Research Report
2010/2011
Preface

The Max Planck Institute for Human Cognitive and Brain Sciences in Leipzig continues to develop rapidly, as we have outlined in detail in this research report covering the years 2010/2011. The extension building is now fully functional and houses the Departments of Neurophysics and Social Neuroscience with a full complement of researchers, in addition to the many of the newly formed and existing research groups. The new lecture hall, which we named after Gustav Theodor Fechner, one of the founders of experimental psychology who was for many years professor at the University of Leipzig, is constantly in use for colloquia, imaging meetings, workshops and guest lectures. The cafeteria has further increased the spirit of communication across the Institute by providing a focal point for meeting and socializing, formally and informally.

The new Department of Social Neuroscience (Tania Singer) was set up over the past year and the other two “young” departments—Neurophysics and Neurology—are now fully established. In addition, several new independent research groups have been initiated: “Auditory Cognition” (Jonas Obleser), “Brain Modes” (Petra Ritter), “Early Social Development” (Tobias Grossmann), and “Neuroanatomy & Connectivity” (Daniel Margulies). Peter Keller and Moritz Daum, to date group leaders at our Institute, have received prestigious professorships in Sydney and Zürich, respectively.

The 7 Tesla MR scanner is running at full speed and, increasingly, is not just a technical development but an extremely useful tool for neuroscience as our researchers harness its potential and get creative with its capabilities. In addition, two more 3 Tesla scanners have been acquired in the last two years, which are used mainly for longitudinal and clinical studies.

Major research grants have been obtained: An ERC Advanced Grant has been awarded to Angela Friederici; the ERC Starting Grant obtained by Tania Singer has been transferred from Zürich to Leipzig; we are actively involved in several Marie Curie European exchange programmes; and two major project grants with the University Hospital Leipzig (on genetics and imaging) are under way. More are to come.

The International Max Planck Research School on Neuroscience of Communication (NeuroCom) has been very productive over the last two years with teaching courses, workshops, and the first two summer schools in Leipzig and London. The first cohort of students will complete their PhDs this year, and a second round of recruitment is currently ongoing.

The aforementioned are, of course, only tasters to whet your appetite for the full content of this book, which we hope you will enjoy reading as you discover more about our Institute and its research.

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Tania Singer
Robert Turner
Arno Villringer
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The Max Planck Institute for Human Cognitive and Brain Sciences

The Max Planck Institute for Human Cognitive and Brain Sciences at Stephanstrasse in Leipzig was established on 1 January 2004 by a merger between the former Leipzig Max Planck Institute of Cognitive NeuroScience and the Munich Max Planck Institute for Psychological Research. The new institute, joining two centres of expertise into one, reflects the development in the last ten to fifteen years, which has seen psychological and neuroscientific research being conducted increasingly closer together. The creation of this centre in Leipzig also established exceptional conditions for interdisciplinary behavioural and neurobiological research into human cognition.

The Institute currently consists of four departments; a fifth department will be initiated in the near future: Neurology, Neurophysics, Neuropsychology, Social Neuroscience. The institute also hosts several research groups, including five Max Planck Research Groups: "Auditory Cognition", "Body & Self", "Early Social Development", "Music Cognition and Action", "Neural Mechanisms of Human Communication", and "Neuroanatomy & Connectivity", as well as a Minerva research group on "Brain Modes" and a research group on "Infant Cognition and Action". The Minerva research group "Neurocognition of Rhythm in Communication" concluded in December 2011, as did the former Max Planck Fellow Group "Attention & Awareness". With the renewal of Professor Heinze as a Max Planck Research Fellow at our Institute, a new group is currently starting its research on "Cognitive and Affective Control of Behavioural Adaptation". Three research and development units facilitate scientists' access to the Institute's state-of-the-art technical equipment, while at the same time conducting research into the methodology of high-resolution methods.

Research foci

Research at the Max Planck Institute for Human Cognitive and Brain Sciences revolves around human cognitive abilities and cerebral processes, with a focus on the neural basis of brain functions like language, emotions and human social behaviour, and music and action. Our many studies investigate the perception, planning, and generation of these brain functions, to reveal the interaction between, and common functional bases of, their production and perception. Other research focuses on plastic changes in the human brain and the influence this has on various cognitive abilities, and also the neuronal and hormonal basis of "modern diseases" such as high blood pressure and obesity. In addition, the further development of imaging methods for the neurosciences is an important focal point of research at the Institute.

The Max Planck Institute for Human Cognitive and Brain Sciences in Leipzig provides an exciting framework for these topical and appealing theoretical domains, with the full gamut of cognitive and neuroscientific methodology available under one roof. A defining characteristic of the Institute—and at the same time a basic principle of our research approach—is the dovetailing of research and technical development. The state-of-the-art technical equipment of the Institute both accentuates Leipzig's long-standing tradition in psychological research and, additionally, contributes to cutting-edge research within relevant areas. Modern imaging techniques, which are increasingly being used in traditional psychological approaches, are utilized and, most importantly, improved at the Institute. Our Institute, hosting the entire bandwidth of techniques and approaches that are established within human cognitive and neurosciences, thus offers ideal conditions for its own and guest researchers.

Cooperation agreements and collaborations

There has been a long-standing collaboration with the University of Leipzig. The first cooperation agreement between the Max Planck Society and Leipzig University, involving the (then) Max Planck Institute of Cognitive NeuroScience and the University of Leipzig, goes back to September 1994. In December 2006/January 2007, the Max Planck Society signed a cooperation agreement with the University of Leipzig and the University Hospital Leipzig with regard to the Max Planck Institute for Human Cognitive and Brain Sciences. The purpose of this agreement is to maintain and promote cooperation between the University, the Hospital, and the MPI in the field of cognitive neurology. Above all, this cooperation is implemented through: 1) the management of the Clinic...
of Cognitive Neurology as part of the hospital by a director of the Max Planck Institute who is also appointed by the University; 2) the exchange of scientific information and experience; 3) the undertaking of joint research projects and cooperation in individual research ventures; 4) the teaching and fostering of junior scientists; and 5) the mutual use of facilities. Currently, a new cooperation agreement between all Leipzig Max Planck Institutes and the University of Leipzig is being drafted in order to further extend and strengthen existing collaborations.

In 2010, a collaboration agreement with the Institute of Cognitive Neuroscience (ICN) at University College London, UK, was signed, establishing a partnership between the ICN and the International Max Planck Research School on Neuroscience of Communication: Function, Structure, and Plasticity (IMPRS NeuroCom). The agreement includes collaborations in the organization and running of the annual IMPRS summer school and student exchange programmes, as well as collaborations between the ICN and the MPI CBS. IMPRS NeuroCom is an interdisciplinary PhD programme originally initiated by the Max Planck Institute for Human Cognitive and Brain Sciences, which is based at the Institute and the University of Leipzig, and also involves the Max Planck Institute for Evolutionary Anthropology, Leipzig and the Institute of Cognitive Neuroscience at University College London, UK. A further cooperation agreement exists between the Max Planck Society and the Otto von Guericke University Magdeburg involving the Max Planck Institute for Human Cognitive and Brain Sciences, dating from October 2005. According to this arrangement, the Max Planck Society and the University of Magdeburg agree for the directors of the Max Planck Institute and Professor Dr Hans-Jochen Heinze to cooperate in the domain of methodological developments in the ultra-high-field area as well as in cognition research. In order to further extend the existing cooperation, Professor Heinze has been renewed as Max Planck Fellow at the Institute for a further duration of five years from October 2010 onwards.

