize the degree of vessel suppression within the images (Fig. 4.10.1.3).

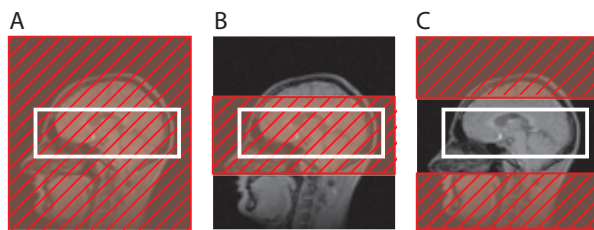


Figure 4.10.1.1 The ASL FAIR technique

(A) a non-selective global inversion pulse is applied in the labelling phase; (B) control phase is acquired with only a selective inversion pulse; (C) only the inflowing blood (both arterial and venous) is present within difference image (everything outside slice-selective inversion region is affected). Imaging slice = white, labelling region = red

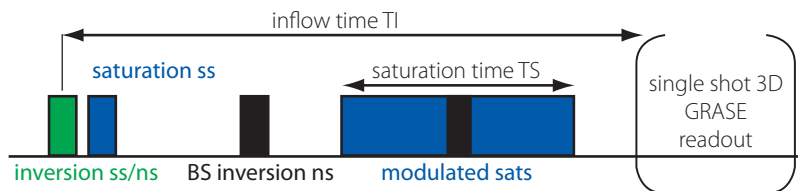


Figure 4.10.1.2 An illustration of the magnetization preparation scheme applied before the conventional 3D GRASE readout

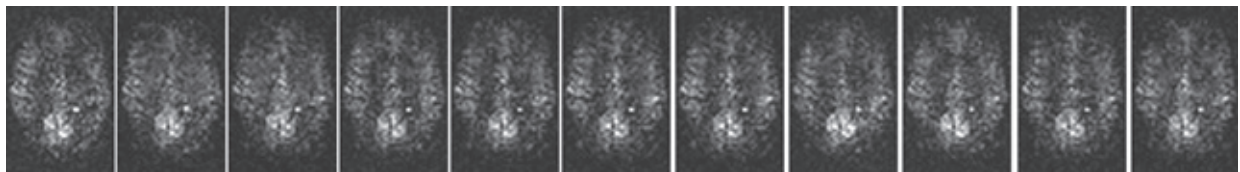


Figure 4.10.1.3 A series of 3D-GRASE-ASL images acquired at different b-values (ranging from 0 to 5000 in steps of 500) to evaluate which degree of diffusion weighting provides the best vessel suppression

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5

Research Groups

Independent Junior Research Group "Neurocognition of Music"

Head

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Senior Researchers and PostDocs

Dr. Ronny Enk (a)

Dr. Daniel Mietchen (*)

PhD Students

Tom Fritz (a)

Julia Grieser

Sebastian Jentschke (a)

Daniela Sammler

Nikolaus Steinbeis

Dr. Katrin Schulze (a) (*) (PhD since 11/2006)

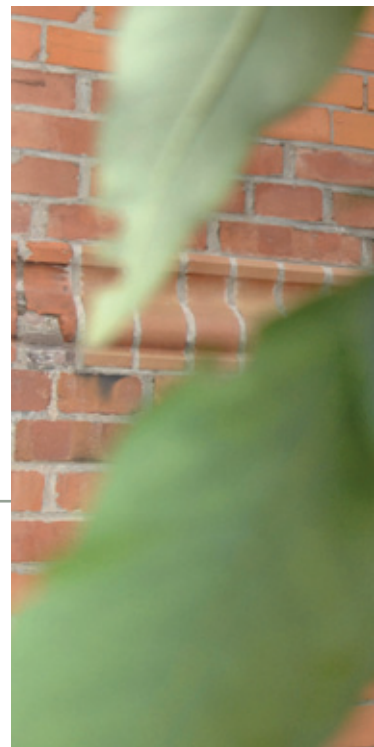
Technical Staff

Sylvia Stasch

Former PhD Students

Dr. Katrin Schulze

Cognition Auditive et Psychoacoustique,
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Independent Research Group "Attention and Awareness"

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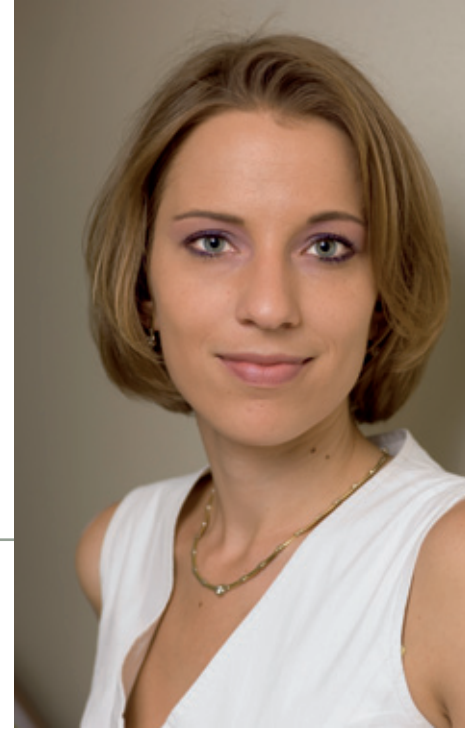
Katja Brüning

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(a) German Research Foundation (DFG)
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5.1

Independent Junior Research Group “Neurocognition of Music”

During the last years, our “Neurocognition of Music” group has increasingly investigated emotion with music. Thomas Fritz conducted a field study in Northern Cameroon (with a solar panel and a Laptop in his backpack), in which he discovered that emotional expressions of Western music such as happy, sad, and fearful, can be universally recognized (5.1.1). His data also revealed that the preference for consonance over highly dissonant music is not specific to Western listeners, because even listeners who had never heard Western music before rated permanently dissonant music as less pleasant than consonant music. With our fMRI in Leipzig, we found that such musical stimuli activate different aspects of the amygdala, revealing that different structures of the amygdala are involved in the processing of pleasant and unpleasant emotion (5.1.2).

In cooperation with the Department of Neuropsychology, we investigated developmental aspects and influences of musical training on language processing in children. These studies showed that neurophysiological substrates of (syntactic) language processing are earlier, and more strongly developed in children with music training (5.1.3). Fascinatingly, we additionally found that children with specific language impairment also have difficulties in processing musical structure, suggesting that musical training provides a new avenue to the treatment of, and perhaps even to the prevention of language disorders in children. Transfer effects from musical skills to linguistic skills are presumably due to the overlap of neural

resources of music and language processing. The assumption of such shared neural resources is supported by findings that patients with brain damage in areas supporting language processing also show differences in music processing, as compared to normal controls (5.1.4). Interestingly, the processing of musical structure appears to share neural resources with the processing of semantic aspects in language, suggesting a link between structure and semantics in music (5.1.5). Also, data collected with fMRI suggest that representations of the meaning of sounds are located in temporal regions along the superior temporal sulcus.

Another large project investigated Working Memory functions for phonemes and tones with fMRI, this project also aimed at investigating possible effects of musical training on verbal Working Memory (5.1.6). Executive functions were also investigated in a project on music production, conducted in cooperation with the Department of Psychology (5.1.7). This study provides the first ERP insight into action-related processes observed while individuals play a musical instrument. The results revealed that when an error occurs during playing, the brain is often aware of such an error – even before this error is actually performed. This project was of particular importance for our group, because it was one of the first leading us into the new territory of music production.

Universals of emotion in music

5.1.1

Fritz, T.¹, Jentschke, S.¹, Gosselin, N.², Sammler, D.¹, Peretz, I.², Friederici, A.D.¹, & Koelsch, S.^{1,3}

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It has long been debated which aspects of music perception are universal and which are developed only after exposure to a specific musical culture. Unfortunately, due to the progressing globalization, opportunities for intercultural comparisons between individuals exposed to completely incongruent music cultures are becoming increasingly rare. Here we performed a cross-cultural study with participants from a native African population (Mafa) and Western participants, both groups naïve to the music of the respective other culture. In one experiment we used a selection of Western music piano pieces specifically designed to express happy, sad, or scary emotion. Results showed that these expressions could clearly be decoded by the Mafa listeners, although less reliably than by Western listeners (Fig. 5.1.1). This demonstrates that a variety of emotional expressions coded in the Western music excerpts can be recognized universally, and that music is a means for the communication of emotional expression inherent to all humans.

Another experiment compared ratings of emotional valence between consonant Western musical pieces, and permanently dissonant counterparts of these pieces. The results showed that the Mafa listeners showed a prefer-

ence for the consonant over the permanently dissonant pieces which was significant, although not as strong as in Western listeners. This shows that preference for rather consonant over highly dissonant acoustic signals is a universal human trait, and that this preference can also be heavily shaped by cultural imprinting.

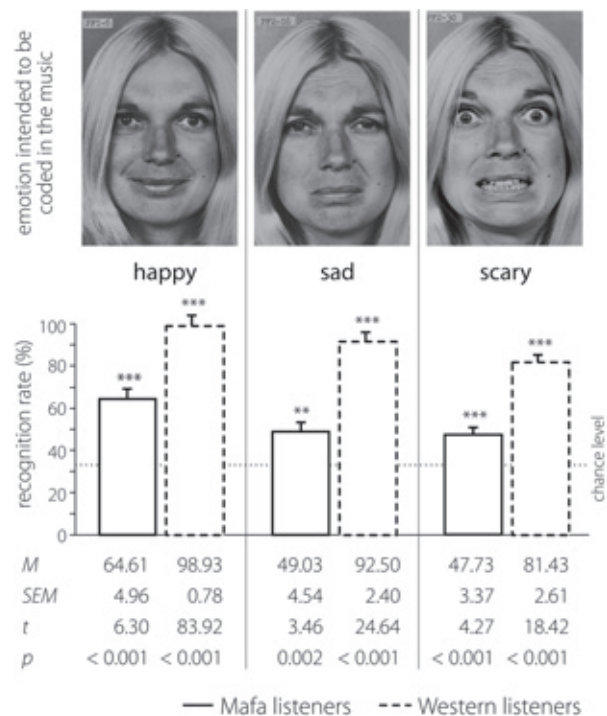


Figure 5.1.1 The figure shows the mean performance (M) in percent for the recognition of each emotional expression (***) $p < 0.001$, ** $p < 0.05$) in Western music excerpts, standard error (SEM), t-values (df = 21 for the Mafa listeners and df = 19 for the Western listeners), and p-values.

To please, or not to please: The amygdala differentiates in an early stage of music perception.

5.1.2

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It is widely believed that the amygdala deals only with unpleasant emotional experience. This idea largely derives from the history of emotion research in neuroscience, where unpleasant emotions such as fear and stress have been easier to operationalize in animal experiments. Recent evidence of amygdala function, however, indicates that it plays a more important role for the processing of stimuli with positive valence than formerly believed. This study investigated amygdala activity during

emotional responses to both pleasant and unpleasant musical stimuli. Functional magnetic resonance imaging (fMRI) showed that two separate amygdala sub-regions are involved in the response to stimuli of positive and negative valence (Fig. 5.1.2): Activity within a central aspect of the amygdala correlated with increasing unpleasantness of participants, whereas activity within a dorsal aspect of the amygdala increased with increasing pleasantness.

Functional connectivity analysis revealed that each of these sub-regions behaves synchronously with a corresponding valence-specific network: A network comprising the hippocampus, the parahippocampal gyrus, and the temporal poles was functionally connected to the central aspect of the amygdala, and a network comprising the ventral striatum and the orbitofrontal cortex was functionally connected to the dorsal amygdala/substantia innominata. The data reveal distinct roles for dorsal and central aspects of the amygdala in governing the response to music stimuli with positive and negative valence. This indicates that the amygdala's role in emotion processing is not confined to negative emotions, and that different subregions of the amygdala respond to different valence dimensions.

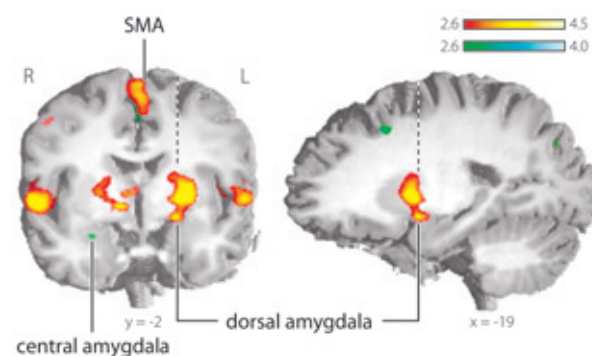


Figure 5.1.2 Parametric analysis with BOLD response correlating with increasing pleasantness in red and BOLD response correlating with increasing unpleasantness in green.

5.1.3 Relations between syntax processing in music and language: Developmental studies

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Language and music consist of perceptually discrete elements combined into hierarchically structured sequences according to syntactic regularities. We investigated language- and music-syntactic processing with the ERAN (Early Right Anterior Negativity, elicited by music-

syntactic irregularities), and the ELAN (Early Left Anterior Negativity, elicited by language-syntactic irregularities). Earlier studies reported larger ERAN amplitudes in adults with formal musical training, indicating that such training leads to more specific representations of musical regu-

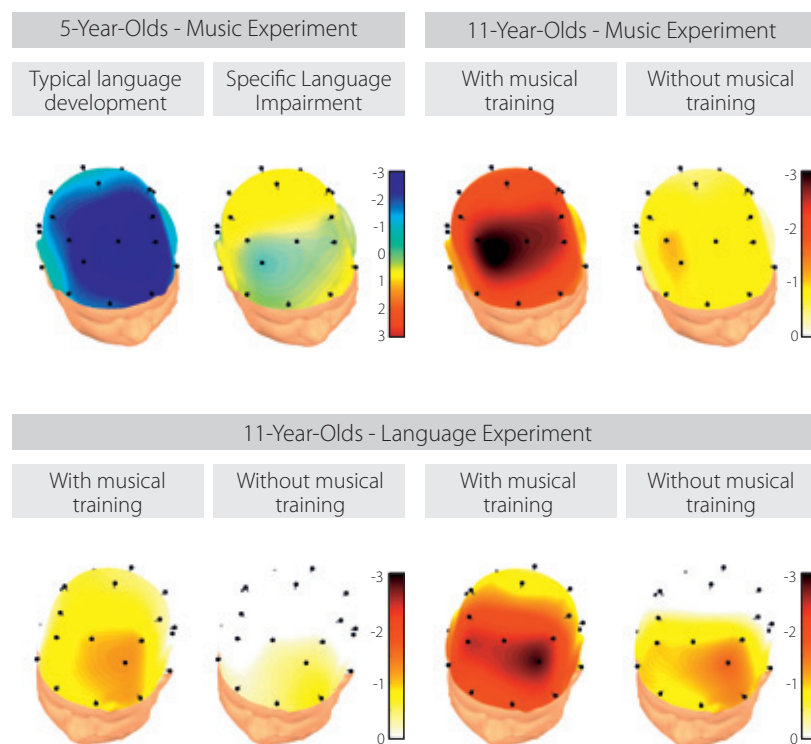


Figure 5.1.3 Scalp topography of the difference in ERPs. In the music experiments (upper row) regular were subtracted from irregular final chords; in the language experiments (bottom row) we compared the brain response to syntactically incorrect and syntactically correct sentences. A violation of music-syntactic regularities usually elicits an ERAN, a violation of linguistic syntax an ELAN. These two brain responses reflect very fast (around 200 to 300 ms) and fairly automatic processes of syntactic structure building. In 5-year-old children with typical language development we observed an ERAN that was not present in children with Specific Language Impairment (top-left panel). In 11-year-old children with musical training this brain response had an enlarged amplitude indicating that these children have an improved processing of musical syntax (top-right panel). The 11-year-old children with musical training also showed an improved processing of linguistic syntax: An ELAN was established in children with, but not in those without, musical training (bottom-left panel). Moreover, the amplitude of a later sustained negativity (which is regarded as a precursor of the ELAN in the time in which this response develops) had an enlarged amplitude in the children with musical training (bottom-right panel).

larities. Moreover, previous studies suggested that ERAN and ELAN are, at least partly, generated in overlapping brain regions, which might lead to effects of musical training to linguistic skills.

We observed that 11-year-old children with musical training show a larger ERAN than children of a control group without musical training, and – even more importantly – that the children with musical training showed an ELAN, while no ELAN was present in the control group. That is, musical training led to an improved processing of both musical and linguistic syntax. Correspondingly, we

observed that 5-year-old children with specific language impairment (SLI, which is characterized by difficulties in the processing of linguistic syntax) did not show an ERP response to music-syntactic irregularities (while such responses were observed in age-matched children with typical language development). These data provide the first evidence for connections between music- and language-syntactic processing in children, supporting the notion that musical training can have beneficial effects on language development in children.

Music-syntactic processing in patients with lesions in left fronto-temporal "language areas"

5.1.4

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fMRI and MEG studies provide evidence that processing of syntactic regularities in language recruits similar neural networks as processing of such regularities in music (including the inferior frontal gyrus, IFG, and the anterior superior temporal gyrus, aSTG). Moreover, syntactic irregularities in either domain elicit similar ERP components originating from these fronto-temporal brain areas, only slightly differing in hemispheric weighting: The ELAN, and the ERAN. We tested the hypothesis of shared resources for linguistic and music syntactic processing by investigating whether patients with lesions in brain regions known to be relevant for language also show deficiencies in the processing of musical structure. Therefore,

the ERPs of 6 patients with circumscribed lesions including the left IFG, 7 patients with focal lesions including the left aSTG (average lesion onset: 6;8 years), and an equal number of matched healthy controls were investigated. Previous language studies have shown that lesions in these areas abolish the ELAN. In the present study, the ERAN amplitude, its scalp distribution, and the behavioural performance of participants were investigated as a function of lesion site. Stimuli were chord sequences ending either on a regular (tonic) or irregular (dominant-to-the-dominant) chord.

Both patients and controls showed a significant ERAN. However, the scalp topography of the ERAN in patients with left IFG lesions differed significantly from the other experimental groups, being more frontally distributed and more strongly right lateralized. Moreover, only in the left IFG patient group the ERAN amplitude was correlated with the time since lesion onset, and also only left IFG

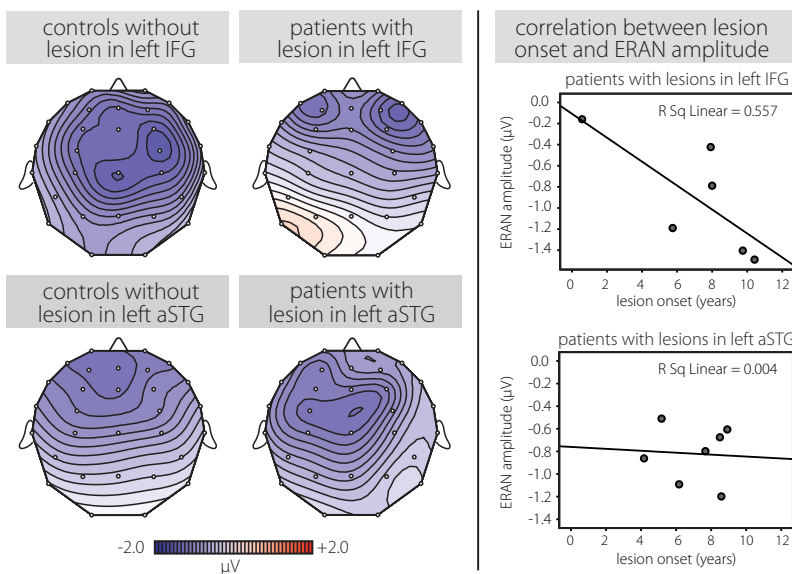


Figure 5.1.4 Left panel: Scalp topography of the ERAN in a time window from 150 to 250 ms after onset of the critical chord. Patients with lesions in the left IFG (upper right panel) show a significantly different scalp distribution of the ERAN than the other experimental groups. Right panel: Only in the patients with left IFG lesions the ERAN amplitude was correlated with the time since lesion onset.

patients performed below chance when asked to discriminate regular and irregular sequence endings. These findings lend support for the involvement of the left IFG, but not aSTG, in the processing of harmonic irregularities,

and, thus, provide evidence for a partial overlap of the neural networks processing linguistic and musical syntax within the left IFG.

5.1.5 Harmonic expectancies represent abstract instances of meaning in music

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This study sought to investigate the functional role of the N500, an event-related potential (ERP) elicited in response to violations of harmonic expectancy. Its close resemblance to the N400 has suggested the possibility of reflecting similar cognitive mechanisms (i.e. semantic processing). The question addressed by the present study was whether the N500 is a mechanism dedicated to either syntax or semantics or reflects more general demands placed on working memory. To test this we used sentences which were either correct or contained a syntactic or a semantic violation at the end. Twenty-six non-musical subjects were visually presented with language material, while simultaneously listening to chord sequences ending either on a harmonically expected or unexpected chord. Sentences and harmonic sequences each contained five items (words and chords respectively), which were presented in synchrony, but of which only the last item was analysed. Assuming that cognitive processes of similar function recruit the same neural resources regardless of modality, we were interested in how the language violations affect the N500. It was found that the N500 was reduced only when presented concurrently with a semantic violation, but not with a syntactic violation. This suggests that the N500 may in fact reflect

some type of semantic processing established by harmonic chord sequences. As well as providing evidence in favour of musicological notions on the potential semantic impact of tension-resolution patterns, this study may also end a long empirical quest for attempting to find a musical match to the language-related ERP for semantic processing.

Modulation of N500 with type of concurrently presented language material

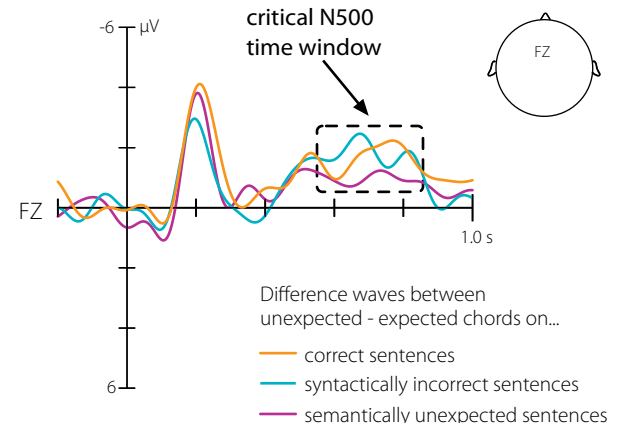


Figure 5.1.5

5.1.6 Neural correlates of working memory for verbal and tonal stimuli in nonmusicians and musicians with and without absolute pitch

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The purpose of these experiments was to compare the mechanisms and underlying neural correlates of perception and working memory (WM) processes for verbal and tonal information in different groups of participants

(nonmusicians and musicians with and without Absolute Pitch). Using fMRI, we observed a strong overlap of the neural networks underlying WM for tonal and verbal stimuli, indicating that similar brain areas serve WM

for language and music. However, there were also areas engaged specifically (or more strongly) in verbal (e.g. Broca's area, premotor cortex, IPL) or tonal (e.g. angular gyrus) WM processes. Compared to nonmusicians, non-AP musicians showed a superior performance during the tonal WM task, and a stronger involvement of premotor areas during tonal rehearsal. Based on the assumption that verbal and tonal material is translated from sensory information into rehearsable (sensori-)motor codes, these data might reflect that musicians have stronger

connections between tonal sensory information and corresponding motor programmes. Further results indicated that AP musicians have a strong tendency to perceive tones categorically (comparable to the normal perception of phonemes). In the fMRI data, AP musicians (compared to non-AP musicians) showed stronger activation of the right pars opercularis/pars triangularis and the left hippocampus during tonal rehearsal. The results of our studies broaden the view on the functional neuroanatomy of WM.

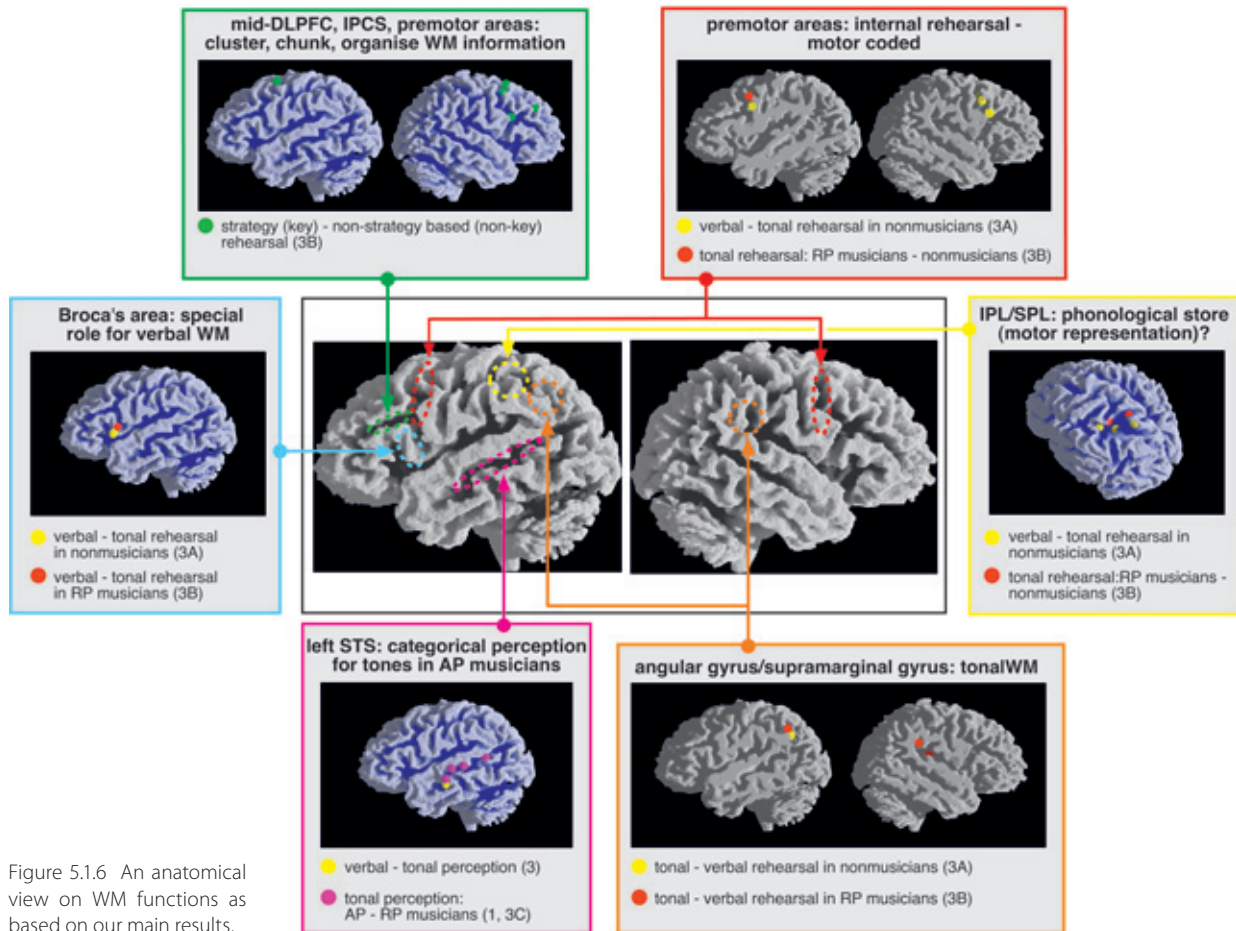


Figure 5.1.6 An anatomical view on WM functions as based on our main results.

Nobody is perfect: Neural correlates of error detection in performing musicians

5.1.7

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This project is part of a cooperation between the music group and the Department of Psychology, Cognition and Action, with the aim to investigate the neural correlates of music production. Playing a musical instrument

is a highly demanding task requiring the planning and execution of fast and complex movements. In addition, the constant and precise monitoring of one's own actions and their effects is necessary to achieve successful

performance. This study investigated neurophysiological correlates of error detection in performing musicians. In an action condition, 12 pianists were blindfolded and asked to play fast sequences bimanually on a digital piano while the electroencephalogram (EEG) was recorded. At random positions, we manipulated the auditory feedback by lowering the pitch of a pressed key by one semitone (sounding as if the pianist made a mistake by pressing the wrong key).

Event-related potentials (ERPs) for pitch manipulations and self-made errors were computed and compared to those of correct notes. Results showed that feedback manipulations in the action condition elicited a "feedback error-related negativity" around 200 ms after the onset of the key press, followed by a positive deflection (Fig. 5.1.7). ERPs of performance errors showed that electric brain responses differed between correct and erroneous performance already 100 ms before the onset of a wrong note (Fig. 5.1.7). This implies that not all error-related mechanisms rely on auditory feedback, and that errors can be neurally detected prior to the completion of an erroneous movement. One possible account for this

finding is that this difference in the ERPs reflects the output of an internal forward model, detecting a discrepancy between the predicted result of a planned movement and the movement goal. Future studies will explore how the musical context (e.g. pitch repetition and tempo) and social settings (e.g. pianists performing a duet) modulate the brain responses to manipulated auditory feedback and to performance errors.

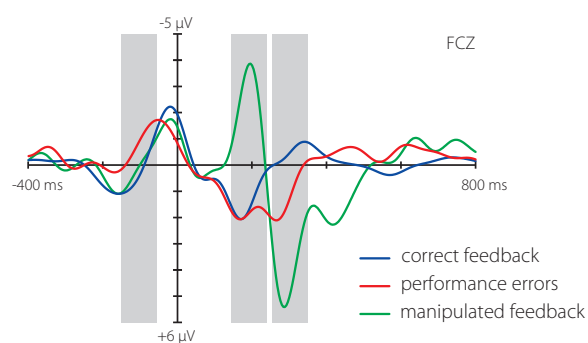


Figure 5.1.7 ERPs for correct feedback, performance errors and manipulated feedback at electrode FCZ in the action condition. The y-axis indicates the onset of the keypress.

Appointment

Koelsch, Stefan. *Senior Research Fellow*. University of Sussex, Brighton, United Kingdom.

■ 2007

Degrees

PhD Theses

Schulze, K. *Neural correlates of working memory for verbal and tonal stimuli in nonmusicians and musicians with and without absolute pitch*. University of Leipzig, Germany. ■ 2006

Jentschke, S. *Neural correlates of processing syntax in music and language - Influences of development, musical training and language impairment*. University of Leipzig, Germany. ■ 2007

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Index of Published Figures

Figure 5.1.6

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5.2

Independent Junior Research Group “Neurotypology”

Language, as a uniquely human cognitive ability, is often used to draw inferences about higher cognition as a whole. At the same time, however, psychologists, linguists, and cognitive neuroscientists continue to debate whether language should be considered “special” in some particular way or whether it is simply a complex instantiation of more general cognitive characteristics. A substantial problem arising in this regard is that conclusions about language architecture are often drawn on the basis of data from English. More precisely, while findings from other languages are increasingly becoming available, most existing models continue to base their underlying assumptions on properties of English (e.g. early availability of the verb, little morphology, strict word order). In view of this situation, we are thus faced with the risk of drawing general conclusions on the basis of language-specific findings.

The primary aim of the Junior Research Group (JRG) Neurotypology is to overcome these problems by pursuing a truly cross-linguistic approach to the neurocognition of language comprehension. To this end, we are examining the processing of simple sentences (comprising the verb and its arguments, the “sentence participants”) within a range of typologically varied languages: English, Chinese, German, Hindi, Icelandic, Japanese, Tamil, and

Turkish. By comparing the neurocognitive processing signatures of these very different languages to one another, we aim to establish cross-linguistic universals of the language architecture. These will then be used to establish correspondences to other cognitive domains.

During 2006 and 2007, research within the JRG Neurotypology was primarily concerned with the cross-linguistic validation and extension of the model-theoretic foundations on which our research is based. Thus, the claims of the extended Argument Dependency Model (eADM; Bornkessel & Schlesewsky, 2006) have been tested in a variety of different languages. This line of research has not only led to several important theoretical developments within the model (cf. section 5.2.1), but has also served to show how a cross-linguistically motivated processing architecture can shed light on more general issues within the neurocognition of language (section 5.2.2). Furthermore, we have investigated possible universal aspects of the processing architecture by means of cross-linguistic comparisons of ambiguous (sections 5.2.3/5.2.4) and unambiguous (section 5.2.5) sentences. In order to examine how neurocognitive signatures of language processing correlate with behavioural output, we have also begun to compare EEG and eye-tracking measures (section 5.2.6).

5.2.1 Theoretical advances in the cross-linguistic modelling of the neurocognition of language comprehension

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In Bornkessel and Schlesewsky (2006), we proposed that incremental argument interpretation is driven by a set of cross-linguistically applicable, hierarchically structured information types known as “prominence hierarchies”. For example, an animate argument is more prominent than an inanimate argument, a definite/specific argument is more prominent than an indefinite/non-specific argument, and a nominative-marked argument is more prominent than an accusative argument. Prominence information serves to establish a hierarchical relation between the arguments during online processing (argument A > argument B), thereby permitting incremental interpretation even in verb-final structures (via a default interpretation of “A acts on B”). In the absence of sufficient information for the establishment of a prominence hierarchy, the processing system defaults to a least-effort principle termed “Minimality”, which leads to a preference for minimal structures and interpretations.

Since the appearance of Bornkessel and Schlesewsky (2006), the notion of prominence has undergone a series of developments. These have led to the formulation

of a new meta-principle termed Distinctness, which states that the arguments within a sentence should be as distinct from one another as possible (Bornkessel-Schlesewsky & Schlesewsky, to appear). In the default case, this leads the processing system to assume that the Actor argument outranks the Undergoer argument on all dimensions of prominence (as, for example, in *The teacher threw a ball*). However, this default preference can be overridden by verb-specific requirements (e.g. with psychological verbs calling for animate Undergoers).

Distinctness provides a range of important theoretical advancements. Firstly, it offers a motivation for prominence hierarchies that is both plausible and appealing from a more general cognitive perspective: distinct argument representations serve to minimize interference during incremental comprehension. Secondly, Distinctness subsumes the Minimality principle: the simplest way for an argument to be distinct is for it to be the only argument. Hence, two fundamental – and potentially universal – principles of online comprehension can be reduced down to one.

5.2.2 Consequences of a cross-linguistic perspective: Deriving “semantic P600” effects

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The literature on the electrophysiology of language comprehension has recently seen a very prominent discussion of “semantic P600” effects, which have been observed in sentences involving an implausible thematic role assignment to an argument that would be a highly plausible filler for a different thematic role of the same verb. These findings have sparked a discussion about underlying properties of the language comprehension architecture, as they have generally been viewed as a challenge to hierarchically organized models of language processing.

In contrast to these widely held assumptions, our research suggests that semantic P600 effects can be derived straightforwardly within the eADM (Bornkessel & Schlesewsky, 2006), i.e. within an independently motivated, hierarchically organized neurocognitive model of language comprehension in which plausibility information is not assumed to have an immediate influence upon interpretation. Furthermore, in addition to accounting for the basic phenomenon of a “semantic P600”, the basic architectural properties of the eADM can explain

apparent empirical inconsistencies within the semantic P600 literature that cannot be addressed within previous approaches. Consider the following sentence examples (from Kuperberg, Kreher, Sitnikova, Caplan, & Holcomb, 2007, *Brain Lang*, 100, 223-237):

- (5.2.2) a. For breakfast, the eggs would eat ...
 b. For breakfast, the eggs would plant ...
 c. For breakfast, the boys would eat ...

Kuperberg et al. (2007) observed a “semantic P600” in response to both (5.2.2a) and (5.2.2b) in comparison to (5.2.2c) and therefore argued that these effects are triggered by an animacy-related thematic processing problem. By contrast, a number of other groups have only observed semantic P600s when there was a semantic association between at least one of the arguments and the verb and an N400 otherwise (e.g. Hoeks, Stowe, & Doedens, 2004, *Cogn Brain Res*, 19, 59-73; Kim,

& Osterhout, 2005, *J Mem Lang*, 52, 205-225; van Herten, Chwilla, & Kolk, 2006, *J Cogn Neurosci*, 18, 1181-1197). This apparent paradox is easily accounted for within the eADM. The relevant aspects of the model architecture are shown in Fig. 5.2.2.

In Kuperberg et al.’s (2007) stimuli, the processing of an inanimate initial argument followed by a modal engenders a passive preference within the linking step of processing. Thus, the processing system predicts an auxiliary (i.e. *be*) as the next category after *would*. When a main verb is encountered instead (as in (5.2.2)) the compute linking step fails (i.e. cannot be initiated). This leads to a blocking of plausibility/semantic association processing such that no N400 is engendered, but only a standard late positivity response to an unexpected category. By contrast, none of the other experiments in this domain led to a category-induced linking failure, thus allowing for a “relatedness/plausibility N400” response.

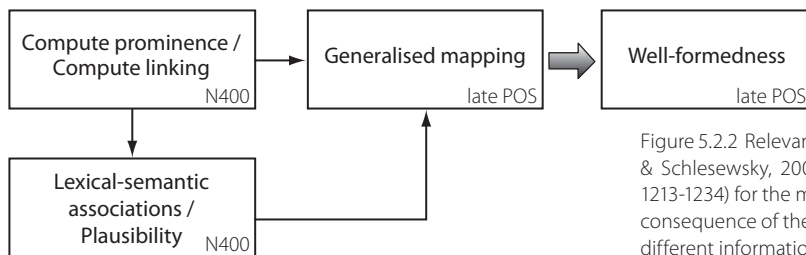


Figure 5.2.2 Relevant architectural properties of the eADM (Bornkessel, & Schlesewsky, 2006; Schlesewsky, & Bornkessel, 2004, *Lingua*, 114, 1213-1234) for the modelling of semantic P600 effects. These arise as a consequence of the “generalized mapping” step, which serves to map different information types onto one another.