The Department of Neuropsychology has long-standing collaborations in the form of joint teaching and supervision projects with the University of Potsdam. Additionally, the department is part of a collaboration agreement with the University Hospital “Carl Gustav Carus”, Dresden, setting out close cooperation in the field of cochlear implants research. Further collaborative links, in the shape of teaching, assessment, and supervision of doctoral students, exist between the Max Planck Institute for Human Cognitive and Brain Sciences and the Excellence Cluster “Languages of emotion” at the Free University Berlin, the doctoral programme “Function of attention in cognition” at the University of Leipzig, and the Berlin School of Mind and Brain at Humboldt University (Speaker: Arno Villringer).

Organizational structure
Professor Dr Arno Villringer
Director
The scientific focus of the Department of Neurology is on neural plasticity in the human brain with a clinical focus on stroke and the main “model system” being the sensorimotor system (Fig. 1).

**Human Brain Plasticity**

At a conceptual level, we develop new theories and models for explaining brain function and plasticity. The overarching goal is to generate theoretical predictions that can then be tested using neuroimaging experiments in both healthy subjects and patients. One major approach (abstract 1.1) uses mathematical modelling to explain neuronal plasticity and learning in terms of self-organizing recurrent neural networks based on the free energy principle. In a controlled experimental setting for understanding mechanisms of plasticity, we investigate spike-timing dependent-like plasticity in the human brain. Using previously established protocols of paired associative stimulation (PAS) with transcranial magnetic stimulation (TMS), we showed that grey
mater thickness in sensorimotor cortex below the TMS coil is a major determinant of PAS effectiveness (Conde et al., in press). We have complemented this approach by establishing novel PAS protocols (ipsiPAS) to provide evidence that the direction of excitability changes induced by PAS can be modulated by changing cortical activation status during the intervention (1.2).

Transcranial stimulation methods have become a methodological focus of our work because they offer unique opportunities for inducing and modulating brain plasticity. To increase the interpretability and reliability of these methods, particularly when studying non-motor areas, we investigated effect sizes in several experiments (e.g. for repetitive TMS: Kaminski et al., 2011). Continuous theta burst stimulation was used to modulate reinforcement learning (1.3), and facilitatory transcranial direct current stimulation (tDCS) to improve speech learning (1.4). A rather new approach to modulate brain activity and induce plasticity is transcranial alternating current stimulation (tACS). Connecting to our research on the role of background rhythms in sensory processing (see below), we tested the hypothesis that tACS allows to modulate the strength of specific brain rhythms and thus interfere with or even enhance learning effects (1.5).

Biofeedback approaches may offer a potentially powerful and practical approach to altering brain function and behaviour by inducing brain plasticity in a controllable fashion. We are investigating the effect of electroencephalography (EEG)-based biofeedback methods and have established a novel, rapid real-time based biofeedback infrastructure for functional magnetic resonance imaging (fMRI) (1.6).

Complementary to these approaches for the effective induction of plasticity, we are developing and applying approaches to assess plasticity effects in brain structure and function in healthy subjects, as well as in subjects after stroke. To assess changes in brain structure, we employ voxel-based morphometry (1.7; 1.8), cortical thickness measurements (Conde et al., in press), and diffusion tensor imaging (Taubert et al., 2010). In the study by Taubert et al., we were able to show for the first time that learning-induced changes in grey matter density are reversible despite continuous further learning of the same task. In particular, there is a shift from early structural changes in motor regions to later changes in prefrontal areas, including the underlying white matter (Taubert et al., 2010; 1.7). A key finding of these studies is that, at a surprisingly early stage, i.e. 45 minutes after the start of training, structural changes in grey matter can be observed when taking advantage of the superior signal to noise ratio of a 7 Tesla magnet (1.7). Besides structural brain imaging, functional connectivity fMRI (so-called “resting-state”fMRI, rsfMRI) has developed into a useful tool for detecting functional connectivity changes in longitudinal studies, as we have shown for the effect of balance training (Taubert et al., 2011), and after stroke (Lohmann et al., in revision). Furthermore, brain parcellation techniques based on rsfMRI can define functional neuroanatomy in an individual brain which seems yet another very promising approach for longitudinal monitoring (Margulies et al., 2009, PNAS, 106, 20069–20074; 1.9). This methodological work has been initiated by a postdoc in the Department (Daniel Margulies) and—with his promotion to a Max Planck Research Group leader at our Institute—will continue in close cooperation.

Sensorimotor System

We have continued our research in this topic in order to use somatosensory processing as a model system to understand specific neurophysiological events measured with non-invasive functional imaging. Taking advantage of high resolution imaging at 7 Tesla (7T), we showed that during electrical finger stimulation the typical response in the somatosensory cortex is not just a somatotopically ordered sequence of activations, but rather an intricate pattern of activations (mostly area 1/2) and deactivations (area 3b), the latter also being somatotopically ordered (1.10). Whether these deactivations correspond to local inhibitory processing remains to be demonstrated in future studies.

We have also continued research on somatosensory processing during subliminal peripheral stimulation for which we previously have provided evidence that it induces selective inhibitory processing in the somatosensory system (Blankenburg et al., 2003, Science, 299, 1864; Taskin et al., 2008, NeuroImage, 39, 1307–1313). We now show that during subliminal stimulation, an evoked potential can be recorded in the EEG, the neural processing of a subsequent supraliminal stimulus is altered, background Mu rhythm increases, and there is a decrease in functional connectivity in the entire contralateral somatosensory network (Nierhaus et al., submitted).
The relevance of background Mu rhythm as a marker of the activation status is demonstrated by a study, in which we show how spontaneous fluctuations of Mu rhythm strength affect the evoked potential of a supraliminal stimulus (1.11). Hence, Mu rhythm may be a marker of plasticity, and therefore, systematic modulation of Mu rhythm strength (e.g., by tACS) is a potential means to shape plastic processes (1.5).

Several models of sensorimotor learning and their effects on brain structure and function are being pursued, e.g., learning a balancing task (1.7), learning a two-point somatosensory discrimination task (1.12), and learning a sequential pinch force task (Vollmann et al., submitted), in healthy volunteers and patient groups after stroke and with Parkinson’s disease. Although the tasks used may be simple, we could provide evidence that subjects’ performance is determined by an interaction of sensory information with previous decisions (1.12). We are currently investigating similar effects when using somatosensory tasks as a test bed for assessing low level perceptual effects with higher level cognitive function.

Such functional results integrate well with findings of two lesion studies: Preusser et al. demonstrates, for the first time, in patients after stroke of the middle cerebral artery without SI involvement, that lesions in SII (opercular I) are associated with deficiencies in somatosensation (1.13). A longitudinal study in thalamic strokes affecting somatosensory relay nuclei shows distant increases in grey matter density in bilateral SII and (peri)-insular regions already about 1 week after the unilateral small thalamic stroke (1.8).