Perspectives on the universality of processing strategies 1: Turkish

5.2.3

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To examine the possible universality of language comprehension strategies, we investigated the so-called “subject preference”, i.e. the tendency to interpret an initial ambiguous argument as the subject of the sentence. While this preference has been observed in European languages like German, Dutch, English, and Italian, these languages all share the property that sentences with initial objects are more difficult to process even when these objects are unambiguously marked. To explore whether the subject-preference also extends to languages of different types (and might therefore be considered a universal of language processing), we explored a language which allows for a natural (unmarked) object reading of an initial ambiguous argument, namely Turkish. Turkish has a basic subject-verb-object order, a preference for subjects

to be dropped and (under certain circumstances) case ambiguity between subjects and objects. Thus, the initial arguments in the sentences in (5.2.3) are ambiguous between a subject and an object reading. Nonetheless, both sentence examples provide optimal expressions of the subject matter at hand in spite of the fact that the initial argument is an object.

- (5.2.3) a. Dün pilot gördüm.
 yesterday pilot see-1sg.past
 ‘Yesterday (I) saw (a) pilot.’
 b. Dün taş gördüm.
 Yesterday stone see-Past-1st.Person.Sing
 ‘Yesterday (I) saw (a) stone.’

In an ERP study, we observed increased processing difficulty in the form of a broadly distributed positivity at the position of the disambiguating verb in (5.2.3a/b) in comparison to minimally differing unambiguously marked control conditions (Demiral, Schlesewsky, & Bornkessel-Schlesewsky, in press; cf. Fig. 5.2.3). This effect was independent of the animacy (i.e. semantic subject prototypicality) of the ambiguous argument. In addition, the ERPs showed no indication of increased processing costs for

unambiguously marked initial objects. Our results therefore speak in favour of a universal tendency to interpret the first argument encountered as the “subject” of the clause, even in languages providing no obvious structural motivation for such a strategy. They further attest to the independence of the subject preference in ambiguous structures from increased processing costs in analogous unambiguous sentences.

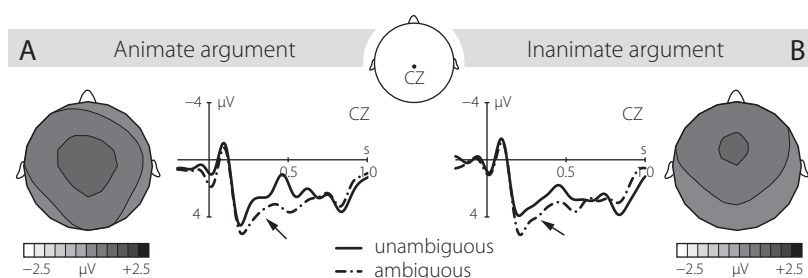


Figure 5.2.3 Grand average ERPs at the position of the disambiguating verb (onset at the vertical bar) in Turkish sentences such as (5.2.3). The topographical maps depict the scalp distribution of the ERP effect at its maximum (ambiguous – unambiguous).

5.2.4 Perspectives on a “universal” processing strategy 2: Japanese

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As discussed in section 3, ERP findings from Turkish suggest that a subject-preference is observable even in languages which allow for unmarked object-initial sentences and in which unambiguous initial objects do not engender increased processing difficulty. This observation suggests that the subject-preference might indeed be a “universal” of comprehension. On the basis of the Distinctness principle (see 5.2.1), we hypothesized that the source of this preference might lie in the processing system’s endeavour to analyse an initial argument as the sole argument in an intransitive relation (and, thereby, as the subject in a language like Turkish). An alternative possibility, however, is that the processing system attempts to saturate subject-verb agreement as soon as possible. These two alternative hypotheses were contrasted in an ERP study on Japanese, a language which is very similar to Turkish in terms of its structural properties but which has no subject-verb agreement. The critical experimental conditions are shown in (5.2.4).

(5.2.4)

- a. 二週間前 判事は 大臣を 招きました
nisyuukanmae hanzi-wa daizin-o manekimasita
two weeks ago judge-TOP minister-ACC invited

‘Two weeks ago, the judge invited the minister.’

- b. 二週間前 判事は 大臣が 招きました
nisyuukanmae hanzi-wa daizin-ga manekimasita
two weeks ago judge-TOP minister-NOM invited

‘Two weeks ago, the minister invited the judge.’

Because of the absence of subject-verb agreement in Japanese and the resulting difficulty in disambiguating a single argument towards an object reading, the sentences in (5.2.4) included two preverbal arguments. In both (5.2.4a) and (5.2.4b), the first argument is marked with the topic particle –wa, which can be used for both subjects

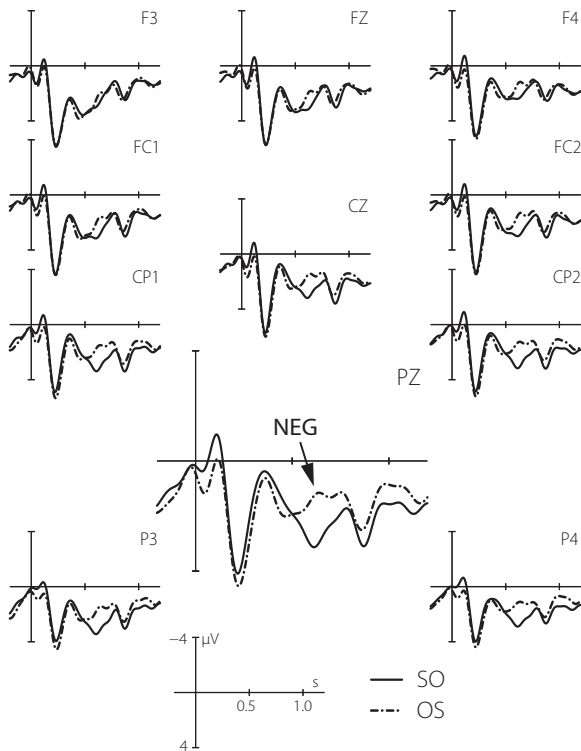


Figure 5.2.4 Grand average ERPs at the position of the disambiguating verb (onset at the vertical bar) in Japanese sentences such as (5.2.4).

and objects. Disambiguation towards an object-initial order is subsequently effected by the verb in (5.2.4b) (the nominative-marked second argument could also be the subject of an embedded clause; see Miyamoto, 2002, *J Psycholing Res*, 31, 307-347). As is apparent from Fig. 5.2.4, disambiguation towards an object-initial order engendered a broadly distributed negativity between 500 and 800 ms post verb onset. The findings from Japanese therefore support the cross-linguistic validity of the subject-preference, thereby indicating that this preference is due to a Distinctness-based preference for single arguments. We attribute the negativity-positivity contrast in the component pattern between Japanese and Turkish to a more general difference between disambiguations involving two preverbal arguments vs. only a single preverbal argument. This distinction between processing constellations in which two arguments compete for positions within a single argument hierarchy and those in which no such competition arises is supported by further findings from German.

The neurocognition of ergativity: Electrophysiological evidence from Hindi

5.2.5

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The incremental comprehension of verb-final languages has long posed a challenge to models of language processing. Previous findings suggest that morphological case marking plays a major role in preverbal argument interpretation in these languages (cf. Bornkessel & Schlesewsky, 2006). To date, however, research on the interpretive consequences of case marking in online processing has been restricted to languages with a nominative-accusative case system. However, roughly a quarter of the languages of the world show a fundamentally different (“ergative”) case system, in which the subject of an intransitive sentence and the object of a transitive sentence are coded by the same morphological case, while the transitive subject is assigned a distinct case, the “ergative”.

The present auditory ERP study examined the processing of ergativity in Hindi, a so-called split-ergative language (i.e. with an ergative system in sentences with perfective aspect and a nominative system otherwise). The critical sentences (see (5.2.5)) capitalized upon the fact that, due to the language’s verb-finality, the requirement for ergative or nominative case does not become clear until the aspect marker of the verb is encountered (i.e. after the arguments have already been processed). The mismatch between case marker and aspect in (5.2.5b/c) therefore does not become clear until this point. To examine the processing of this critical information, we calculated ERPs time-locked to the onset of the aspect markers (-taa/-aa) of our four critical sentence types.

(5.2.5)

- a. shikshak maalii-ko dekh-taa hai
teacher gardener-Acc see-Impf.3sg.m Pres
'The teacher sees the gardener.'
- b. *shikshak-ne maalii-ko dekh-taa hai
teacher-Erg gardener-Acc see-Impf.3sg.m Pres
'The teacher sees the gardener.'
- c. *shikshak maalii-ko dekh-aa hai
teacher gardener-Acc see-Perf.3sg.m Pres
'The teacher has seen the gardener.'
- d. shikshak-ne maalii-ko dekh-aa hai
teacher-Erg gardener-Acc see-Perf.3sg.m Pres
'The teacher has seen the gardener.'

The ERP results showed a biphasic pattern of an N400 followed by a late positivity for the violation condition including an ergative (5.2.5b) in comparison to the imperfective control condition (5.2.5a) (see Fig. 5.2.5 A). By contrast, the violation condition with nominative case (5.2.5c) only engendered an N400 relative to control

condition (5.2.5 d). The general appearance of an N400 in response to a violation of split-ergativity is particularly interesting as this component has been observed in response to increased costs of argument interpretation (e.g. Frisch and Schlesewsky, 2001, *Neuroreport*, 12, 3391-3394) and differs markedly from effects typically observed in response to violations of subcategorized case, i.e. case called for by a particular verb form (namely a left-anterior negativity, LAN; see Friederici & Frisch, 2000, 43, 476-507). This finding therefore suggests that increased processing demands in the domain of split-ergativity arise from processing problems related to argument linking rather than simply reflecting a formal mismatch. With respect to the differences in the positivity for the two violation conditions, the present results are in line with previous findings (e.g. from German) showing that well-formedness problems arising in restricted case marking contexts engender larger late positivities (i.e. the ergative is more marked and more restricted in its distribution than the nominative).

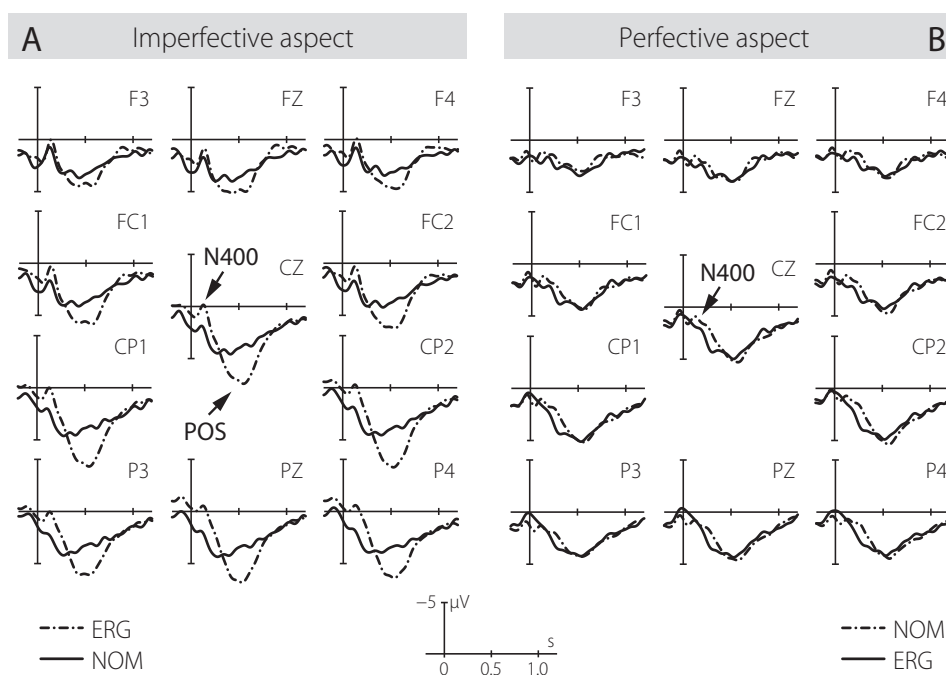


Figure 5.2.5 Grand average ERPs at the position of the disambiguating aspect marker (onset at the vertical bar) in Hindi sentences such as (5.2.5). Note that the early onset of the N400 effect is likely due (i) to the direct timelocking to the critical morpheme, and (ii) to effects of intra-word coarticulation.

From the neural response to the behavioural output: Evidence for the influence of prominence information on eye movements

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A hitherto unresolved puzzle in the language comprehension literature concerns the timing mismatches observed between event-related potentials and measures of eye movements during reading (e.g. Sereno & Rayner, 2003, *Trends Cogn Sci*, 7, 489-493). The frequent finding that the eyes appear to respond more quickly to a particular stimulus dimension than the corresponding ERP effect calls into question the widely held assumption that ERP latencies serve to provide a record of processing in real time. However, direct comparisons between eye-tracking and ERP data are currently difficult to undertake because of a lack of systematic investigations in this domain (i.e. there exist only very few directly comparable studies that have employed both methods). To address this issue, we have recently begun to use eye-tracking to examine manipulations that are well established in the neurocognitive domain (i.e. using ERPs and fMRI), with the aim of developing a model that can derive both the neural correlates of language processing and their behavioural output.

In an initial series of experiments, we examined the role of prominence information (case marking, definiteness, thematic roles; see section 5.2.1) on the eye movement record in the processing of locally ambiguous German sentences such as (5.2.6).

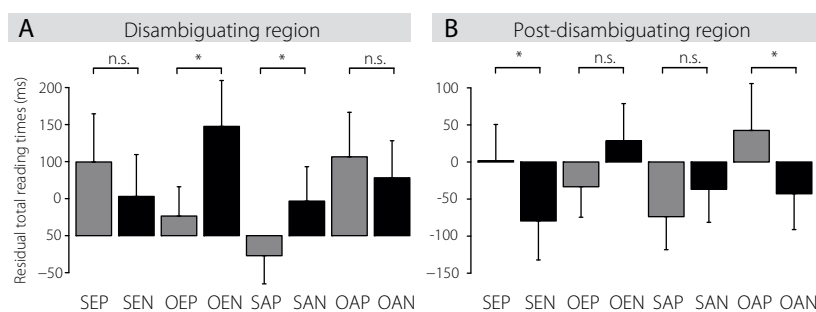
(5.2.6)

Dass Rudolf Präsidenten gefallen, hat alle überrascht.
that Rudolf_{AMB.SG} presidents_{AMB.PL} please_{PL} has everyone surprised
'That presidents are pleasing/appealing to Rudolf surprised everyone.'

At the position of the underlined verb, sentences were disambiguated either towards a subject- or an object-initial order. In addition, the disambiguating verb either assigned the higher thematic role to the subject or to the object (dative active verbs such as *folgen*, 'to follow' vs. dative object-experiencer verbs such as *gefallen*, 'to be pleasing/appealing to') and the first argument was either more or less prominent than the second in terms of definiteness (proper noun preceding bare plural or vice versa). Previous ERP studies (e.g. Bornkessel et al., 2004, *J Mem Lang*, 51, 495-522) have shown that all of these dimensions interact within the N400 time window at the disambiguating verb position.

Eye-tracking, by contrast, showed a much more complex overall data pattern. Whereas a main effect of word order was observable from first pass reading times of the disambiguating region onwards, the definiteness and thematic hierarchies interacted in total reading times for both the disambiguating and post-disambiguating regions. Strikingly, effects of definiteness were only observable at the disambiguating region (see Figure 5.2.6 A) when there was a correspondence between word order and the thematic hierarchy (i.e. for subject-initial sentences with active verbs and object-initial sentences with experiencer verbs), whereas this pattern reversed in

the post-disambiguating region (see Figure 5.2.6 B). The similarities and differences of the data patterns suggest that a combination of neurocognitive and multidimensional behavioural measures may be optimally suited to providing fine-grained information about the language comprehension architecture.



5.2.6 Total reading times for the eight critical conditions in the disambiguating (Panel A) and post-disambiguating regions (Panel B). Condition labels encode word order (S/O = subject- or object-initial), verb type (A = active, E = experiencer) and definiteness (P = proper name first; N = Bare plural noun first).

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- 2007** ■ Bickel, B., Bornkessel-Schlesewsky, I., Comrie, B., Cysouw, M., Haspelmath, M., Junghanns, U., et al. (April). *Grammar and Processing of Verbal Arguments*. Workshop. University of Leipzig, Germany.
- Bornkessel-Schlesewsky, I., & Schlewsky, M. (December). *Theoretical Approaches to the Processing of Verb-Final Constructions*. Workshop. Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.

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- 2007** ■ Demiral, S. B. *Incremental argument interpretation in Turkish sentence comprehension*. University of Leipzig, Germany.
- Mahlstedt, A. *The acquisition of case marking information as a cue to argument interpretation in German: An electrophysiological investigation with pre-school children*. University of Potsdam, Germany.

Awards

- 2006** ■ Bornkessel, I. *Elf der Wissenschaft [Eleven Scientists]*. Stifterverband für die deutsche Wissenschaft und Bild der Wissenschaft.
- Bornkessel, I. *100 Köpfe der Zukunft [100 Heads of the Future]*. Part of the Federal Government's initiative "Germany – Land of Ideas".

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5.3

Independent Research Group “Attention and Awareness”

Is it possible to predict what a person is thinking of – or even what they are planning to do – based alone on their current brain activity? The projects in the “Attention and Awareness” group investigate ways to decode and predict a person’s thoughts from functional magnetic resonance imaging (fMRI) data. The key is that each thought is associated with a unique brain activation pattern that can be used as a signature for that specific thought. If we train a classifier to recognize these characteristic signatures we can read out a person’s thoughts from their brain activity alone. Such “thought reading” is a useful tool in basic cognitive neuroscience because it can reveal how information is neurally encoded in the brain. For example, it is possible to address the important question which specific brain regions carry information related to specific

cognitive representations (e.g. visual images, memories, or intentions). In addition to its use for studying storage of information in the human brain, this research also has many potential applications, for example in the control of computers and artificial prostheses by brain activity. The potential future applications in lie detection and market research are more controversial and thus require careful ethical consideration.

Unconscious determinants of free decisions in the human brain

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There has been a long debate whether subjectively "free" decisions are determined by brain activity ahead of time. Previous claims that subjective decisions are preceded by brain activity have been highly criticized as inaccuracies in the participants' subjective reports. Also, it has remained unclear whether an intention to act is initiated in motor-related brain regions, or if high-level brain areas are involved.

We show that the outcome of a subject's free decision can be decoded – and thus predicted – even up to ten

seconds before it enters awareness from patterns of brain activity in prefrontal cortex and parietal cortex. This delay is too long to be accounted for by inaccuracies in measuring the onset of conscious intentions. Instead it presumably reflects the operation of a network of high-level control areas that begin to prepare an upcoming decision long before it enters awareness. This suggests that our free choices are determined by brain activity much earlier than commonly appreciated.

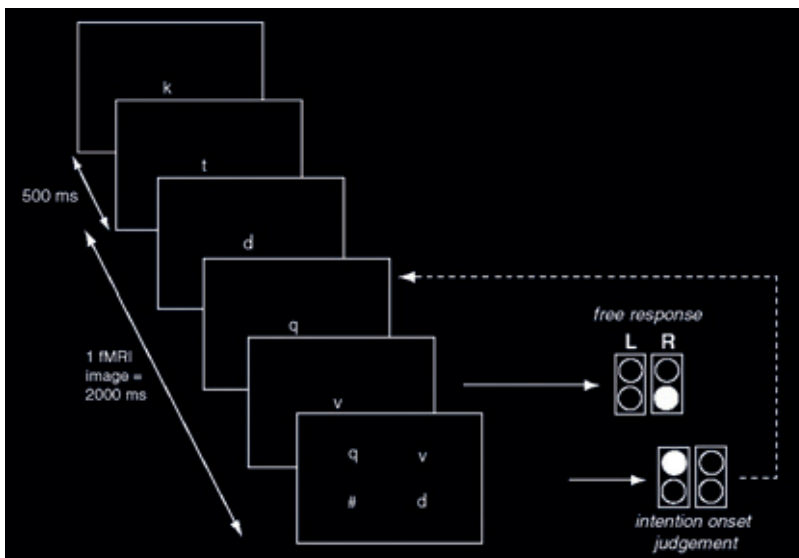


Figure 5.3.1.1 Experimental paradigm. In a variant of Libet's task, subjects viewed a letter stream updated every 500 ms. At some point they spontaneously made the decision for either their left or right index finger and pressed the corresponding button ("free response"). Subsequently, a response-mapping screen instructed subjects which second button to press to report the time when they consciously made the decision.

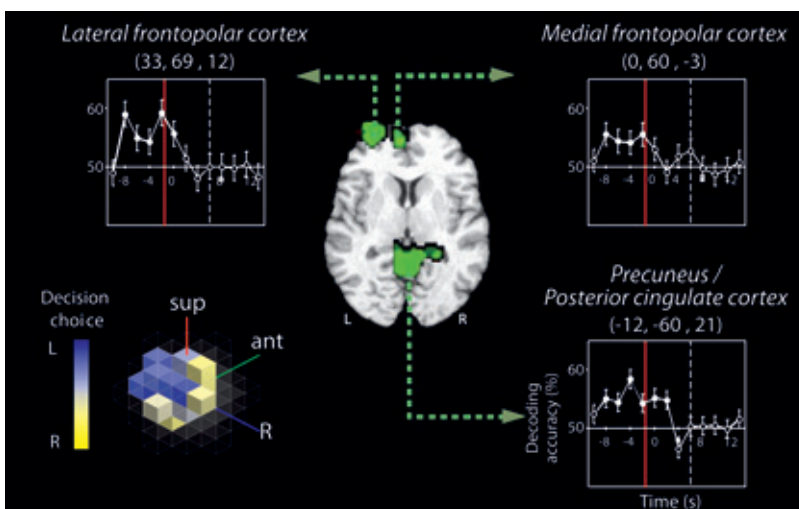


Figure 5.3.1.2 Cortical regions where the outcome of decisions could be decoded before reaching awareness. The graphs depict the accuracy with which a "free choice" could be decoded from the spatial pattern of brain activity in each region (error bars = SEM; chance level is 50%; vertical red line: earliest time when subjects became aware of their choices; dashed vertical line: onset of next trial). The inset in the bottom left shows a representative spatial pattern of preference in frontopolar cortex for one subject.

5.3.2 Decoding the information flow through the human brain

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Information flow in the brain can be considered a process that maps a set of sensory stimuli to a set of motor responses. The stimulus-response mapping is flexible and can be reconfigured by changing the task assigned to the subject. Here we sought to identify which brain regions encode representations at different stages of the flow of information through the brain. We used functional magnetic resonance imaging (fMRI) in combination with multivariate pattern recognition and decoding techniques to dissociate cortical representations of the sensory stimuli, motor responses and stimulus-response mapping rules ("task-sets"). On each trial subjects were presented with one of two possible stimuli, prior to which a response-mapping cue instructed them which of two joystick movements to make in response to each stimulus. Multivariate pattern classification was applied to identify cortical brain

regions encoding stimuli, responses, specific stimulus-response combinations and task-sets. To search for brain regions encoding information in an unbiased fashion, we used a moving searchlight that analysed the activation pattern of a sphere of locally clustered voxels around every voxel in the brain. Stimulus identity was found to be encoded in early visual cortex whereas the motor responses could be decoded from premotor cortex, the cerebellum, postcentral sulcus and posterior temporal cortex. Specific stimulus-response combinations could be decoded from early visual cortex as well as from pre-SMA and SMA. The task-sets were found to be encoded in left lateral prefrontal cortex (PFC) and the left intraparietal sulcus (IPS) (see Figure). Using this approach, we were able to go beyond classical fMRI analyses and demonstrate where information about task-sets is encoded in the human brain. Our

findings provide strong evidence for models that implicate lateral prefrontal regions in encoding of tasks that follow external instructions.

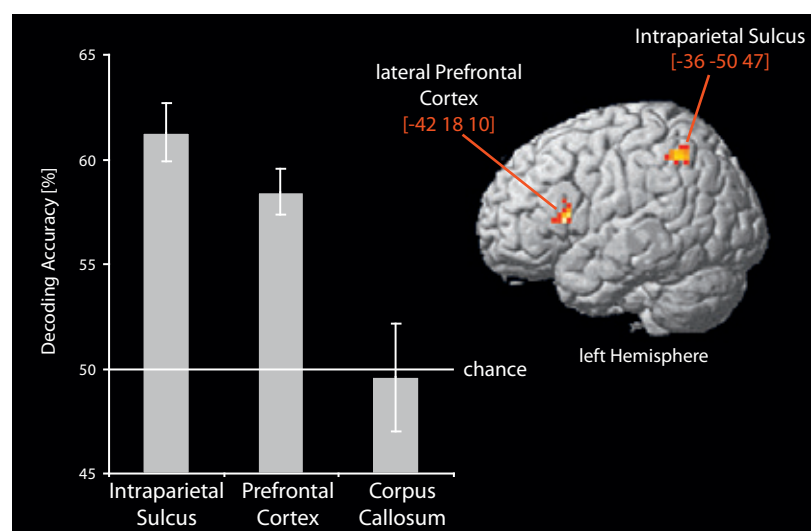


Figure 5.3.2 Decoding of task-sets from spherical voxel clusters. The figure shows decoding accuracy for the task-sets while viewing a target stimulus. Decoding accuracy is significantly above chance with $p < .00001$ (uncorr., 3 voxel threshold) in the brain regions displayed. The graph shows mean decoding accuracy and standard errors (SE) for voxels with the strongest effect in predictive brain regions. Prediction is at chance level in control regions like corpus callosum. Coordinates displayed refer to the Talairach coordinate system.

5.3.3 High-resolution imaging of subcortical visual processing at 7T

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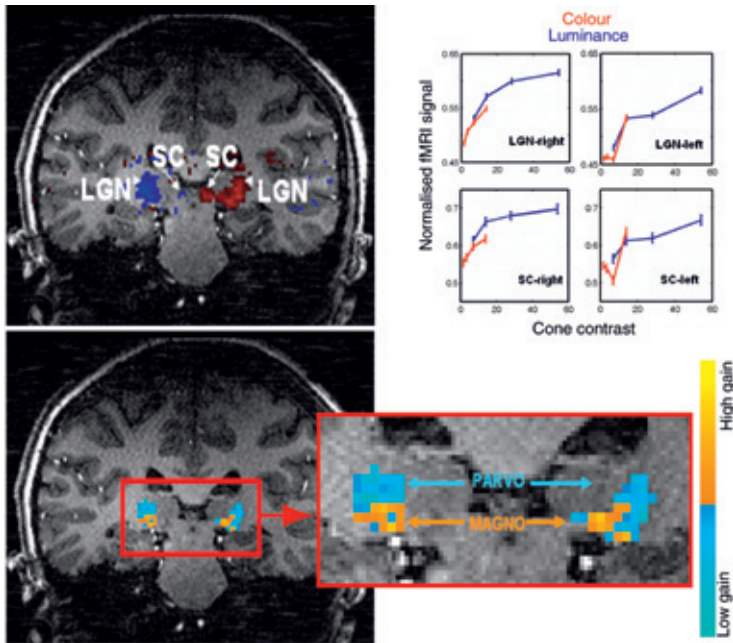
³ Department of Neurology II, Otto von Guericke University Magdeburg, Germany

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⁵ Department of Biomedical Magnetic Resonance, Institute for Experimental Physics, Magdeburg, Germany

This project investigates processing in the subcortical visual pathway using high-field high-resolution imaging at 7T. Based on previous work from our group, where we

used high-resolution fMRI at 3T to investigate eye-selective processing in the human LGN we addressed three main questions: (1) Can visual processing in the human



superior colliculus be reliably studied using fMRI in humans? (2) Is it possible to obtain parametric responses to visual stimulation from subcortical visual structures? (3) Is it possible to map magno- and parvocellular layers of the human LGN based on differences in response gain?

Figure 5.3.3 Top left: Subcortical regions of the visual pathway identified using alternating stimulation in the left and right visual hemifield (LGN: lateral geniculate nucleus; SC: superior colliculus). Top right: Contrast response functions in cone-contrast space in LGN and SC. Bottom: Subdivisions of the human LGN with high and low response gain, presumably reflecting magno- and parvocellular layers.

Saliency signals in the near-absence of attention

5.3.4

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It is classically assumed that salient locations or objects from a visual scene are represented in a spatial saliency map. For the calculation of such a saliency map different feature contrast maps for luminance, orientation, motion, colour, etc. are combined. Brain regions that are candidates for encoding such a saliency map are the pulvinar, superior colliculus, the frontal eye fields and the posterior

parietal cortex. But there is also evidence for a saliency map within the ventral visual pathway. In the experiment presented here we investigated the neural correlates of orientation pop-out in humans. Two types of stimuli were used: (a) homogenous stimuli consisting of an array of bars all of which had the same orientation (randomly chosen to be 0°, 45°, 90° or 135°), and (b) pop-out stimuli consisting of homogenous arrays but with one bar in each quadrant orientated differently (0°, 30°, 60° or 90°) relative to the background. We used an event-related stimulation protocol and stimulated with pop-out stimuli for 4 sec after which the homogenous background stimuli were presented for 7, 10 or 13 sec.

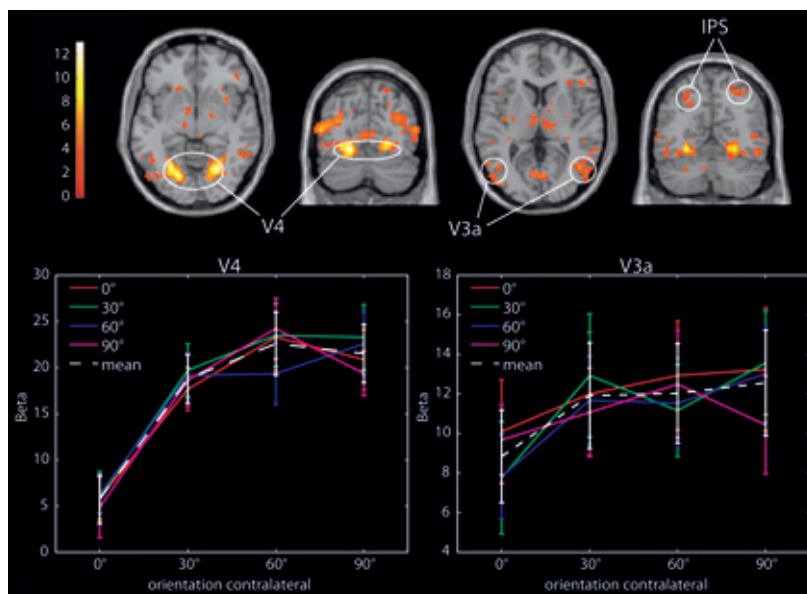


Figure 5.3.4 Top: Regions where gradual increases in pop-out cause monotonic increases in fMRI signals (V1, V3a and V4 and IPS). Bottom: The different colours show signals in retinotopic representations of pop-out stimuli as a function of pop-out in the contralateral visual field. No interaction is observed suggesting an independent processing of saliency signals in retinotopic cortex.

Importantly, during stimulation attention was directed to the fixation using a task that demanded attending the centre. This way no voluntary attention was drawn to the salient positions at the two quadrants. Eleven subjects participated twice in the experiment. BOLD activity in striate and extrastriate cortex showed a significant increase for the salient positions in V1, V3a, V4. A trend was also observed in intraparietal sulcus. Furthermore single subject analysis revealed that the increase in BOLD in V3a and V4

was monotonic in reference to the relative orientation of the bars on the contralateral hemisphere. Interestingly, the orientation of the bars on the ipsilateral hemisphere did not influence the BOLD signal in a systematic manner pointing to an independent processing of pop-out signals in the absence of attention. The results show that bottom-up saliency is represented automatically and implicitly in the visual cortex without requiring voluntary attention.

5.3.5 Control regions for visual spatial attention in prefrontal cortex

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It has been repeatedly shown that a network of brain regions (mainly intraparietal sulcus and frontal eye fields) is involved in goal-directed top-down control of attention to spatial locations. However, it has remained unclear to which degree these brain regions encode specific signals for the direction of attention to particular locations. Activity in these regions may instead reflect non-specific or general factors such as task difficulty or perceptual load. Using a novel technique, namely multivariate decoding of fMRI signals, we investigate the degree to which the spatial focus of attention can be decoded from different regions of the brain. To achieve this, we train a pattern classifier to decode the subject's focus of

attention from spatial patterns of fMRI signals in each local brain region using a moving "searchlight".

There are several brain regions from which it is possible to decode at an above chance level where a subject is attending to. These regions include occipital, parietal (intraparietal sulcus), and especially right prefrontal areas. Since traditional topographic mapping approaches fail to identify specific signals encoding the spatial distribution of visual attention in prefrontal areas, we assume that these control signals are encoded in a less topographic fashion. This reinforces the use of multivariate decoding as a powerful tool for revealing cortical information that goes beyond traditional topographic methods.

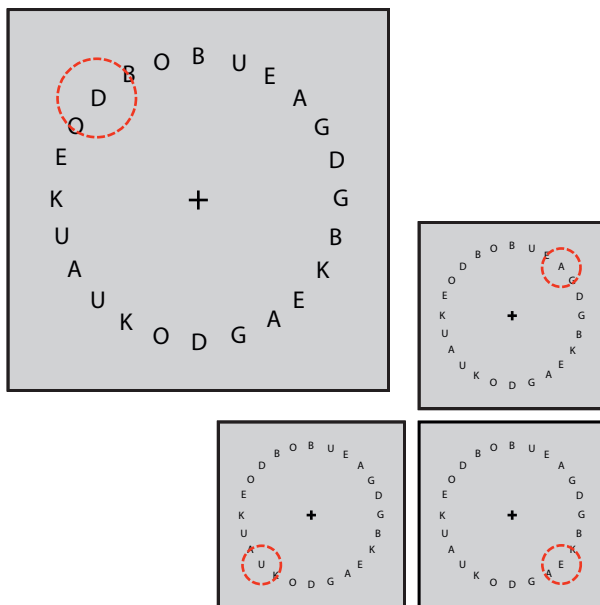


Figure 5.3.5.1 Stimuli were circles of letters at an eccentricity of 5.5°. In a block design 18 subjects indicated by button press whether the letter at one of four previously cued positions oblique to middle fixation was a vowel or consonant. Attentional shifts were done covertly (confirmed by eye movement recording) and had to be maintained during a block of eight stimulus presentations. We recorded 6 runs a 192 volumes of BOLD fMRI at 3T using an birdcage head coil (42 slices, TR = 2800 ms, 3x3x3 mm resolution). Blocks of attentional shifts to the four spatial locations were repeated four times resulting in 16 blocks of 22.4 s.

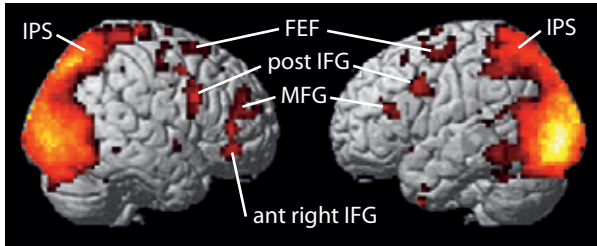


Figure 5.3.5.2 Brain regions from which it is possible to decode where in the visual field a subject is attending to. Second level analysis on distributions of decoding accuracies across 18 subjects (uncorrected, $p < 0.0001$). Classification was done by separating activation patterns of the four conditions.

Invariant decoding of object categories from human visual cortex

5.3.6

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Categorical representations of objects in ventral temporal cortex have been repeatedly investigated using fMRI in humans. However it has remained unclear to which degree specific brain regions encode objects invariant of their defining features, such as brightness, contrast or colour. One promising way to investigate the mechanisms of object representation is to apply pattern-classifiers to distributed responses of object-selective brain regions. It has been shown that such classifiers can predict the perceived object categories of static 2D images precisely. However, it is currently not clear to which degree these classifiers rely on retinotopic differences between stimuli rather than their specific object categories. In this study, we first approached the problem using rendered 3D meshes of objects rotating along a randomly changing axis. The time-average representations of these rotating objects in retinotopic cortex should be approximately matched. Support vector machine (SVM) based pattern classification algorithms were used in combination with a spherical searchlight technique to decode objects from

fMRI signals in multiple local regions. Decoding was possible from high-level object selective cortex; however, it was also still possible to decode object identity from retinotopic visual cortex (V1). Next, we matched the stimuli to minimize differences in time-average retinotopic representation (based upon a Gabor filter model of V1). This had the desired effect of reducing decoding accuracy in V1, whereas decoding in high-level object processing regions of the ventral stream was still possible. Finally, we assessed a cross-scale and cross-colour decoding by training on one scale or colour and testing on the other. This again reduced decoding accuracy in retinotopic cortex, while decoding from object-selective cortex was still possible. Taken together, our results support the notion that object representations in ventral temporal cortex can be decoded independently of their spatial representation in retinotopic visual cortex.