**Stroke**

In the context of stroke, we study brain plasticity in three domains.

**A) Development of stroke risk factors.** We pursue the hypothesis that pathologic brain plasticity is a major factor underlying the development of two major risk factors for stroke, hypertension and obesity. In the case of obesity, the specific hypothesis is the gradual development of addiction-like alterations in the brain, which is supported by our finding of structural changes in reward areas associated with increased body mass index (BMI) (Horstmann et al., 2011), and alterations in reward-based decision making and learning in obese subjects (1.14). In the case of hypertension, the hypothesis assumes the development of increased neuro-vegetative coupling (= higher blood pressure response) during situations of stress which—by repetitive stress exposure—leads to fixed hypertension. To investigate the coupling between brain activity and blood pressure response, we measured fMRI responses to emotional stimuli simultaneously with continuous blood pressure monitoring, and were able to show a correlation between activity in amygdala and reaction of blood pressure (1.15).

In two cohort studies which are performed as part of two large scale project grants together with the University Hospital Leipzig ((i) LIFE: Leipzig Interdisciplinary Research Cluster of Genetic Factors, Clinical Phenotypes, and Environment, (ii) Integrated Research and Treatment Center (IFB) AdiposityDiseases), we pursue these two hypotheses by performing longitudinal studies in cohorts of 2500 and 1200 subjects, respectively, in whom comprehensive medical examination, genetics, cognitive testing, and brain imaging are combined.

**B) Effect of focal lesions.** We study the effect of focal lesions due to stroke in several phases: we use rsfMRI as a tool to give similar information to perfusion MRI (Lv et al., in revision), and we assess the effect of the focal lesion on functional connectivity networks (Lohmann et al., in revision). Structural MRI is used for the assessment of behavioural effects of lesions in the chronic stage of stroke (1.13), and in longitudinal studies of thalamic stroke (1.8). These studies are performed in close co-operation with the Clinic of Cognitive Neurology at University Hospital Leipzig and the Center for Stroke Research, Charité, Berlin.

**C) Rehabilitation.** In several studies which are performed at the Clinic of Cognitive Neurology, we assess the effect of new rehabilitation protocols for a new adaptive working memory training protocol (1.16), the potential improvement of phonological learning in aphasic patients with gestures (1.17), and the electrophysiological correlates of word production after a verb naming training in aphasic patients (1.18).
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Adaptive processes are fundamental for survival and associated brain plasticity can be observed at the macroscopic level, e.g. using functional magnetic resonance imaging (fMRI) and magneto- and electroencephalography (M/EEG). The mechanistic principles underlying these plasticity phenomena are currently unknown. The computational understanding of brain plasticity would enable us to derive and experimentally test concrete predictions about brain changes, e.g. induced by learning motor skills or, more drastically, due to stroke. One way of deriving such computational models is to use (i) knowledge at the microscopic and mesoscopic level combined with (ii) insights about fundamental physical principles to constrain the construction of plasticity models at a macroscopic level. A novel way of doing this, in a principled fashion, has emerged recently: The free energy principle describes mathematical models of how one can explain brain plasticity expressed in terms of self-organizing recurrent neural networks. We have used this modelling approach to describe learning at multiple spatiotemporal scales. In three theoretical studies, we have modelled the emergence of learning as the consequence of acting in an Bayes-optimal fashion (Friston, Daunizeau, Kilner, Kiebel, 2010), as the result of synaptic reconfiguration using self-organizing principles at a microscopic level (Kiebel & Friston, 2011; Fig. 1.1), and translated the free energy principle approach to experimental learning paradigms, where we described a Bayesian modelling approach to inferring subjects’ learning strategies (Daunizeau et al., 2010) from their behavioural responses. In a next step, these modelling approaches will be used to derive computational predictions for task-based and resting-state fMRI experiments, where we will predict learning induced changes in effective connectivity between cortical regions.

Figure 1.1 Sequence learning based on synaptic reconfiguration. (A) Synaptic weights reconfigure over time to learn a specific input sequence, where each row shows a specific synaptic weight over reconfiguration cycles. (B) The objective function, the negative free energy, is increasing over time during synaptic reconfiguration. (C) The induced changes in connectivity structure from an unordered to an ordered synaptic configuration. (Reproduced from Kiebel & Friston, 2011).
Induction of reversed timing-dependent plasticity in the human brain

Conde, V., Vollmann, H., Taubert, M., Sewerin, S., Sehm, B., Villringer, A., & Ragert, P.

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Spike-timing-dependent plasticity (STDP) has been suggested as one of the most important underlying mechanisms in learning and memory. Time-dependent plasticity has been studied in the living human brain by application of non-invasive brain stimulation protocols such as paired associative stimulation (PAS), first described by Stefan et al. (Stefan et al., 2000, Brain, 123(3), 572–584). However, in contrast to STDP, as studied at a cellular level, PAS involves the interaction among functionally relevant cortical areas at a systems level in a time-dependent manner (Müller-Dahlhaus et al., 2008, Exp Brain Res, 187, 467–475). Here, we applied a new PAS protocol that required communication between hemispheres (interhemispheric inhibition) within a constraining time window in order to induce a plastic change (Fig. 1.2.1). Interestingly, the time-dependent induction of effects was reversed in relation to standard PAS (Fig. 1.2.2), where a temporally asymmetric Hebbian-like rule for the induction of plasticity has previously been shown (Wolters et al., 2003, J Neurophysiol, 89, 2339–2345). Until now, previous PAS studies mainly focussed on the induction of plasticity over an activated area (for review see Chen et al., 2008, Clin Neurophysiol, 119, 504–532). In the present study, however, we induced plastic changes within a deactivated cortical area (M1) as a result of interhemispheric inhibition of an interconnected brain area (S1). Our findings suggest the existence of a reversed time-dependent plasticity mechanism in the human cortex that probably depends on the cortical activation patterns during intervention. This new protocol (ipsiPAS), in turn, provides a new tool for studies investigating sensorimotor integration, interhemispheric processing, plasticity-related disorders or corpus callosum abnormalities.