Congresses, Workshops, and Symposia

- 2006** ■ Haynes, J.-D. (June). *Brain-reading of consciousness*. Symposium. 10th Annual Conference of the Association for the Scientific Study of Consciousness (ASSC), Oxford, United Kingdom.
- 2007** ■ Haynes, J.-D., & Curio, G. (May). 11. *Berliner Kolloquium der Gottlieb-Daimler- und Karl-Benz-Stiftung "Gedankenforscher – Was unser Gehirn über unsere Gedanken verrät"*. Conference. Academy of the Konrad Adenauer Foundation, Berlin, Germany.

Appointment

- 2006** ■ Haynes, John-Dylan. *Professorship for Theory and Analysis of Large-Scale Brain Signals*. Bernstein Center for Computational Neuroscience Berlin.

Publications

Published papers

- Ansari, D., Dhital, B., & Soon, C. S. (2006). Parametric effects of numerical distance on the intraparietal sulcus during passive viewing of rapid numerosity changes. *Brain Research*, 1067(1), 181-188.
- Bode, S., Koeneke, S., & Jäncke, L. (in press). Different strategies do not moderate primary motor cortex involvement in mental rotation: A TMS study. *Behavioural and Brain Functions*.
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- Venkatraman, V., Soon, C. S., Chee, M. W.-L., & Ansari, D. (2006). Effect of language switching on arithmetic: A bilingual fMRI study. *Journal of Cognitive Neuroscience*, 18(1), 64-74.

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6

Research and Development Units

Nuclear Magnetic Resonance

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Dr. Yun Nan (*) (PhD since 11/2006)

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Mathematical Methods in fMRI

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- (a) German Research Foundation (DFG)
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- (p) National Institute of Mental Health
- (r) partly financed by the German Federation of Industrial Research Associations (AiF), Programme Pro Inno
- (*) Left the Institute during 2006/2007

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6.1

Nuclear Magnetic Resonance

Activities of the Nuclear Magnetic Resonance Unit comprise three interrelated core areas: (1) The development and optimization of magnetic resonance (MR) methods in general to provide an infrastructure for application, (2) mapping of cortical activation and investigation of the underlying signal changes, and (3) a parametric characterization of the human brain by quantitative MR approaches.

In all MR applications, a careful choice of the radiofrequency (RF) coil is of paramount importance for optimizing the signal-to-noise ratio (SNR). We have developed a multi-channel transmit/receive helmet coil for imaging at 3 T based on microstrip transmission line technology (6.1.1). Adaptation to 7 T was pursued in collaboration with the Harvard/MIT Martinos Center for Biomedical Imaging. Further collaboration exists with the University of Leipzig and the *Physikalisch-Technische Bundesanstalt Berlin* to investigate a head coil with octahedral symmetry. Besides hardware design, sophistication of MR sequences and theoretical simulations of spin dynamics have been subjects of ongoing interest. An example is an improved standard EPI sequence serving as the workhorse in functional magnetic resonance imaging (fMRI) applications to include internal navigators and to support arbitrary matrix dimensions. To improve auditory experiments, interleaved silent steady state (ISSS) imaging was implemented in collaboration with the Cambridge MRC Cognition and Brain Sciences Unit. Finally, simulation of MR experiments using intra-voxel magnetization gradients proved to be an efficient tool for understanding the process of image formation.

Research in the field of functional brain mapping is related to exploring novel contrast mechanisms for fMRI and investigating the physiology and biophysics underlying blood oxygen level dependent (BOLD) and alternative contrast mechanisms. To achieve better specificity of BOLD-based methods, non-invasive imaging of the vessel size in activated voxels was a subject of extensive research (6.1.2; funded by the *Deutsche Forschungsgemeinschaft*). A cooperation on this subject was initiated with the University of Jena. Examples of non-conventional fMRI approaches include the extensive use of perfusion imaging, diffusion imaging (in collaboration with the MPI for Biological Cybernetics), or intermolecular multiple-quantum techniques. Contrast based on intermolecular double-quantum coherences is also related to the BOLD effect but further depends on the so-called correlation distance, which can be adjusted by the operator (6.1.3). Perfusion imaging with two-coil continuous arterial spin labeling (CASL) has been rewarding for many years. Strategies were developed to map dynamic information on transit times and perfusion territories (6.1.4). More recently, methods for quantitative brain imaging and spectroscopy have found increasing interest, in particular relaxometry and magnetization-transfer imaging to characterize the white matter and myelination. Application of a novel regularization method to spectroscopy aims at the separation of signals from macromolecules (6.1.5; funded within the 6th Framework Programme).

A microstrip transceive array coil for imaging at high magnetic fields

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To optimize the SNR in human magnetic resonance imaging (MRI), a volume RF coil transmitter decoupled from a phased-array receiver is often used. However, high-field MRI scanners may not have whole-body RF coils for transmission due to design challenges and the problem of high specific absorption rates. Therefore, a prototype four-channel transmit/receive (T/R) array coil for imaging the brain at 3 T or above was built (Annual Report 2004/2005, Section 7.1.3). Extension to larger arrays is straightforward.

For the coil design, four semi-open microstrip transmission-line (MTL) elements with an electrical length equal to one quarter-wavelength were arranged to form an overall dome-like shape surrounding the human head (Fig. 6.1.1 A). They consisted of two thin copper strips separated by polypropylene (i.e., a low-loss dielectric substrate) and terminated with a short at the end near the neck. Each channel was tuned with a parallel capacitance and matched to 50 Ω with a series capacitance. The transmit power was split by a four-way power divider to produce a circularly-polarized B_1 field inside the array coil. Power was controlled by a T/R switch for each channel that used actively switched PIN diodes to provide sufficient isolation between transmitter and receiver. For minimizing

the mutual coupling between array elements, preamplifier decoupling was used.

Images recorded with counterclockwise and clockwise rotation senses of the transmission phases verified numerical simulations of the generated field and polarization: Areas of high signal intensity included a circularly-polarized central region and linearly-polarized regions near the MTL elements. Small areas of reduced signal intensity between the MTL elements were consistent with regions of a negative rotation sense of the transmission field. In comparison with a commercial standard T/R birdcage head coil, an SNR improvement by up to 30% was achieved. Noise correlations between the MTL elements were well below 20%, which was regarded negligible. Consistently, phantom images recorded with parallel-imaging reconstruction (GRAPPA) indicated low noise amplification. Even with only four channels, an image quality comparable to a full- k -space reference image was obtained using an acceleration factor, $R = 2$ (Fig. 6.1.1 B,C). With increasing acceleration, subtle residual aliasing artifacts became visible. The open design provides sufficient space for additional audiovisual stimulation devices that may be needed in functional studies.

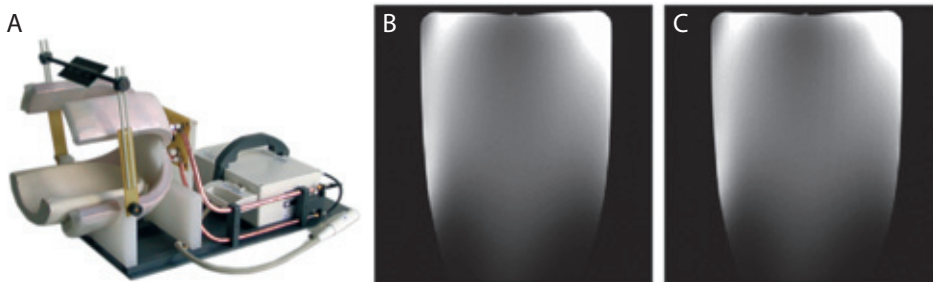


Figure 6.1.1 (A) Prototype of the four-channel T/R array with a helmet-like shape and spin-echo images (repetition time, $T_R = 800$ ms; echo time, $T_E = 8.9$ ms; resolution $0.9 \times 0.9 \times 5.0$ mm³) obtained (B) without parallel imaging (SNR = 410) and (C) with GRAPPA reconstruction (32 auto-calibration signal lines; $R = 2$; SNR = 324).

Increased specificity in functional magnetic resonance imaging by integrated estimation of vessel sizes

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Detecting neuronal activity by fMRI based on the BOLD effect is derogated from the fact that the contrast reflects changes in blood oxygenation which may be distant from the activated site, for example, in the presence

of large veins. To increase the specificity of BOLD-fMRI (i.e., to confine the origin of the BOLD contrast to the microvasculature), a novel approach was developed for predicting the average venous-vessel radius in activated

voxels. The average vessel radius was derived from the combined changes in the transverse relaxation rates R_2 and R_2^* upon activation which were measured by a sequence comprising parallel imaging and single-shot, multiple gradient-echo (GE) sampling of a spin echo (SE). A GE sequence generally provides better sensitivity but is subject to signal from large vessels compared to a SE sequence. It is therefore advantageous to use GE for the initial pattern of activated voxels. From the GE and SE relaxation rates, the venous vessel radius was calculated exploiting existing models of susceptibility-induced MR signal dephasing, and voxels with contrast dominated

by large veins were filtered out. An inherent advantage of this strategy is that the radius was derived from the fMRI data itself so that error-prone coregistration was not necessary. Due to the high temporal and spatial resolution, the imaging sequence is suitable for routine fMRI applications. The feasibility of the method was demonstrated by a study with visual stimulation. Results were well reproducible between trials, and voxels in the vicinity of large veins (e.g., the sagittal sinus) were robustly eliminated (Fig. 6.1.2). In addition, the technique provided additional insight into the origin of the BOLD contrast, such as the impact of the significance threshold on the macrovascular contribution to the fMRI signal.

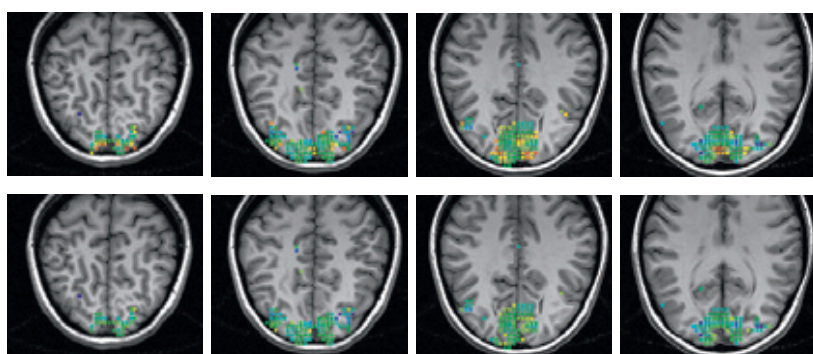


Figure 6.1.2 Maps of the average vessel radius in activated voxels recorded in a healthy subject under visual stimulation. Voxels are color-coded by the logarithm of the average vessel size (between 1 and 100 μm). The top row shows results with all voxels included. In the bottom row, activated voxels with average radii above 30 μm were removed.

6.1.3 Influence of the correlation distance in functional imaging based on intermolecular double-quantum coherences

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In fMRI exploiting intermolecular double-quantum coherences (iDQC), image contrast is based on dipolar couplings between nuclear spins in molecules separated by the so-called 'correlation distance' d_c (Annual Report 2003, Section 2.7.8). The signal is a function of the frequency difference of the two interacting spins, which is sensitive to the distribution of local field gradients whereas conventional BOLD experiments reflect the average gradient strength within an imaging voxel. It was previously postulated that the selection of a length scale for the detection of susceptibility changes – which can be manipulated externally by adjusting d_c – might also imply a selection of blood vessels of a particular size. This would be most valuable as iDQC-based fMRI might permit focusing only on hemodynamic changes in the microvasculature located at a minimal spatial offset from the site of neuronal activity.

For a thorough investigation, iDQC-based fMRI was performed under visual stimulation with variation of d_c be-

tween 60 and 300 μm . Robust activation was obtained in all experiments (Fig. 6.1.3 A) with average signal changes exceeding those normally associated with BOLD-fMRI. Relaxation-rate changes ($\Delta R_2 = 0.33 \pm 0.36 \text{ s}^{-1}$ and $\Delta R_2^* = 0.77 \pm 0.54 \text{ s}^{-1}$) were similar to those commonly obtained for the extravascular BOLD effect. The number of activated voxels increased with increasing d_c until a plateau was reached at approximately 120 μm . Similar trends were observed for the activation-induced percent signal change and for the maximal Z-scores. These effects were quantitatively explained by a reduced sensitivity at short d_c due to increasing signal attenuation related to diffusion and an increasing amount of signal fluctuations in the fMRI time series due to imperfect suppression of unwanted coherence pathways (Fig. 6.1.3 B). Consistent indications of a preferential selection of susceptibility changes in blood vessels of a particular size were not obtained.

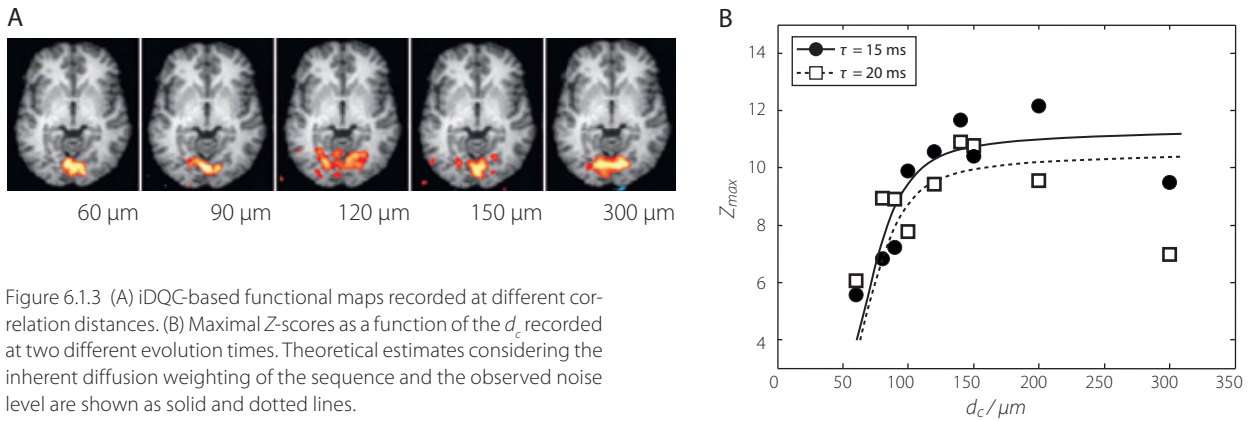


Figure 6.1.3 (A) iDQC-based functional maps recorded at different correlation distances. (B) Maximal Z-scores as a function of the d_c recorded at two different evolution times. Theoretical estimates considering the inherent diffusion weighting of the sequence and the observed noise level are shown as solid and dotted lines.

MATISSE—mapping of arterial transit times by intravascular signal selection

6.1.4

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In perfusion studies, the arterial transit time (ATT) is the duration a tagged bolus of blood needs to travel from the labeling plane to the imaging plane (Annual Report 2003, Section 2.7.5). It is therefore an essential parameter for the quantification of cerebral blood flow and the characterization of vascular diseases, such as stroke. The present work introduces a novel method for ATT mapping in the human brain dubbed 'Mapping of Arterial Transit times by Intravascular Signal SElection' (MATISSE). Goal was the measurement of the phase shift between perfusion-weighted time series recorded from different groups of voxels. The specific implementation was based on continuous arterial spin labeling (CASL). Experimental conditions were chosen to relate the phase shift directly to the ATT difference. This was achieved, firstly, by modulating the inversion efficiency smoothly from repetition to repetition instead of acquiring pairs of label/no-label images. Secondly, short repetition times ($T_R = 500 \text{ ms}$) were applied. An inherent benefit of these conditions is the gain in sensitivity that can be obtained by the application of efficient frequency filtering methods.

In a first study, 10 healthy young subjects were investigated. A single MATISSE scan consisted of 420 repetitions.

The frequency offset of the labeling RF was swept between repetitions to achieve a quasi-sinusoidal inversion efficiency. The labeling RF was applied continuously at the neck with a separate label coil during the first 400 ms of each T_R interval, and two imaging slices were acquired from the brain during the remaining 100 ms. Nine scans (i.e., 18 slices) were recorded sequentially for whole-brain coverage. Fig. 6.1.4 shows an ATT difference map averaged over all subjects. Similar distributions, with increasing ATT differences from inferior to superior and from anterior to posterior, were observed in all subjects. Maximal ATT differences were about 1.9 s.

Although MATISSE is not a direct means for flow territory mapping, results were in good agreement with the known vascular territories of the human brain. A unique feature of MATISSE is its sensitivity to all sizes of arterial vessels: Inflowing blood through the major brain-feeding arteries was identified as was flow through arterioles or capillaries in the border zones between territories. Such zones of late perfusion may be of clinical relevance because they are prone to watershed or low-flow infarctions in case of vascular pathologies and general hypoperfusion.

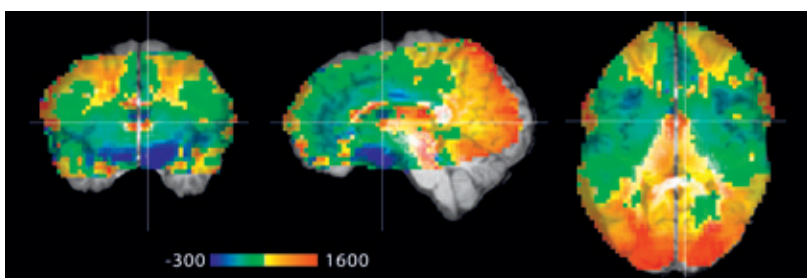


Figure 6.1.4 Coronal, sagittal, and axial slices showing the ATT difference (in msec) with reference to the left and right frontal insula. Maps were averaged over ten subjects and overlaid onto a normalized brain.

6.1.5 Characterization of macromolecular components by cross-regularized inverse Laplace transform of in-vivo proton spectra

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Single-voxel proton spectra of the brain measured at short TE contain a strong baseline signal arising from macromolecules and lipids. The widely used quantitation tool LCModel represents this broad signal as a regularized sum of cubic B-splines. Other algorithms apply weighting of the first data points in the time domain (AMARES). Both approaches benefit from incorporation of prior information, typically obtained from inversion-recovery measurements with nulling of the signals from low molecular-weight molecules (subsequently referred to as 'metabolites'). Among the disadvantages of this strategy are imperfections in the metabolite nulling due to differences in the longitudinal relaxation times, T_1 , of metabolites and the assumption that macromolecules share a common T_1 , which is not necessarily fulfilled.

We propose a method to extract the macromolecular baseline by inverse Laplace transform (ILT) of a series of 64 spectra recorded with STEAM and variation of the mixing time, T_M . The ILT is an ill-posed computation re-

quiring a strong regularization of the non-negative least-squares fit. This is typically achieved by penalizing non-smooth solutions and, hence, returning broad peaks in the relaxation domain that proved inadequate for separation of macromolecules and metabolites. To enhance the T_1 resolution, we applied a novel cross-regularized ILT, which computed a two-dimensional map as a function of the resonance frequency and $\log T_1$ by imposing smoothness in the frequency domain rather than the relaxation domain.

The proposed cross-regularized ILT yielded a good T_1 -based separation of macromolecules and metabolites as shown in Fig. 6.1.5 A. In order to identify the macromolecular signals, an integration of the metabolite cluster was performed by combining basis sets of metabolites, which were reliably detected by LCModel: *N*-acetylaspartate, cholines, total creatine, glutamate, glutamine (Gln), and myo-inositol. Each proton group was fitted to a Gaussian distribution along the $\log T_1$ dimension. The

resulting metabolite signal was used to iteratively update a boundary defining the separation between macromolecules and metabolites.

An assessment of the macromolecular baseline is shown in Fig. 6.1.5 B. In addition to the macromolecular signals labeled M1 – M10 (as already known from metabolite-nulled approaches), five additional peaks were identified in the macromolecular baseline (m6a, m8a, m8b, m8c, m9a). The γ -methylene signal of Gln displayed a broad distribution of $\log T_1$, which was attributed to either an interaction of its side-chain with binding sites or to an interference with the macromolecular cluster forming beneath (m6a).

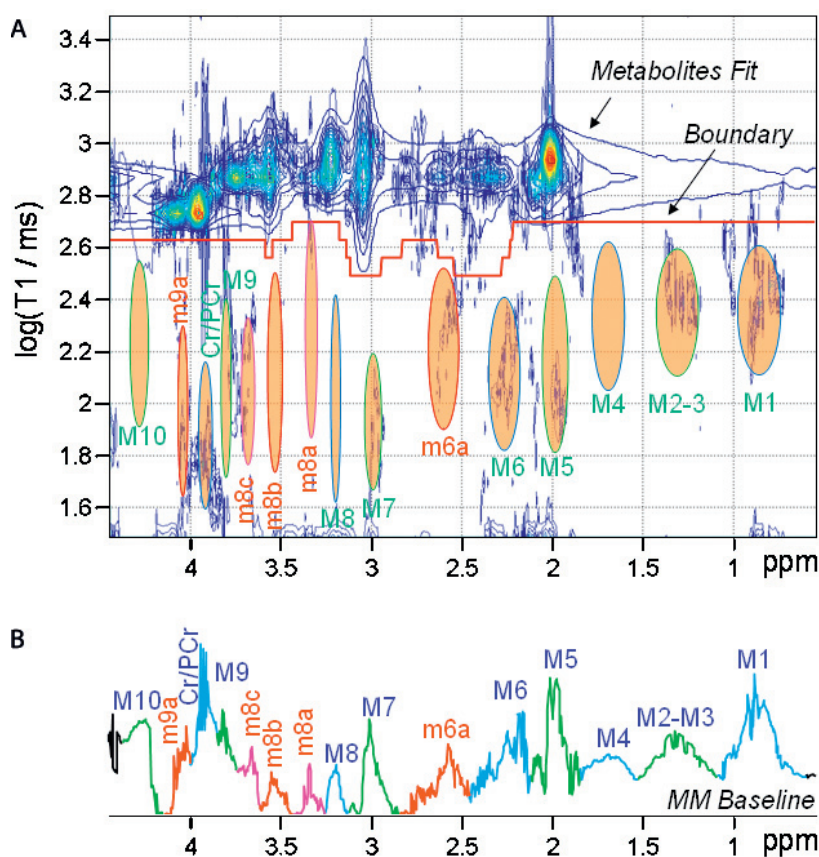


Figure 6.1.5 (A) Relaxogram obtained with cross-regularized ILT of a series of STEAM spectra ($T_R = 6$ s, $T_E = 20$ ms) with varying T_M and (B) extracted macromolecular baseline.

Congresses, Workshops, and Symposia

Möller, H. E. (December). *Annual Plenary Meeting "Advanced signal processing for ultra fast magnetic resonance"*. Conference. Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.

■ 2007

Appointment

Möller, Harald E. *Honorary Professorship*. University of Leipzig, Germany.

■ 2007

Degrees

Habilitation

Pampel, A. *Hochauflösende MAS-NMR-Spektroskopie kombiniert mit gepulsten Feldgradienten – Neue Möglichkeiten zur Untersuchung des Stofftransports in komplexen Materialien [High-resolution MAS NMR spectroscopy in combination with pulsed field gradients – Novel possibilities for the investigation of transport phenomena in complex materials]*. Faculty of Physics and Earth Science, University of Leipzig, Germany.

■ 2006

PhD Thesis

Schäfer, A. *Funktionelle Bildgebung mittels magnetischer Resonanz (fMRI) auf der Grundlage intermolekularer Multiquantenkohärenzen [Functional imaging using magnetic resonance (fMRI) on the basis of intermolecular multi-quantum coherences]*. University of Leipzig, Germany.

■ 2006

Award

Lepsien, J. *Merit Award*. Department of Experimental Psychology, University of Oxford, United Kingdom.

■ 2006

Publications

Books and Book Chapters

Möller, H. E. (2006). Grundlagen der MRT [Fundamentals of MRI]. In E. J. Rummeny, P. Reimer, & W. Heindel (Eds.), *Ganzkörper-MR-Tomographie* (pp. 2-23). Stuttgart: Thieme.

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6.2

Mathematical Methods in fMRI

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. Lipsia has by now evolved into a mature software package that allows for a very efficient data analysis. A recent study has shown that a typical analysis sequence from the raw data to the final result takes no more than about five minutes per test subject on a standard Linux workstation.

As in recent years, we have continued our research into the development of new mathematical methods for meta-analysis of fMRI data. We have now established a very fruitful international collaboration with research groups at the University of Texas, at Nottingham University and at Georgetown University. This project is funded by a National Institutes of Health (NIH) grant. Here, our aim is to identify relationships between brain areas using coordinate data of a meta-analysis data base located in San Antonio, Texas.

At the same time, we have also developed new methods for identifying relations between brain areas on the basis of single subject fMRI time series data. In this context, we

have further refined the replicator dynamics approach. An entirely new mathematical approach that we have recently developed is based on the analysis of single trial data. The primary idea is to correlate the BOLD responses in different brain areas on a trial-by-trial basis. As the raw data of single trials would be far too noisy for this purpose, we first extract their most salient features using a matrix factorization called “non-negative matrix factorization (NMF)”. This method allows us to tackle the problem at a more abstract level. Applications to fMRI data have already yielded promising results.

Finally, we have continued our research into understanding human cortical folding. In a recent study, we investigated locally deepest regions of the cortical sulci and found that they are arranged in a strikingly regular pattern suggesting that their locations are under a close genetic control.

6.2.1 Deep sulcal landmarks provide an organizing framework for human cortical folding

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The folding pattern of the cerebral cortex and its relation to functional areas is notoriously variable, and there is a need to identify more consistent 3D topographical cortical features. We analysed magnetic resonance brain images of 96 normal adult human volunteers using automated 3D image analysis methods. We examined the deeper parts of the sulci, because they generally show

less inter-individual variability than more superficial parts, especially in monozygotic twins, and deepest parts of primary sulci are the first to develop embryologically and change least as the cortex expands. Along the length of each sulcus we found that there is generally one well defined zone where depth is maximal, which we term the sulcal pit. Long sulci may have two or three pits. The spatial arrangement of pits is strikingly regular, forming alternating chains of deeper and shallower pits. We hypothesize that the pits are encoded in the protomap described in (Rakic 1988) and are under closer genetic control than the rest of the cortex, and are likely to have a more consistent relationship to functional areas.

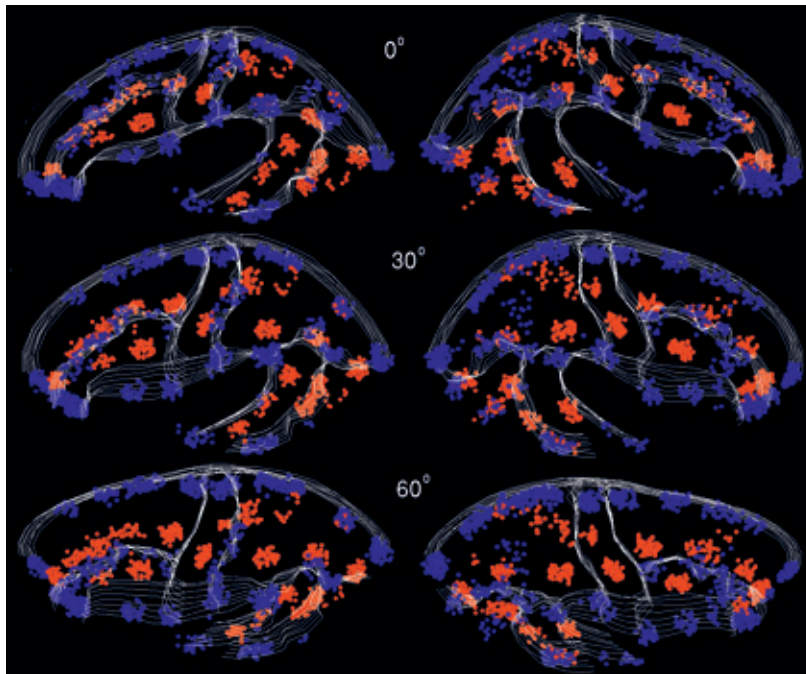


Figure 6.2.1 Location of major and minor sulcal pits from the group of 96 subjects. Left and right lateral views are shown in the left and right columns; rows show degrees of rotation from true lateral (top row) towards a more superior viewpoint. Pits of major sulci are shown as red spheres, minor as blue. The pit clusters are arranged in interleaved chains that mark a clear spatial separation between these two types of pits. For clarity, only regions where pit density was maximal are shown.

6.2.2 Non-negative matrix factorization for single trial analysis of fMRI data

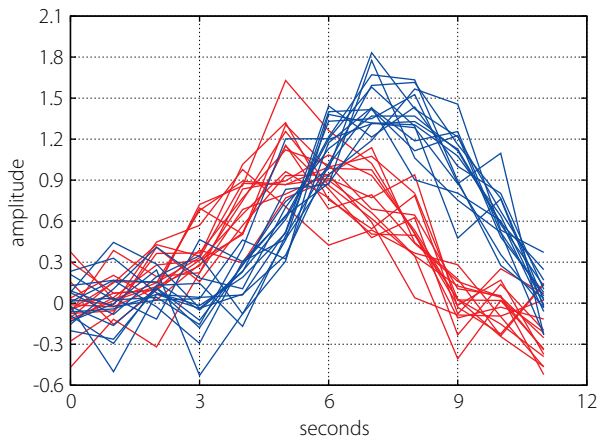
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The analysis of single trials of an fMRI experiment is difficult because the BOLD response has a poor signal to noise ratio and is sometimes even inconsistent across trials. We propose to use non-negative matrix factorization (Lee & Seung, 1999, *Nature*, 401, 788-791) as a new technique for analysing single trials. NMF yields a matrix decomposition that is useful in this context because it elicits

the intrinsic structure of the single trial data. In addition to analyzing single trials in one brain region, the method is also suitable for investigating interdependencies between trials across brain regions. The method even allows to analyze the effect that a trial has on a subsequent trial in a different region at a significant temporal offset. This distinguishes the present method from other methods



that require interdependencies between brain regions to occur nearly simultaneously. The method was applied to fMRI data and found to be a viable technique that may be superior to other matrix decomposition methods for this particular problem domain.

Figure 6.2.2 A synthetically generated set of 30 trials. The example simulates fMRI trial data where the BOLD response to the same stimulus type varies across the duration of the experiment. In this example, there are two distinctly different groups of trials that peak at different times that are color-coded for better visualization. We found the NMF provides a data representation that is well suited for capturing salient features such as these.

The parcellation of cortical areas using replicator dynamics in fMRI

6.2.3

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⁴ NordicNeuroLab, Bergen, Norway

One of the main goals in functional magnetic resonance imaging (fMRI) is the parcellation of cortical areas with respect to their different functionality. Model-based approaches facilitate the dissociation of cortical areas by directly manipulating the underlying cognitive processes. In contrast, exploratory analysis techniques examine the inherent structure of the data independently of the experimental design or any pre-defined model of the hemodynamic response.

We have developed a new exploratory method for the detection of sub-regions of cortical areas on the basis of the similarity between fMRI time series. Our method facilitates two well-known mathematical concepts, replicator dynamics and canonical correlation. More specifically, the method exploits the structure of a similarity matrix

derived from the canonical correlation between fMRI time series by means of a replicator process.

Canonical correlation computes the correlation of groups of variables, in our context two voxels and their respective neighbors. Using this multivariate approach is advantageous, since it takes into account the spatial dependencies of neighboring voxels present in fMRI data. The resulting similarity matrix is then subjected to a replicator process in search of the so-called dominant network, in our context the group of voxels showing the highest correlation between them. A repeated application of the replicator process facilitates the detection of several such groups. These highly correlated groups of voxels might be interpreted as functional sub-regions of the investigated region of interest. (Fig. 6.2.3)

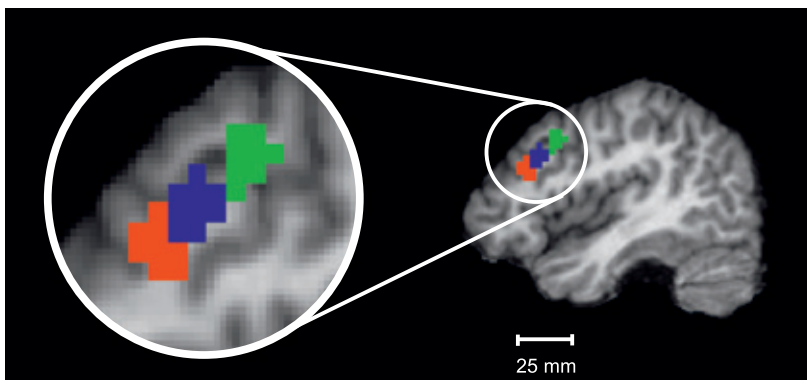


Figure 6.2.3 Results from applying our method to a region of interest in the lateral frontal cortex derived from fMRI measurements of a subject performing a task switching experiment.

6.2.4 Model-based clustering of meta-analytic functional imaging data

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The comparison and integration of imaging results on a meta-analytic level has become a much researched topic, given the increasing availability of experimental results in publicly accessible imaging data bases. Coordinate-based meta-analyses, for example, explore activation coordinates reported from independently performed imaging experiments in search of functional cortical areas that are relevant for the investigated cognitive task.

We have developed a new method for the coordinate-based meta-analysis of functional imaging data. The method is based on Activation Likelihood Estimation (ALE) and subsequent model-based clustering using Gaussian

mixture models, expectation-maximization (EM) for model fitting, and the Bayesian Information Criterion (BIC) for model selection. Our method facilitates the clustering of activation maxima in a hierarchical fashion. Regions with a high concentration of activation coordinates are first identified using ALE. Activation coordinates within these regions are then subjected to model-based clustering for a more detailed cluster analysis (Fig. 6.2.4).

Our method offers several advantages compared to the application of ALE alone. Most importantly, it is less sensitive to the parameterization of the Gaussian applied in ALE. Moreover, the size of the determined sub-clusters of ALE regions is independent of the overall distribution of the activation coordinates.

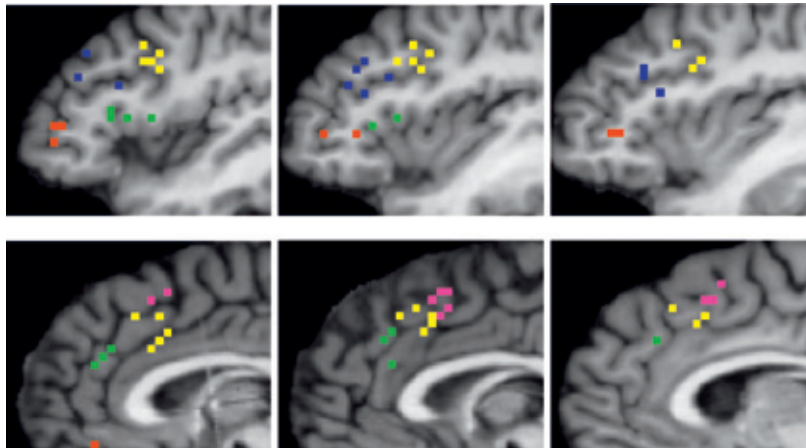


Figure 6.2.4 Results from applying our method to activation coordinates in the left pre-frontal cortex (top) and the medial frontal cortex (bottom). Both areas were identified as large continuous ALE regions. Different colors represent different sub-clusters within these regions as determined by model-based clustering. Activation coordinates were extracted from the BrainMap database and represent results from 26 Stroop experiments.

6.2.5 Detecting groups of coherent voxels in fMRI data using spectral analysis and replicator dynamics

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In order to detect groups of coherent voxels in fMRI data, we propose the combination of the approaches of spectral analysis and replicator dynamics.

We investigated simulated and real fMRI time courses using the coherence, a bivariate measure resulting from spectral analysis. The coherence values were placed in coherence matrices which encode the relationship between the time courses. These coherence matrices were investigated twice. First, groups of coherent voxels were

detected from the matrix by choosing a reference voxel j and determining all voxels k whose coherence with j exceeds a given threshold. The reference voxel was automatically determined using the so-called number of coherent voxels (NCV). Second, a replicator process was applied in order to search for groups of maximally coherent voxels.

Simulations as well as real fMRI data showed that the group of coherent voxels detected by the NCV method

depends critically on the threshold which has to be chosen in advance. The lower the threshold, the larger the detected group. Higher thresholds lead to less sensitivity of the method. Using higher NCV thresholds in our simulations, the method did not detect all voxels that were constructed to have a high coherence among each other. In contrast, the replicator process was detecting the whole group in all simulations (Fig. 6.2.5.1). A replicator process is able to determine groups of voxels with the property that each voxel in the group exhibits a high coherence with every other group member. In contrast to the NCV approach, this method is parameter-free and does not require the a priori selection of a reference voxel.

We also investigated the advantage of using spectral coherence instead of correlation coefficients as a similarity measure for the replicator process. In our simulations, the replicator process detected only a part of the coherent voxels when the Pearson correlation was used. These results were comparable with the analysis of the real fMRI data. For all subjects, the application of a replicator process to correlation matrices revealed only a fraction of the group of coherent voxels detected by using the coherence matrix. This is most likely caused by the dependence of the correlation on temporal shifts between the fMRI time series (Fig. 6.2.5.2).