Figure 1.2.1 (A) Experimental setup of standard PAS with "Baseline" pre-measurements (TMS measures of corticospinal excitability in M1), "Intervention" (TMS paired with median nerve stimulation (MNS)) and post-measurements (TMS measures of corticospinal excitability in M1). (B) Intervention setup for standard PAS and the new ipsiPAS (the hand coloured in grey depicts the site of MNS in each type of intervention) and assumed pathways and latencies for the MNS to reach contralateral (standard PAS) or ipsilateral (ipsiPAS) M1. Red and blue coloured circles represent assumed cortical activations and deactivations, respectively.
Continuous Theta-Burst Stimulation (cTBS) over the lateral prefrontal cortex alters reinforcement learning bias

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We examined the influence of continuous theta-burst stimulation (cTBS)—a special transcranial magnetic stimulation (TMS) protocol—on probabilistic learning, if applied either to the left or the right dorsolateral prefrontal cortex (DLPFC), or the vertex as a control region. In a recent fMRI experiment, we showed that the DLPFC is active during a reinforcement learning paradigm in which subjects constantly have to integrate trial outcomes in order to optimize performance. While fMRI is a purely correlative method, leaving the causal role of activated areas in a given paradigm a matter of hypotheses and speculation, TMS directly interferes with neural activity and enables causal inference about the dependence of task performance on circumscribed brain areas. After stimulating the left or right DLPFC or the vertex, respectively, with 40 s cTBS, we saw no influence of stimulation on learning performance per se; however, we observed a stimulation-dependent modulation of reward vs punishment sensitivity: Left-hemispherical DLPFC stimulation led to a more reward-guided performance, while right-hemispherical cTBS induced a more avoidance-guided behavior. Post-stimulation learning was performed during fMRI acquisition and imaging results showed enhanced prediction error coding in the ventral striatum in subjects stimulated over the left as compared to the right DLPFC. Both behavioural and imaging results are in line with recent findings that left, but not right-hemispherical, stimulation can trigger a release of dopamine in the ventral striatum.
ventral striatum, which has been suggested to increase the relative impact of rewards rather than punishment on behavior. However, anatomical comparison of our fMRI results with previous dopamine-receptor labelling PET-studies show only limited correspondence which is most probably due to methodological issues; this would be an interesting starting point for future studies combining PET, fMRI, and TMS.

Facilitatory tDCS over left inferior frontal gyrus improves perceptual learning of degraded speech

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Perceptual learning of degraded speech is associated with the modulation of activity in a left-lateralized network, comprising of inferior frontal (IFG) and angular gyrus (AG) (Eisner et al., 2010, J Neurosci, 30, 7179–7186). Here we investigate whether facilitatory transcranial direct current stimulation (tDCS) might improve perceptual learning processes in a sham-controlled design. Thirty-six volunteers were allocated to three intervention groups: anodal tDCS over left IFG, left AG or sham stimulation (Fig. 1.4A). Volunteers were trained to discriminate minimal pairs (e.g. “Fisch – Tisch”) from identical pairs (“Fisch – Fisch”). The first word in each pair was acoustically presented, degraded to 4 different intelligibility levels (2, 3, 4 and 6 bands; number of bands corresponds to spectral detail and intelligibility), while the second word appeared written on a screen. Volunteers performed a forced same-different choice task. In total, 100 minimal pairs were trained on each of three consecutive days. During the first 20 minutes of this training, tDCS was applied. A pre- and post-test assessed discrimination performance (d-prime) for the trained and untrained word pairs before and after the training. Here increases in d-prime indicate perceptual learning for the untrained words and a combination of associative and perceptual for the trained pairs. The training resulted in an improved discrimination performance of trained item pairs on all intelligibility levels (p < .05) without differences between groups. Anodal tDCS over left IFG improved the discrimination performance of untrained items at the lowest intelligibility level (2 bands) as compared to sham (p < .05, Fig. 1.4B). No group differences were observed on higher intelligibility levels. Our results suggest that facilitation of higher-order language areas might support perceptual learning processes of degraded speech comprehension.

Figure 1.4  (A) tDCS electrodes were placed over left IFG (n = 12) and AG (n = 12), by means of neuronavigation based on individual structural MRIs. For the sham group (n = 12), electrode placements were randomly chosen. (B) Change in discrimination performance (Δd’) of untrained items indicating perceptual learning. Only anodal tDCS over left IFG improved in discrimination performance in severely degraded speech (2 bands). There was no such improvement when using tDCS over AG or in the sham condition.
Modulation of somatosensory oscillations by means of transcranial alternating current stimulation

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Major functional modes of the human brain rely on neuronal oscillatory activity. Ongoing oscillatory activity can be associated with brain functions such as sensory perception. For example, the amplitude of the Mu rhythm, the predominant sensorimotor background oscillation, could be linked to perceiving near-detection-threshold somatosensory stimuli (Linkenkaer-Hansen, Nikulin, Palva, Ilmoniemi, & Palva, 2004, J Neurosci, 24(45), 10186–10190). Transcranial alternating current stimulation (tACS) may offer the possibility to modulate such oscillatory activity, as shown recently for visual alpha oscillations (Zaehle, Rach, & Herrmann, 2010, PLoS One, 5(11), e13766).

Here, we systematically examined the effect of different stimulation frequencies on the modulation of the somatosensory Mu rhythm. Specifically we hypothesized that application of tACS, using each subject’s individual Mu frequency ($\mu_{\text{ind}}$), has stronger modulatory effects than tACS with neighbouring frequencies ($\mu_{\text{ind}} \pm 1$ Hz) or using a fixed frequency in a different range (20 Hz).

A total of 18 healthy volunteers took part in a combined EEG/tACS experiment. In a pre-test, each subject’s individual Mu frequency was derived from the event-related desynchronization over the left somatosensory cortex (S1) induced by electric pulses to the right index finger (Fig. 1.5A). Subsequently in the EEG/tACS experiment, tACS was delivered in a bilateral montage over both S1 during 4 blocks of 5 min length each. The order of the blocks was counterbalanced across subjects and differed only in stimulation frequency: $\mu_{\text{ind}}$, $\mu_{\text{ind}} + 1$ Hz, $\mu_{\text{ind}} - 1$ Hz and 20 Hz. Furthermore, one sham stimulation block was applied (Fig. 1.5B). For analysis, we compared the Mu amplitude during 120 s before to 120 s after each block. Application of tACS using the individual Mu frequency resulted in an increase of the Mu-rhythm amplitude ($F = 3.475, p < .05$). No effects were seen during the other stimulation conditions (Fig. 1.5C). We conclude that tACS is capable of modulating ongoing somatosensory oscillations only when the exact individual frequency of the respective rhythm is applied.

Figure 1.5  (A) Averaged pre- and post stimulus frequency spectra of a representative subject measured at C3 before (red line) and after (blue line) electric finger pulses were applied; the green line represents the difference curve showing an event-related desynchronization of Mu-rhythm at 12.6 Hz. (B) Blocks (counterbalanced) of different stimulation frequencies were applied during EEG. (C) tACS with the individual Mu frequency results in an increase of the Mu-rhythm amplitude (difference in amplitude post vs pre stimulation).
Real-time functional magnetic resonance imaging: Technique and application

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Real-time functional magnetic resonance imaging (rt-fMRI) allows acquisition and subsequent analysis of neural brain responses over the course of an fMRI experiment (Weiskopf et al., 2007, MagnResonImaging, 25; deCharms, 2008, NatRevNeurosci, 9). For the analysis of fMRI data in 'real-time', the time for processing of each single brain scan on an external computer must be shorter than the repetition time in MRI scan acquisition (Fig. 1.6 for technical details). Real-time fMRI enables several useful applications: (1) Real-time observation and correction of scanning artefacts such as head-motion for the assurance of high data quality. (2) Real-time adaption of experimental designs and external systems based on subjects’ brain states. (3) Real-time feedback of neural responses from the brain (neurofeedback).

The latter application is the most widely used for rt-fMRI. Over the course of an experiment, a subject’s own task-related brain states are translated into feedback signals, which are back-projected to the subject in the scanner. Using this technique, the subject learns to control his/her own brain activation, which directly influences his behaviour and hence associated brain function and structure.

Our focus is on two applications: (1) rt-fMRI neurofeedback to train subjects in the self-regulation of neural responses from posterior insular cortex. We hypothesize that several feedback sessions improve subjects’ interoceptive and perceptual abilities. To this end, we use a custom-made software package for rt-fMRI data analysis (Hollmann et al., 2008, JNeuMeth, 175). (2) Development of a new software framework that allows for real-time analysis and integration of different physiological brain and body signals (e.g. ECG, EEG, eye tracking, skin conductance) into the experimental design (Hellrung et al., 2011, Proceedings OHBM). For instance, our system enables monitoring eye-gaze positions to present visual stimuli only if subjects fixate a specific point on the projection screen and to dynamically adapt the rt-fMRI analysis.

Figure 1.6 Real-time fMRI system as installed at two Siemens MRI scanners at the Max Planck Institute for Human Cognitive and Brain Sciences Leipzig, Germany.
Brain plasticity during learning of a balancing task

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Recent findings in neuroscience showed that learning can change the macroscopic structure of the adult human brain (Draganski et al., 2004, Nature, 427, 311–312). While subsequent studies demonstrated structural changes within different brain tissues (Scholz et al., 2009, Nat Neurosci, 12, 1370–1371), nothing is known about (1) the spatial and temporal development of structural changes in grey matter (GM) and white matter (WM) during an extensive learning period, or (2) about the temporal onset of training-induced GM changes.

To address these open questions, we first acquired structural magnetic resonance and diffusion weighted images at 3 Tesla (3T) on four time points during a six weeks balance training period. Second, a follow-up 7T MRI study was conducted to test for rapid structural GM changes immediately after training (45 minutes) since rapid GM changes have been identified on the microstructural level immediately after training (Xu et al., 2009, Nature, 462, 915–919).

In the 3T study, we observed structural changes in frontal and parietal GM (Fig. 1.7A), as well as in frontal WM tracts, after 2 weeks of training (p < 0.05, corrected). While these changes decreased in the later learning period, GM and WM changes in the left anterior prefrontal lobe evolved gradually during the 6 weeks (Fig. 1.7A; p < 0.05, corr.; see Taubert et al, 2010). Moreover, the 7T study revealed rapid but transient GM changes in the parietal and temporal cortex immediately after training (Fig. 1.7B; p < 0.05, corr.). These areas are part of the vestibular cortical system (Guldin & Grüsser, 1998, Trends Neurosci, 21, 254–259).

Together, our results highlight distinct wavelike patterns of balance training-induced structural plasticity from (vestibular) sensory areas (minutes) to sensorimotor-associated regions (weeks) to higher-order cognitive areas in the prefrontal cortex (months). Furthermore, our findings revealed the extraordinary capacity of the adult human brain for structural plasticity after a brief period of stimulation.
Rapid and extensive structural compensatory mechanisms in secondary somatosensory areas following thalamic sensory stroke in humans: New evidence for stroke-induced morphological plasticity

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Depending on stroke localization and extent, a large variety of syndromes can emerge that may impede a patient’s quality of life. It is well established, however, that the individual clinical course may undergo considerable improvement: Its underlying processes and mechanisms are summed together in the unspecific and relatively poorly understood term “plasticity.” Our broader aim is to identify plasticity processes following localised ischemic stroke— as a sudden lesion models in humans—to study the subsequent local and long-distance alterations within the interconnected network; with this knowledge, perhaps one day it will even be specifically possible to pharmacotheapeutically foster plasticity processes.

We previously investigated the functional consequences of ischemic lesions in the ventroposterolateral nucleus of the thalamus using fMRI during bilateral index finger stimulation (Taskin et al., 2006, Cereb Cortex, 6, 1431–1439). This approach bears several potential confounds (duration of fMRI protocols, variation of attentional levels, different sensory deficits and selection of appropriate test stimuli). In this study, we therefore used the stimulation-free approach of voxel-based morphometry: MPRAGE $T_1$-weighted MRI image data was acquired at days 0, 6, 30, and up to 120 after stroke onset and underwent multivariate analysis.

We found that, locally in the diencephalon, there is a large loss of white matter, possibly related to axonal damage and degeneration of local connections to neighbouring thalamic nuclei (Fig. 1.8). Approximately a single week after onset, however, a massive system-specific distributed structural alteration can be observed (Fig. 1.8B): In secondary somatosensory cortex (located around the perisylvian fissure), and, more rostrally in the insular and periinsular region, an extensive volume exhibiting an enhancement in structural density can be delineated.

Figure 1.8 Structural grey matter (GM) changes induced by isolated thalamic stroke affecting the ventroposterolateral nucleus as measured with 3 Tesla MRI. A: Decreases in grey matter density after 180 days when compared to the initial examination. B: Increases in grey matter density after 6 days when compared to the initial examination.
Functional parcellation of brain areas with resting-state fMRI

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The clear delineation of functionally similar brain areas using non-invasive imaging tools in humans is a challenge. While reliance on standard template brains has proven useful for comparison across individual research participants and studies, this approach lacks information derived from the brains themselves. Connectivity-based mapping offers a promising avenue to describe individual regions. We have developed various techniques using fMRI data acquired independent of any externally driven task demands (‘resting-state’) to characterize circumscribed brain regions based on unique patterns of functional connectivity. These approaches all benefit from
the short acquisition time required (~6 minutes) using standard fMRI protocols, and the subsequent flexibility during data analysis, to investigate any number of functional systems.

In the basic investigation of connectivity-based cortical parcellation, the gold-standard technique is tract-tracing in the macaque monkey. Although techniques such as those described here and diffusion tensor imaging (DTI)-based tractography can offer the methods necessary for studying the human brain, the only approach available to specify termination points of a single neuron are found in the literature on the macaque monkey brain. Nonetheless, the knowledge gained from the macaque can serve to generate hypotheses for study in the human. We previously implemented this approach to investigate subdivisions within the precuneus, a region commonly thought to be homogeneous in the human, but having three connectivity-based subdivisions in the macaque. Using resting-state functional connectivity, we were able to demonstrate the presence of three similar subdivisions in both the human and macaque brain, which greatly overlapped with predictions from the tract-tracing literature (Margulies et al., PNAS, 2009, 20069–20074). In addition, our study provided evidence that the patterns of connectivity mapped using resting-state fMRI data are generally consistent with known anatomical connections.

One of the most difficult areas of the brain to study in the human, using non-invasive anatomical connectivity methods (such as DTI-based tractography), is the cerebellum. This is primarily due to all axons converging in the pons nucleus before travelling to the cerebrum. Functional connectivity, however, offers a method for interrogating these cerebellar-cortical connectivity patterns, focusing specifically on the sensorimotor system. Through refining the analytic approach for delineating specific regions of the cerebellum, and removing covariant signal from adjacent regions, we have been able to demonstrate highly specific cerebello-subcortico-cerebral connectivity in the human that is consistent with known connections in the monkey (ongoing thesis of Judy Kipping). In addition, using the techniques validated on known connections, we mapped the connectivity of regions less well understood in the cerebellum, such as lobular segments beyond the primary fissure (lobuli HVI and HVIII). We found that these regions, which are involved in motor-related activity, have connections that extend beyond bilateral association cortex and secondary motor areas. HVI demonstrated substantial functional connectivity to prefrontal regions, indicating its role in both complex motor as well as non-motor function.