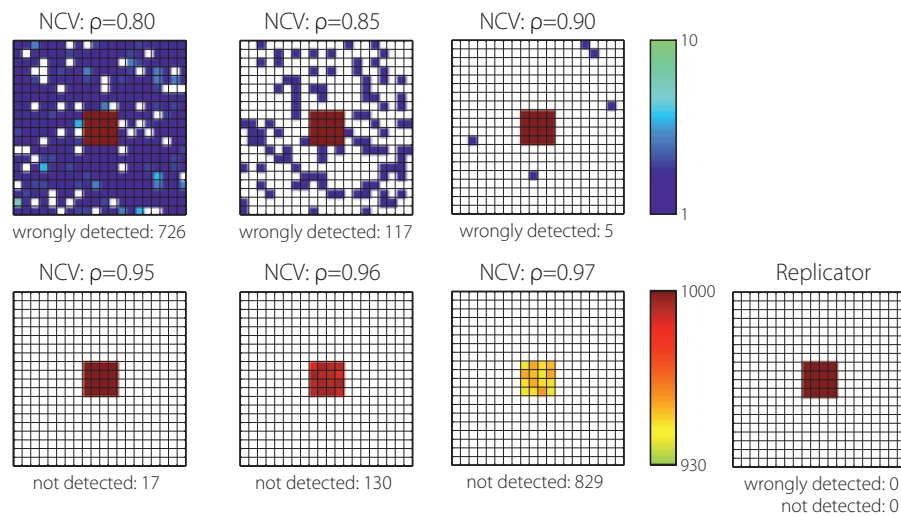


Figure 6.2.5.1 Analysis of the coherence between simulated fMRI time courses using replicator dynamics and NCV with different thresholds. Each of the six sub-figures is the result of 1000 runs with 20x20 simulated fMRI time series. In the center of the grids, 4x4 time series were constructed to be coherent among each other. The simulations show that the analysis of coherence matrices using NCV critically depends on the selected threshold. Using a lower threshold, all 4x4 coherent time series were detected in all 1000 cases. However, the method found also voxels outside the 4x4 group. Using a higher threshold, no voxels outside the 4x4 group were detected. However, then the NCV method did not find all 4x4 coherent time series. The replicator process (left sub-figure) identified the entire group of the 4x4 coherent time courses in all 1000 runs without detecting any voxels outside the 4x4 grid.

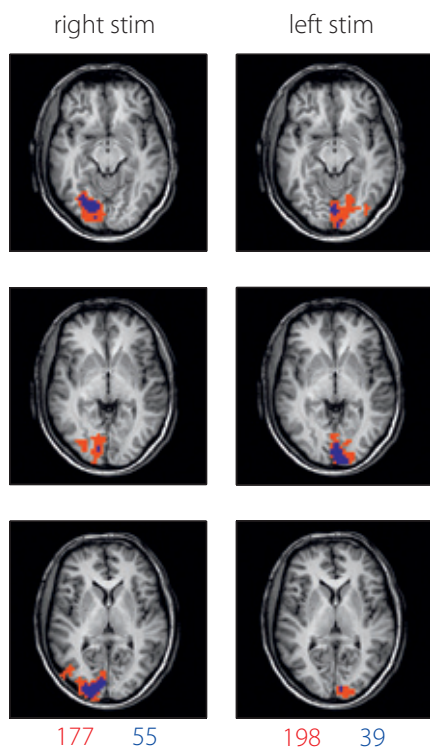


Figure 6.2.5.2 Three axial slices of a single subject showing the application of a replicator process to a spectral coherence matrix (voxels in red) and to a correlation matrix (voxels in blue). At the bottom, the number of voxels in the coherent groups are printed in red and blue, respectively. Time courses in both hemispheres were analyzed separately. Taking the results of the simulations into account, the reduced group size for the correlation is likely to be caused by the phase displacements between the fMRI time courses.

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Degree

Habilitation

- 2006** ■ Müller, K. *Die Anwendung von Spektral- und Waveletanalyse zur Untersuchung der Dynamik von BOLD-Zeitreihen verschiedener Hirnareale [Using spectral and wavelet analysis to investigate the BOLD dynamics of different brain regions]*. Faculty of Medicine, University of Leipzig, Germany.

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Zysset, S., Schroeter, M. L., Neumann, J., & von Cramon, D. Y. (2007). Stroop interference, hemodynamic response and aging: An event-related fMRI study. *Neurobiology of Aging*, 28(6), 937-946.

Zysset, S., Wendt, C. S., Volz, K. G., Neumann, J., Huber, O., & von Cramon, D. Y. (2006). The neural implementation of multi-attribute decision making: A parametric fMRI study with human subjects. *NeuroImage*, 31(3), 1380-1388.

6.3

MEG and EEG: Signal Analysis and Modeling

In 2006 and 2007 two events were especially important for our working group. Firstly, we split into two groups. The new group, 'Cortical Networks and Cognitive Functions', led by Thomas Knösche, focuses on the characterization of cortical networks for modeling brain functions. The group does this by combining structural measures as provided by e.g. T1-MRI and DTI data with data from functional methods (EEG, MEG, fMRI) into dynamical cortical models. Central to the group is the close cooperation with the MPI for Neurology in Cologne as well as with our group 'MEG and EEG: Signal Analysis and Modeling'. Secondly, a new magnetoencephalography device was bought by the Institute. The new device, a whole head system Vectorview (by Elekta Neuromag, Helsinki, Finland), has been operational since the end of 2006. It offers a number of great improvements over the previous one since it permits combined recording of EEG and MEG and offers twice as many channels as before. Importantly, it provides a head position indicator system which can be activated during measurements, thus providing almost continuous head position tracking.

Our group is involved in both methodological and neurocognitive research and has benefited considerably from close collaborations with researchers from other institutions in Jena, Münster, Leipzig, Berlin, Hamburg, Graz, Havana, and Beijing.

One important branch of our research concerns the forward modeling of the human brain. The Finite Element method (FEM) opens promising new avenues for the more precise analysis of electro- and magnetoencephalographic data (EEG and MEG) of children and patients. Anwander et al. (6.3.1) discuss alternatives for defining volume conductors as well as in modeling electrical sources within the brain. They also consider the influence of anisotropic conductivity profiles for the more accurate localization of EEG and MEG measurements.

Another important part of our recent research involves the modeling of functional connectivity based on EEG or MEG data. We believe the method of partial directed coherence (PDC) will be capable of revealing the direction of information transfer between two coupled regions. However, thorough investigation of the PDC method as applied to EEG data by simulations of dynamical interactions between different brain areas (Grigutsch, 6.3.2) showed that the method under certain conditions displays connectivities that are not in fact present in the brain. The PDC method was applied to analyze the dynamics of the estimated brain activity pattern and has revealed the directional connectivity between centers of oscillatory brain activity (Supp. 6.3.3). A promising way to determine anatomical connectivities from diffusion tensor imaging (DTI) data is shown in 6.3.4. Furthermore, Gruber (6.3.5) demonstrated that MEG measurements are well suited to observing and localizing induced Gamma band responses (iGBR) avoiding the confounds that are typically introduced by the EEG reference electrode.

Research on processing auditory stimuli like speech and music is probably the most established branch in our group. Cross-cultural comparisons between Chinese and Western styles of music described in Knösche, Nan, Zysset, & Friederici (2.1.20). Männel, Neuhaus, & Friederici (2.2.3) investigated how phrasing in spoken sentences and music is processed in infants and adults. Recently, we also started research into mathematical processing. A first contribution here is our ERP-study on arithmetical processing by Wang (6.3.6). Finally, we investigated how the magnetic counterpart of the well-known mismatch negativity (MMNm) is localized in the brain by applying the so-called controlled paradigm. This paradigm can disentangle deviancy detection from refractoriness. We found temporally distinct but spatially overlapping activities for both types of automatic change detection (Maess, 6.3.7).

Influence of meshing, dipole modeling and anisotropic conductivity on EEG source analysis

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Source reconstruction from EEG and MEG data is strongly influenced by the modeling of the head volume conductor and the current dipole representation. We first evaluated the influence of improved mesh generation on Finite Element (FE) method based source analysis. We proposed smoothing regular hexahedral finite elements at material interfaces using a node-shift (ns) approach. Two different techniques for modeling a current dipole in FE volume conductors, a subtraction and a direct potential method were compared. We computed and visualized potential distributions for a source in the somatosensory cortex in regular and smoothed three-compartment hexahedra FE volume conductor models of the human head using both the subtraction and the direct potential method. Node-shifting reduces both topography and magnitude

errors by more than a factor of 2 for tangential and 1.5 for radial sources for both potential approaches.

To quantify the influence of electrical and structural anisotropy on the source reconstruction, we performed simulations and source localization based on invasive measurements in a rabbit head. Anisotropic conductivity information was obtained from diffusion MRI. Anisotropy influenced source location of up to 1.3 mm with a mean value of 0.3 mm. The averaged orientation deviation was 10 degrees and the mean magnitude error of the dipole was 29%. The expected average source localization error due to anisotropic white matter conductivity was within the accuracy limits of current inverse procedures. By contrast, dipole orientation and dipole strength were influenced significantly by the anisotropy.

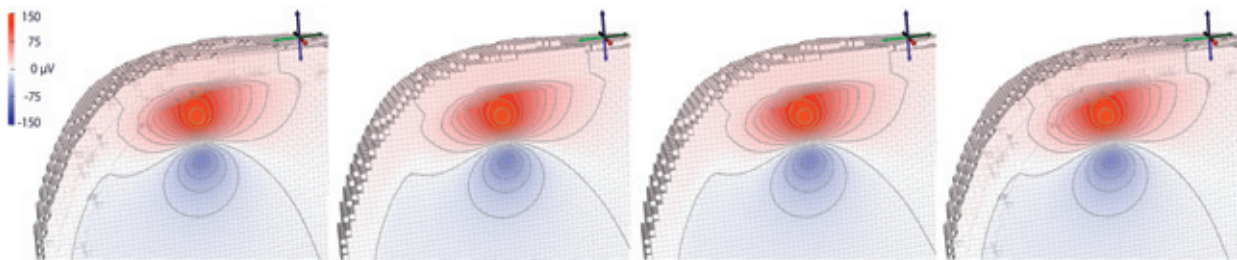


Figure 6.3.1.1 Potential distribution for a dipole in the somatosensory cortex in a regular and a node-shifted hexahedra FE model. Left: subtraction dipole (smooth, regular), right: direct dipole modeling (regular, smooth).

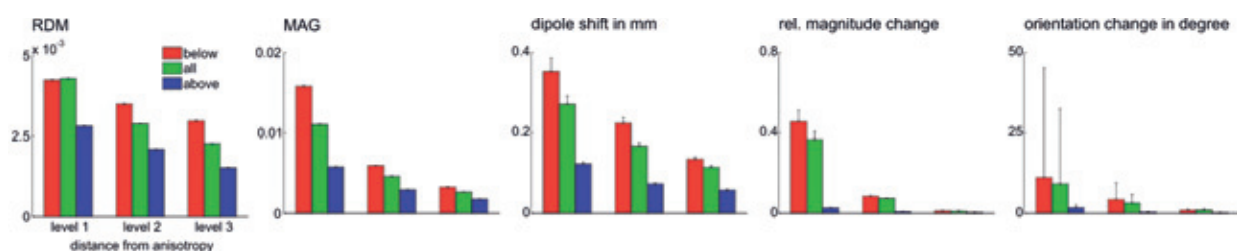


Figure 6.3.1.2 Analysis of the influence of the distance on relative difference measure (RDM), magnification factor (MAG), dipole shift, relative magnitude change and orientation change. Level 1–3 indicates decreasing distances of source locations with respect to the anisotropic volume. The results are presented for deep sources (below anisotropy volume, red), superficial locations (above, blue) and all positions.

6.3.2 Specificity of PDC and DTF – An EEG simulation study

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Modeling the dynamic interactions between brain regions is a key issue for the understanding of higher cognitive functions in humans. In this simulation study, we used partial directed coherence (PDC) and the directed transfer function (DTF) to reveal the directionality of information flow between hypothetical brain regions. We utilized forward simulations for a 4-shell spherical head model to generate scalp EEG data with known underlying cortical interactions. Multivariate autoregressive (MVAR) models were then fitted to subsets of the simulated channels and the frequency-dependent PDC and DTF coefficients were calculated. The observed scalp connectivity patterns were found to depend strongly on the chosen reference signal and on the orientation and depth of the interacting source dipoles. Especially for deep or tangential sources, a number of spurious interactions as well as missing links were detected. For shallow sources with nearly radial orientation (deflections < 45 deg), the specificity of the estimated connectivity coef-

ficients could be substantially improved by computing local estimates of the surface Laplacian derivation prior to MVAR analysis (Fig. 6.3.2).

In contrast to previous suggestions (Kaminski and Blinowska., 1991, *Biol Cybern* 65, 203-210; Kaminski and Liang, 2005, *Crit Rev Biomed Eng* 33, 347-430; Ginter et al., 2001, *J Neurosci Meth* 110, 113-124), the present study shows that PDC and DTF cannot distinguish between true time-lagged interactions of distant neuronal populations and simultaneous cross-talk between sensor measures due to the spatial smearing of cortical signals by volume conduction or the existence of a non-silent common reference. The inference of true cortical interactions requires the preprocessing of scalp recordings in order to increase their spatial resolution and to remove the influence of the EEG reference. Future investigations will aim to combine MVAR analysis with inverse source modeling techniques.

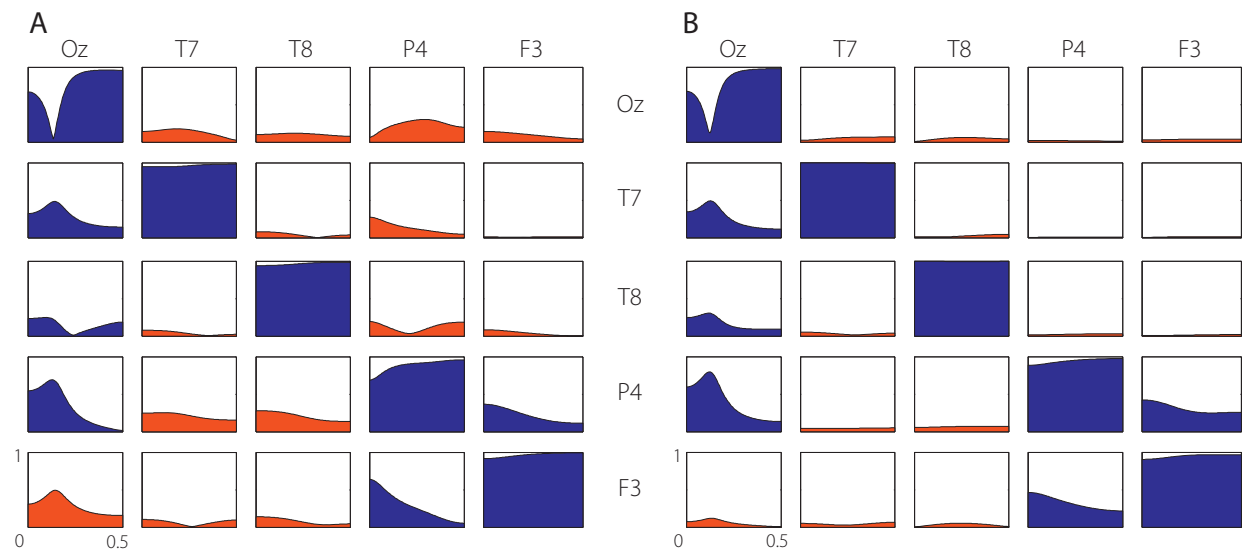


Figure 6.3.2 Estimated PDC coefficients versus normalized frequency obtained from (A) simulated scalp recordings and (B) surface Laplacian derivations. Coupled cortical regions were simulated as 5 correlated current dipoles located in the middle occipital, right posterior parietal, left and right temporal, and left frontal brain regions located beneath the electrodes Oz, P4, T7, T8, and F3, respectively. The sources of information flow are given in the columns. Identified true interactions are shown in blue, spurious interactions are highlighted in red.

Information transfer and long-range synchrony during human object recognition: Analyzing EEG gamma responses in brain's source-space

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The increase of induced gamma-band-responses (IGBRs; oscillations >30 Hz) elicited by familiar (i.e., meaningful) objects is well established in electroencephalogram (EEG) research (e.g., Kaiser and Lutzenberger, 2003, *Neuroscientist*, 9, 475-484; Gruber and Müller, 2006, *Brain Res*, 1097, 194-204). This frequency-specific change at distinct electrodes is thought to indicate the dynamic formation of local neuronal assemblies during the activation of cortical object representations. However, power increase, as a single-channel property, does not reveal

oscillatory interactions between spatially distant locations. Therefore, power change alone is not sufficient to investigate the formation of large-scale networks.

This study is the first to identify the directionality of oscillatory brain interactions in source space during human object recognition and suggests that familiar, but not unfamiliar, objects engage widespread reciprocal information flow. Directionality of cortical information-flow was calculated based upon a Granger-Causality coupling measure, partial directed coherence (PDC)

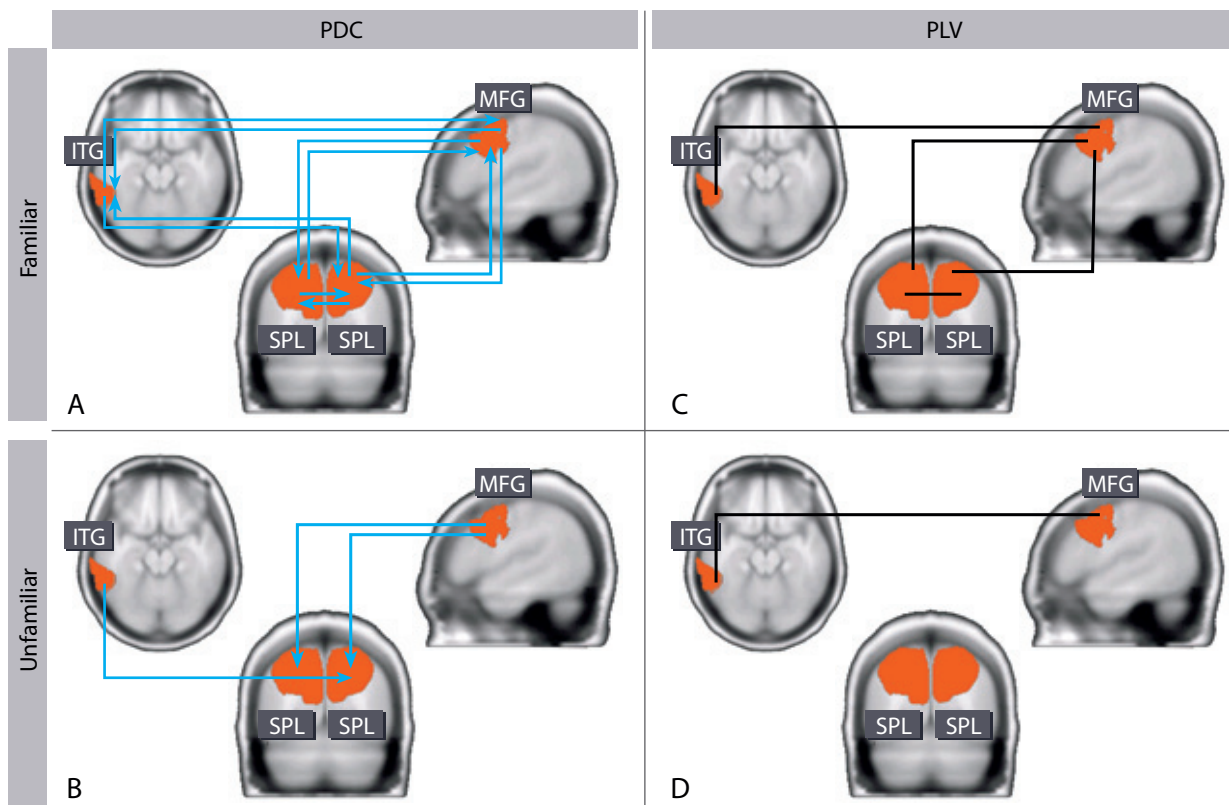


Figure 6.3.3 The inverse solutions of the induced gamma effect are mapped at their corresponding anatomical locations as red areas. The arrows of the PDC results (on the left side) represent the direction of information transfer and were only drawn if the PDC values were significant ($p < 0.001$). The lines on the right display significant increases of phase-synchrony ($p > 0.001$) calculated between all pairs of source-reconstructed brain areas. Both coupling measures were applied to the time-window of the increased gamma band responses (150 to 400 ms post-stimulus onset) elicited by meaningful (familiar) and meaningless (unfamiliar) pictorial object presentation.