As the acquisition of data for functional connectivity approaches can be easily standardized across repeated scanning sessions, this methodology offers a promising tool, and complementary method, for longitudinal studies of brain plasticity (Taubert et al., 2011).

In this study we demonstrate that the human contralateral primary somatosensory cortex (S1) concurrently exhibits positive and negative blood oxygenation-level dependent (BOLD) signal changes in response to suprathreshold peripheral stimulation that are subarea-specific and essentially depend on stimulation intensity and frequency. We performed high-field (7 Tesla) BOLD-sensitive functional magnetic resonance imaging (fMRI) during electrical finger nerve stimulation (on a total of 36 subjects) to benefit from both an increased MR signal gain and a comparatively high spatial resolution. We found that stimulation at amplitudes at near-threshold intensity of 25% throughout to higher intensities up to 200% above the perceptual threshold (Fig. 1.10A1), as well as frequencies between 2 Hz and 12 Hz (Fig. 1.10A2), consistently elicited differential signal changes within the hand area of contralateral S1: a negative BOLD response (“deactivation”) which was unequivocally assigned to area 3b and was most prominent at high stimulation intensities, and, in areas 1 and 2, a positive BOLD response as it is commonly established. Moreover, stimulation of different fingers (experiment B) revealed a somatotopic
Figure 1.10  (A1) Average changes in BOLD signal intensity upon 2 Hz stimulation of finger II at different stimulation intensities above threshold (25 %, 50 %, 100 %, 150 % above sensory threshold, respectively) observed in area BA 1/2 and BA 3b. (A2) Average changes in BOLD signal intensity upon stimulation of finger II at different stimulation frequencies observed in BA 1/2 and BA 3b. (B1) Positive (upper part) and negative (lower part) BOLD responses to stimulation of digit 2 and digit 4 in four individual subjects. (B2) Positive (upper part) and negative (lower part) BOLD responses to stimulation of digit 2 and digit 4 (group analysis).

arrangement of negative BOLD responses in area 3b that exhibited a marked overlap (Fig. 1.10B1, single subjects, Fig. 1.10B2 fixed-effects model for the group). This sub-area-specific differential response pattern possibly reflects diverse neural signalling processes in S1, which possesses features both of hierarchical (area 3b operating as “S1 proper”), as well as parallel, organisation. We propose that the discovered negative BOLD response to electrical finger nerve stimulation might be a correlate of a strong concomitant activity of inhibitory neuronal ensembles in the initial cortical target region (area 3b) of projections originating from the thalamic relay nuclei. It thus potentially corresponds to the phenomenon of intracortical “afferent inhibition” characterized electrophysiologically in animal models.
Power and phase of ongoing Mu-oscillation at stimulus onset differentially influence the Somatosensory Evoked Potential (SEP)

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Several studies have reported that prestimulus alpha power has an impact on the amplitude of the evoked potential (EP) (Becker et al., 2008, NeuroImage, 39(2), 707–716). Studies on the influence of the phase of ongoing alpha at stimulus onset have so far focused on post-stimulus latency effects, investigating potential phase resetting (Hanselmayr et al., 2007, Cereb Cortex, 17(1), 1–8, Risner et al., 2009, NeuroImage, 45(2), 463–469). Evaluation of the phase-dependent EP amplitude is difficult since phase-selective averaging introduces phase artifacts, which mask the EP.

Here, we investigate how power and phase of prestimulus central alpha (Mu) activity affect the somatosensory evoked potential (SEP). Healthy subjects (n = 22) were electrically stimulated on the left index finger and EEG was recorded continuously. Raw-data trials were divided into (1) two phase-dependent subgroups (positive [0–π] and negative [π–2π] phase) and (2) two power-dependent subgroups (low and high prestimulus Mu power). Phase artefacts are eliminated by subtraction of individual Mu templates.

Mere power sorting shows the N80 component is decreased and the N140 is increased for high power trials (Fig. 1.11G). This N140 increase is consistent with our previous results (Reinacher et al., 2009, J Neurosci Methods, 183(1), 49–56). The N80 decrease may be due to larger desynchronization effects for high vs low power trials. Mere phase sorting leads to phase artefacts around stimulus onset, masking the SEP (Fig. 1.11B). Subtraction of the Mu template (Fig. 1.11D) reveals a phase effect on the P50 component (Fig. 1.11F). At first view, this effect could still be a residual of the phase sorting artefact, but after additional power sorting (Fig. 1.11H) the effect is even more pronounced for the low power trials, arguing strongly against a sorting problem. In general, oscillations in the alpha range are thought to be inhibitory driven. The P50 phase effect thus may reflect different stages of excitability of the sensory cortex.

Figure 1.11 Different effects of prestimulus power-sorting (high vs low power, right column) and phase-sorting (positive vs negative phase, left column) on the SEP. Template subtraction is necessary to reveal phase-effects. Combined power- and phase-sorting is depicted in H.
Implicitly memorized decisions bias assessment of tactile spatial 2-point discrimination threshold

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In a neurological examination, the tactile 2-point discrimination task is the standard instrument for assessing the skin’s tactile spatial resolution. Here we show that, during the assessment, participants’ decision on presented distances at or around threshold are biased by the implicitly memorized preceding decision. If, for instance, distances were presented at threshold in a series of three or even more stimuli, participants made the same decision on each presentation, although decisions at threshold per definition are at chance level (i.e. 50% 1 point, 50% 2 points felt). In other words, each decision participants made in this series of presentations is memorized to bias the directly following decision, resulting in a sequence of similar decisions. To assess whether the decision was explicitly or implicitly memorized, we systematically asked for the decision strategy subjects used, right after the task. Surprisingly, participants were not aware of this trial-to-trial bias suggesting that decisions were in fact implicitly memorized. Our findings have important consequences for the interpretation of the 2-point discrimination threshold as a standard marker of tactile spatial accuracy. First, they indicate that using an unbalanced assessment with unsymmetrically distributed distance pairs around threshold, which provoke sequences of similar decisions, will artificially lower or elevate the 2-point discrimination threshold. Although using a fully symmetric design is general practice, and we used a fully symmetric design as well, we found that decisions in this standard sensory assessment are cognitively supported and not based on pure tactile evidence. Consequently, the 2-point discrimination threshold should be seen as a tactile-cognitive rather than a purely tactile marker of spatial accuracy.

Figure 1.12 Trial-to-trial decision bias. Only for a difficult decision (here one distance above threshold, i.e., threshold+1), subjects were more likely to make the same decision as for the preceding distance if this was a decision on a threshold–1 or threshold distance. For easy decisions on threshold–2 or +2, subjects did not seem to rely on memorized decisions. Note that subjects are not aware of this trial-to-trial update in the decision process suggesting that decisions are implicitly memorized.
Does secondary somatosensory cortex contribute to somatosensation? A lesion mapping study on stroke patients

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In this study, we aimed at a better understanding of the role of human S2 in somatosensation, which is still a matter of ongoing debate. To this end, we collected structural MRI scans of stroke patients from our MPI/clinic database. We retrospectively compared MRI-based lesion maps of 29 patients presenting a somatosensory deficit to 10 patients without a deficit after contralateral stroke in the medial territory of the middle cerebral artery, in whom S1 was not affected. Using the non-parametric mapping toolbox of MRIcron (http://www.cabiatl.com/mricro/mricron/index.html) we unveiled a significant (FDR corrected) effect within opercular 1 (OP 1) which together with OP 2 to 4 comprises the anatomical site of S2 (Fig. 1.13). Furthermore, we found these effects spreading into premotor and prefrontal cortex. These regions might be associated with reorganizational processes since stroke in all patients occurred at least 3 months before MRI. In summary, our findings are, to our knowledge, the first causal proof of S2 being involved in somatosensation.

Figures 1.13 Results of the lesion mapping. Lesion mapping revealed the operculum (OP), in particular OP1, as being causally associated with the occurrence of somatosensory deficits after stroke.

Obesity- and gender-related effects on performance and strategy use in implicit multi-cue learning

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Recent evidence points to obesity- and gender-related differences in cognitive control mechanisms and learning. In this study, we investigated obesity- and gender-related effects on implicit multi-cue learning, implemented by the Weather Prediction Task (WPT; Knowlton et al., 1994, Learn Mem, 1, 106–120). In this task, subjects learn the association between four different symbols and "sun" or "rain" as two possible outcomes which the sym-
bols predict (Fig 1.14A). Sixty-eight healthy participants (35 female, 18 obese [BMI >= 30, < 40], 17 lean [BMI >= 19, <= 25], 33 male, 17 obese), matched for educational background and age (19–44 years), performed 200 trials of the WPT. Analysis of learning behaviour revealed a significantly decreased learning performance of obese subjects over the entire task (Fig 1.14B). This effect was particularly pronounced in the second half of the experiment. Moreover, participants’ BMI correlated negatively with task performance at the end of the task. In a second analysis, a computational model for various learning strategies (Meeter et al., 2006, Learn, Mem, 13, 230–239) was employed to assess subjects’ strategy with respect to prediction accuracy and the number of considered cues. In correspondence with the increased task performance, lean subjects used the most successful strategies (> 80 % prediction accuracy) more often than obese participants. Accordingly, obese subjects relied more frequently on strategies with lower prediction accuracy (50–80 %). Moreover, lean women used a multi-cue strategy significantly more often than lean men to predict outcomes, whereas lean men used single-cue strategies for their predictions to a greater extent than lean women (Fig 1.14C). No such effect was observed for obese subjects. The results indicate an influence of obesity on learning performance and of gender and obesity on strategy use in a task requiring the integration of multiple cues for decision-making.

Figure 1.14 (A) Weather Prediction Task, example trial. (B) WPT outcome probabilities for the four symbols. (C) Learning performance: Lean subjects outperformed obese participants in the number of correctly learned stimulus-response associations. (D) Number of considered cues: Lean women used multi-cue strategies to a greater extent than lean men. Lean men based their cue-outcome predictions more often on one cue only.
Recent evidence suggests that the brain is causally involved in the initiation and progress of cardiovascular diseases, by failing to regulate blood pressure responses to emotional events (Gianaros & Sheu, 2009, NeuroImage, 47, 922–936; Jennings & Zanstra, 2009, NeuroImage, 47, 914–921). This study examines the neural regions regulating phasic blood pressure reactions to negative stimuli. Twenty-four healthy subjects were asked to ignore task-irrelevant emotional content, while engaging in an emotional Stroop task and an emotional modification of a perceptual load task. fMRI data was collected simultaneously to continuous blood pressure recording. In the emotional Stroop task, negative words resulted in enhanced activation in the left inferior frontal gyrus and bilateral amygdala. Blood pressures positively correlated with neural activation in the left amygdala (Fig. 1.15A). In the perceptual load task, high perceptual load resulted in reduced activation in bilateral amygdala and orbitofrontal cortex. These results are in line with previous evidence that emotional reaction depends on sufficient resources. Blood pressure positively correlated with activation in a network including the right amygdala, bilateral parahippocampal cortices, pons, SMA and PFC (Fig. 1.15B). These findings corroborate previous evidence for the role of bilateral amygdala in blood pressure regulation. Furthermore, these results show, for the first time, that this regulation is online and continuous, and, furthermore, might depend on the specific task. In line with recent evidence, these findings suggest that early therapeutic interventions at the neural level might prevent the development of cardiovascular diseases. Further studies aimed at investigating further attention systems, as well as other negative emotions (i.e. anger) are currently in a pilot phase.

Training of working memory – Development and evaluation of an adaptive working memory training

Weicker, J.¹, Frisch, S.², Lepsien, J.¹, Müller, K.¹, & ² Cooperation: HASOMED GmbH

Working memory (WM) is a system with a storage and a manipulating component, with selective attention and inhibition playing an important role (Baddeley, 2000, Trends Cog Sci, 4(11), 417–423.; Miyake, et al., 2000, Cogn Psychol, 41, 49–100). Deficits in WM occur frequently after brain injury and cause severe impairments in everyday functioning (Johansson & Tornmalm, 2011, Scand J Occup Ther, Aug 15). Although recent studies have in-
Plasticity

dicated that WM can be trained (Brehmer et al., 2011, NeuroImage, 58, 1110–1120), existing studies often lack methodological quality and theoretically based training tasks. The aim of the study is to develop and evaluate an adaptive training programme in which different aspects of WM, including selective attention and inhibition processes, can be exercised by subjects. In cooperation with HASOMED GmbH, a training programme was developed which was evaluated in a pilot study with 7 healthy elderly subjects. The results confirmed the feasibility of the training and the control condition. Subjects reported subjective improvement of alertness, memory performance, and self-confidence. On psychometric tests, we found tendencies in the expected direction on measures of WM (PASAT, OSPAN) and mental control (STROOP, task switching). The results also revealed the necessity to redesign difficulty levels. After reprogramming the tasks, a RCT training study will be conducted with healthy elderly subjects. Aside from behavioural variables, we will examine training effects with voxel based morphometry (VBM) and "resting-state" measures. In addition, the programme will be evaluated in patients with brain injury and stroke.

Differential efficiency of gesture-supported phonological learning in aphasic patients with phonologic versus semantic deficits

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Lexical retrieval is regularly impaired in patients suffering from aphasia. Clinical case studies suggest that iconic gestures facilitate object naming. Therefore, we addressed the question of whether phonological learning of novel words can be supported by gestures in residual aphasia. A second goal was to find out whether efficiency of gesture-supported learning is affected by phonotactic complexity of the novel word.