(Baccala and Sameshima, 2001, *Biol Cybern* 84, 463-474; Schlögl and Supp, 2006, In Neuper and Klimesch, eds., Amsterdam: Elsevier. pp. 137-152). To validate the plausibility of this advanced coupling measure resting on autoregressive modeling, PDC results were contrasted with conventional phase-locking analysis (PLA), a symmetric measure derived from wavelet-based signal decompositions lacking directional information. Both, autoregressive modeling and wavelet analysis, revealed an augmentation of iGBRs during the presentation of familiar pictorial objects relative to unfamiliar controls, which were localized to inferior-temporal, superior-parietal and frontal brain areas by means of distributed source reconstruction. PLA between these sources replicated previous findings (Gruber et al., 2006, *Neuroimage*, 29, 888-900), showing a dense pattern of significant long-range gamma-band phase-synchrony as opposed to control stimuli (see Fig. 6.3.3).

PDC, however, instead of merely describing pair-wise synchronicity, was capable of tracing a network of extensively reciprocal information transfer between frontal, temporal and parietal iGBR generators elicited by familiar stimulus presentation. In contrast, unfamiliar objects entailed a sparse network of only unidirectional connections from temporal and frontal areas which converge on parietal areas.

The bidirectional PDC coupling pattern in response to familiar objects may be seen as direct empirical support for the idea that functional brain networks successfully implementing object feature integration are realized by reciprocal (feed-forward and feed-backward) oscillatory interactions between functionally specific brain locations (inferior temporal, superior-parietal and frontal areas). In contrast, the sparse pattern of unidirectional connections possibly reflects the restricted processing of isolated object features that remain present in unfamiliar stimuli, but fail to activate distinct structural information. This restricted processing seems to be realized by frontal activity and inferior temporal activity, which both converge to parietal areas, a brain site repeatedly associated with visual feature integration.

All in all, the PDC coupling patterns associated with the activation of cortical object representation were generally in agreement with those of the traditional PLV analysis, but qualitatively extended them by delivering the directionality of brain interactions. Given that the PDC results do not only match widely assumed theoretical expectations regarding visual object processing, but also fit into experimental data addressing the functional role of specific brain areas, PDC seems to be a potentially useful tool for providing functionally plausible results regarding the directionality of brain interactions.

6.3.4 Parametric spherical deconvolution: Inferring anatomical connectivity using diffusion MR imaging

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The human brain forms a complex neural network with a connectional architecture that is still far from being known in full detail, even at the macroscopic level. The advent of diffusion MR imaging has enabled the noninvasive exploration of the nerve fiber system in vivo. We propose a new forward model that maps the microscop-

ic geometry of nervous tissue onto the water diffusion process and further onto the observable MR signals. Our spherical deconvolution approach completely parameterizes the fiber orientation density by a finite mixture of Bingham distributions, which yield a closed form expression. In addition, we define the term anatomical connec-

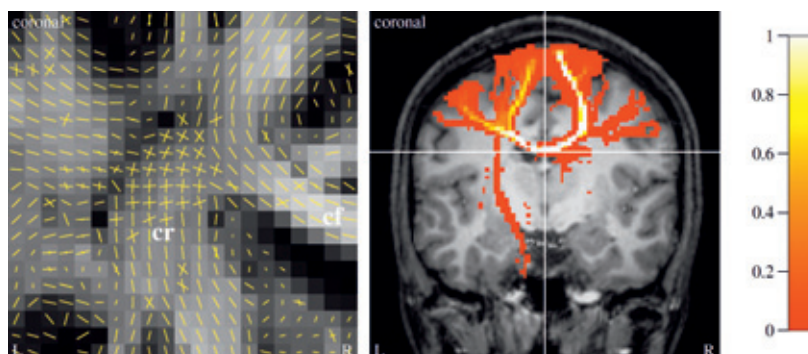


Figure 6.3.4 Mean fiber bundle orientation of the callosal fibers (cf), the corona radiata (cr) and their crossing (left). The right panel shows the posterior probability map (that the anatomical connectivity exceeds the threshold 10%) of the radiation of the corpus callosum.

tivity, taking the underlying image modality into account. This neurophysiological metric represents the percentage of the nerve fibers originating from a source area which intersects a given target region. The specified inverse problem is solved by Bayesian statistics. Posterior probability maps denote the probability that the connectivity value exceeds a chosen threshold, conditional upon the noisy observations. These maps allow us to draw inferences about the structural organization of white matter. For example, the proposed approach is capable of disentangling the crossing of the callosal fibers and the corona

radiata using diffusion-weighted data sets featuring high angular resolution. Moreover, we demonstrate that the commissural fibers passing along the central part of the corpus callosum do not only project into the medial and superior areas as suggested by the traditional diffusion tensor model, but also radiate towards the lateral regions of the cerebral cortex, thus replicating the known connective neuroanatomy.

Sources of synchronized induced Gamma-Band Responses during a simple object recognition task: A replication study in human MEG

6.3.5

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Natural stimuli are comprised of numerous features, which are cortically represented in dispersed structures. Synchronized oscillations in the Gamma-Band (>25 Hz; induced Gamma-Band Responses, iGBRs), are regarded as a plausible mechanism for re-integrating these regions into a meaningful cortical object representation. Using electroencephalography (EEG), it was demonstrated that the generators of iGBRs can be localized to temporal, parietal, posterior, and frontal areas. The present magnetoencephalogram (MEG) study intended to replicate these findings in order to contribute to the ongoing debate regarding the possible functional difference of high-frequency signals as measured by both techniques.

During a standard object recognition task we found an augmentation of the iGBR after the presentation of meaningful as opposed to meaningless stimuli at ~160-440 ms after stimulus onset in a frequency range of ~60-95 Hz. This peak was localized to inferior temporal gyri, superior parietal lobules and the right middle frontal gyrus (see Figure 6.3.5). Importantly, most of these brain structures were significantly synchronized with each other.

The implications of these results are twofold: (1) they present further evidence for the view that iGBRs signify synchronous neuronal activity in a broadly distributed network during object recognition. (2) MEG is well suited to detecting induced high-frequency oscillations with a

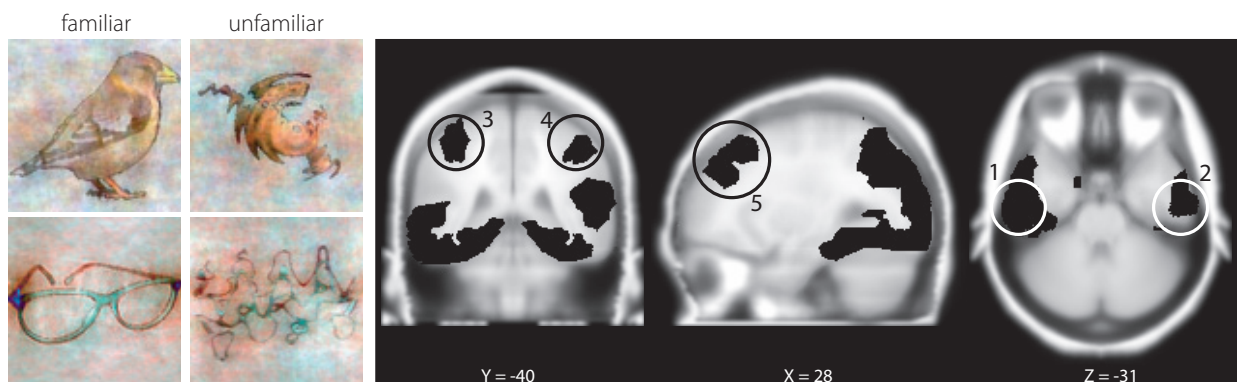


Figure 6.3.5 Left: Excerpt of stimulus sequence. Familiar (meaningful) and unfamiliar (meaningless) color pictures were presented in randomized order. Right: Statistical Parametric Maps of the inverse solutions of the effect of stimulus type of the iGBR (160-440 ms; 60-95 Hz). Voxels showing a significant effect ($P < 0.01$) are marked black. Circles indicate regions for which coupling analyses were performed (1,2 - inferior temporal gyri; 3,4 - superior parietal lobules; 5 - right middle frontal gyrus). X, Y and Z-coordinates values represent the location of each of the displayed slices in MNI space.

very similar morphology as revealed by EEG recordings, thereby eliminating known problems with electroencephalographical methods (e.g., reference confounds). Additionally, the localization of the generators of event-related fields and evoked Gamma-Band Responses re-

vealed sources in early sensory areas, and, thus, seem to mirror complementary functions during object identification.

6.3.6 Executive inhibition in mental arithmetic

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In a series of studies focusing on inhibitory executive control, a frontocentral N2 was suggested as an ERP correlate reflecting response inhibition. However, as previous studies were mainly restricted to Go/NoGo tasks, flanker tasks and Stroop tasks, a question is raised whether the modulation of the frontocentral N2 amplitude is present in other cases of response competition as well. In the present study, event-related potentials (ERPs) were measured to investigate executive inhibition in a mental arithmetic task. Subjects had to compute arithmetic expressions visually presented in four chunks, each of which comprised a number followed by an operator. The first operator was a "+" or a "-". The second operator was either another "+" or "-" ("Calculate" condition) or a "x"

("NoCalculate" condition). ERP analyses were conducted for the second chunk comparing the "NoCalculate" to the "Calculate" conditions. In the NoCalculate condition, subjects were required not to compute the intermediate result since the second operation was a multiplication, which had priority over the addition or subtraction. The results showed a negative response (N380) over frontocentral regions at about 380 ms, and a late posterior positivity (LPC) which was similar in amplitude across both conditions. The N380 can be differentiated from the classical N400 in two aspects. Firstly, a semantic violation associated with the N400 was involved in neither condition of the present study. Secondly, while the N400 usually shows a central or centroparietal distribution, the N380 was frontocentrally distributed. The N380 was interpreted as a late NoGo-N2 effect, reflecting the calculation inhibition demanded in the NoCalculate condition. Additionally, the dN380 (NoCalculate-Calculate difference) was more pronounced in the right hemisphere. This is consistent with the findings of previous fMRI and PET studies which report that the right prefrontal cortex is closely associated with response inhibition. Our results further support the generalization of the frontocentral N2 as a neurobehavioral tool for investigating inhibitory executive functions.

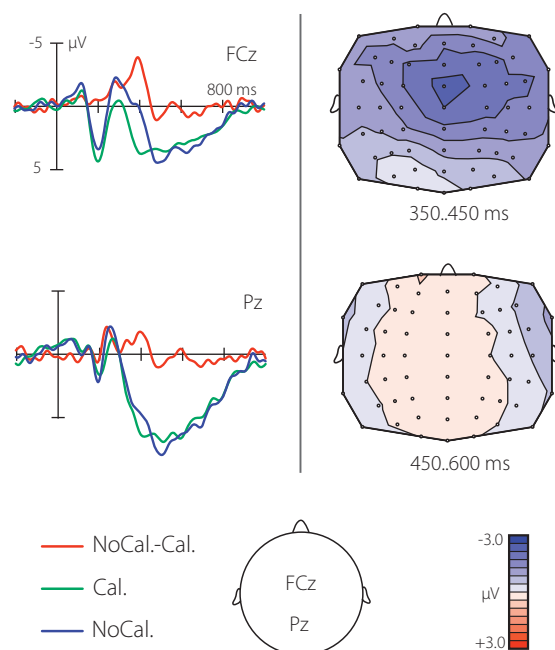


Figure 6.3.6 Left panel: grand averaged ERPs for the two conditions and the difference wave (NoCalculate minus Calculate). Right panel: scalp topographies for the difference wave of NoCalculate minus Calculate in the time range corresponding to the N380 (upper plot) and the LPC (lower plot).

Localizing pre-attentive auditory memory-based comparison: Magnetic mismatch negativity to pitch change

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Changes in the pitch of repetitive sounds elicit a mismatch negativity (MMN) of the event-related brain potential (ERP). There exist two alternative accounts for this index of automatic change detection: (1) A sensorial, non-comparator account according to which ERPs in oddball sequences are affected by differential refractory states of frequency-specific afferent cortical neurons, (2) a cognitive, comparator account stating that MMN reflects the outcome of a memory comparison between a neuronal model of the frequently presented standard sound with the sensory memory representation of the changed sound. Using a condition controlling for refractoriness effects, the two contributions to MMN can be disentangled. The present study used whole-head MEG to further elucidate the sensorial and cognitive contributions to frequency MMN. Results replicated ERP findings that MMN to pitch change

is a compound of the activity of a sensorial, non-comparator mechanism and a cognitive, comparator mechanism which could be separated in time. The sensorial part of frequency MMN consisting of spatially dipolar patterns was maximal in the late N1 range (105–125 ms), while the cognitive part peaked in the late MMN-range (170–200 ms). Spatial principal component analyses revealed that the early part of the traditionally measured MMN (deviant minus standard) is mainly due to the sensorial mechanism, while the later part is mainly due to the cognitive mechanism. Inverse modeling revealed sources for both MMN contributions in the gyrus temporales transversus, bilaterally. These MEG results suggest temporally distinct but spatially overlapping activities of non-comparator-based and comparator-based mechanisms of automatic frequency change detection in auditory cortex.

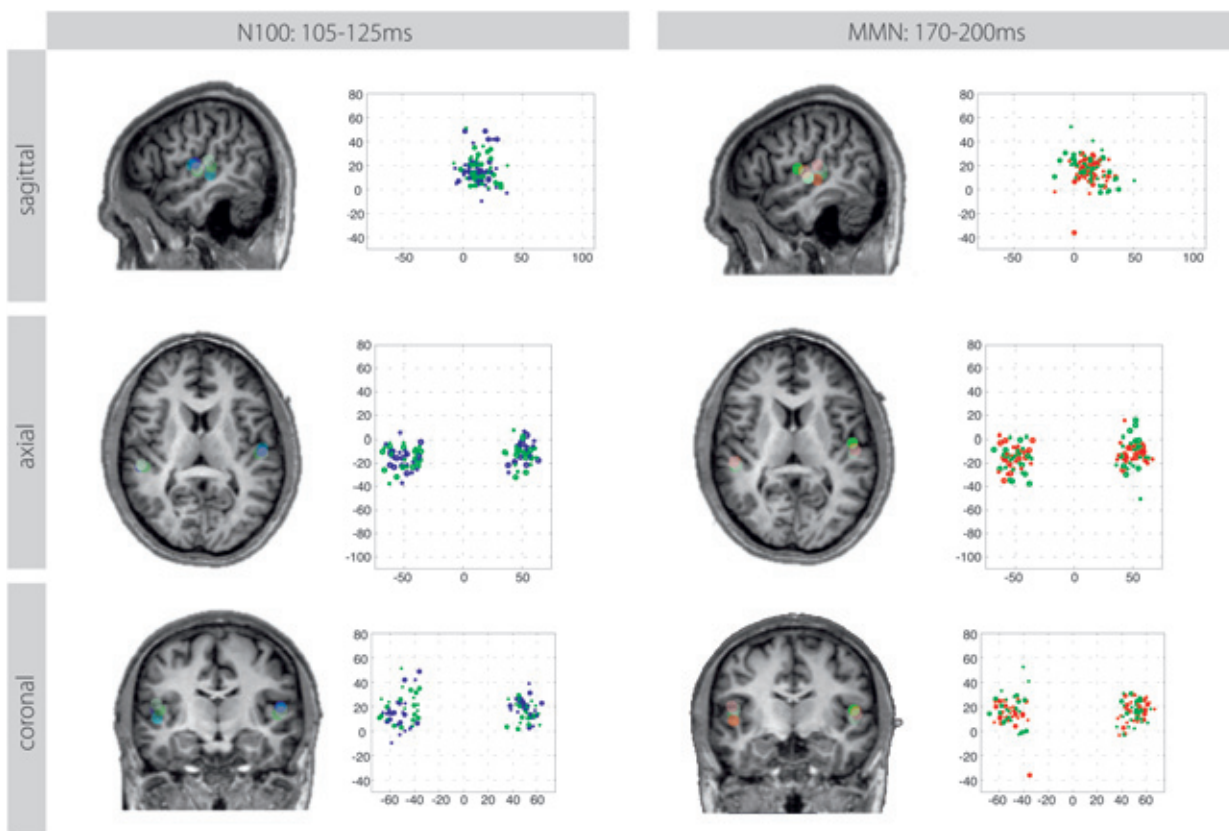


Figure 6.3.7 Average dipole localizations for two conditions and for two sound frequency ranges in the N1 and MMN time ranges. Mean and individual locations of differences between deviants and standards are displayed in red, of differences between deviants and controls in green; finally differences between standards and controls are visualized in blue. Graded reductions in brightness of the colors reflect distance from the displayed slice (partially transparent brain).

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- 2006** ■ Knösche, T. R., & Haueisen, J. (August). *Decomposition Methods for Multidimensional Data*. Workshop. 1st International Summer School in Biomedical Engineering, Ilmenau University of Technology, Germany.
- 2007** ■ Haueisen, J., & Knösche, T. R. (August). *Diffusion-Weighted Magnetic Resonance Imaging: Principles and Applications*. Workshop. 2nd International Summer School in Biomedical Engineering, Ilmenau University of Technology, Germany.

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- Sivonen, P. *Event-related brain activation in speech perception: From sensory to cognitive processes*. University of Leipzig, Germany.

Award

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