13 patients with residual aphasia (6 females, age: 37–71) learned 30 novel words (NW) for 30 root words (RW), referring to manipulable objects (e.g. "flute", "cup", "gun"). Novel words differed with regard to phonotactic complexity (PC), including 10 simple (no consonant onset-cluster, e.g. "bafo"), 10 medium (legal German onset-cluster, e.g. "kruti") and 10 complex items (non-German consonant-cluster, e.g. "tkase"). Following the written presentation of the RW, patients were asked to either simply repeat the NW (verbal condition) or to repeat the NW while imitating an iconic gesture (gesture condition). Memory performance for NW was assessed by cued recall and other memory tasks. Memory performance for NW after 4 days of training (35 minutes, daily) varied between 93 % and 17 %. As predicted, memory was better for simple words, compared to medium and complex words. While no effect of training-condition was found across the group, patients who benefitted from the gesture-condition had specific impairments on the phonologic-segmental level, whereas patients who did not benefit from the gesture-condition showed impairments mainly at the lexical-semantic level (Fig. 1.17).

The results provide evidence for gesture-aided phonological learning being efficient only in a subgroup of aphasia-patients, whose impairments are most pro-

Figure 1.17 Scatterplot shows that gesture-benefit correlates positively with a lexical-semantic score (left) and negatively with a segmental-phonologic score (right).
nounced at the phonologic-segmental level. We suggest that an intact semantic lexicon is necessary for successful integration of the meaningful gesture and the novel word form.

Electrophysiological correlates of word production after a verb naming training in medium proficient L2 speakers and aphasic patients

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Naming is regularly impaired in aphasia, partially due to problems with the activation of the lexico-semantic entry. Similarly, medium proficient second language (L2) speakers often have difficulties in retrieval of the L2 lexicon. To assess the electrophysiological correlates of such enhanced demands on lexico-semantic retrieval, the present study used a delayed naming task in medium proficiency L2 speakers and aphasic patients. In healthy adults, overt naming of real objects in their medium proficient L2 and their native language (L1) were compared (Rossi, Aurig & Obrig, in prep.). To avoid contamination by articulation, subjects had to name pictures in German (L1) and English (L2) after a delay period of 3 s. Phonological similarity between L1 and L2 was varied across three levels, and subjects rated the subjective ease of lexical retrieval for each item. Event-related potentials (ERPs) for L2 but not L1 production were modulated by phonological similarity. For immediate L2 retrieval, a larger negativity 200–350 ms after picture onset was seen for words with high compared to medium L1/L2-similarity, as well as for low compared to medium-similarity words (Fig. 1.18). Similar effects were observed for short retrieval and tip-of-the-tongue phenomena, but not when lexical retrieval failed. Results suggest that while substantial overlap in high-similarity entries may ease L2 entry access, no-overlap entries may strongly reduce inhibition demands for the L1 entry necessary to retrieve the weaker L2.

In an ongoing study, the ERP procedure was used in aphasic patients prior to and after intensive repetitive naming training. Verb training was administered for 3 h over 5 days following a vanishing cues (“errorless learning”) strategy. Results in the first five patients confirm that training-induced modulation of early ERP components associated with lexical access can be used to assess neuronal correlates of training success, and may be used to also investigate potential transfer effects.

Figure 1.18  ERP results for different phonological L1/L2-similarities and subjective ease of lexical retrieval in German (L1) and English (L2).
Inter-individual influences on human performance monitoring – A multimodal approach using genetic and patient data

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Monitoring the course and outcome of actions is a prerequisite for adaptive, goal-directed behaviour. The overarching aim of our research is to investigate inter-individual influences on human performance monitoring, that is, the ability of subjects to detect errors, adapt to errors, and learn from errors. Previous research has shown potential genetic influences on human error processing (Klein et al., 2007, Science, 318(5856), 1642–1645). While this study used a candidate gene approach, our current project (funded by the German Research Foundation, KL2337/2-1) aims to investigate genetic influences on error processing on a genome-wide level. Participants are genotyped using the Affymetrix 6.0 SNP-array. Phenotypes are established by means of event-related potentials acquired while participants work on classical performance monitoring related tasks. So far, nearly 400 subjects have been included in the study; the aim is to reach a final sample size of about 750 subjects. Another source of inter-individual differences in error processing is brain pathology. There exists a close anatomical connection between performance monitoring related brain areas and brain areas involved in working memory and motor programming. Therefore, subjects with age-related white matter changes that influence connectivity between these brain areas, are of particular interest for understanding the role of intact brain connectivity in error processing. We invited subjects from which a rating of age-related white matter changes was available, to take part in an EEG experiment measuring brain responses to performance errors. Results show a relationship between the amount of white matter changes and the subjects’ brain response to performance errors: Larger white matter pathology is related to slower erroneous responses, smaller ERP differences between erroneous and correct responses, and higher latencies of brain responses to errors.

Executive deficits are related to the inferior frontal junction in early dementia

Schroeter, M. L.\textsuperscript{1,2,3}, Vogt, B.\textsuperscript{1,2}, Frisch, S.\textsuperscript{1,2}, Becker, G.\textsuperscript{4}, Barthel, H.\textsuperscript{5,6}, Müller, K.\textsuperscript{1}, Villringer, A.\textsuperscript{1,2,3}, & Sabri, O.\textsuperscript{3,4}

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\textsuperscript{4} Department of Nuclear Medicine, University of Leipzig, Germany

Executive functions describe a wide variety of higher-order cognitive processes that allow the flexible modification of thought and behaviour in response to changing cognitive or environmental contexts. This impairment is very common in neurodegenerative disorders. Executive deficits negatively affect everyday activities and hamper the ability to cope with other deficits, such as memory impairment in Alzheimer’s disease (AD), or behavioural disorders in frontotemporal lobar degeneration (FTLD). Our study aimed to characterize the neural correlates of executive functions by relating respective deficits to regional hypometabolism in early dementia (Schroeter et al., 2011). Executive functions were assessed with two classical tests, the Stroop and semantic fluency test, and various subtests of the Behavioral Assessment of the Dysexecutive Syndrome (BADS) test battery capturing essential aspects of executive abilities relevant to daily living. Impairments in executive functions were correlated...
with reductions in brain glucose utilization as measured by [18F] fluorodeoxyglucose positron emission tomography (FDG-PET) and analysed voxelwise using statistical parametric mapping (SPM) in 54 subjects with early dementia, mainly AD and FTLD, and its prodromal stages, subjective and mild cognitive impairment. Although the analysis revealed task-specific frontoparietal networks, it consistently showed that hypometabolism in one region in the left lateral prefrontal cortex—the inferior frontal junction area—was related to performance in the various neuropsychological tests. This brain region has recently been related to the three component processes of cognitive control—working memory, task switching, and inhibitory control. Group comparisons additionally showed hypometabolism in this area in AD and FTLD. Our study underlines the importance of the inferior frontal junction area for cognitive control in general, and for executive deficits in early dementia.

Figure 1.20 Brain regions that showed consistently reduced glucose metabolism in association with executive deficits. (A) Overlap of all five executive function tests. Maximum is located in the vicinity of the inferior frontal junction area. Scale represents number of overlapping tests. (B) Minimum z score for all five executive function tests which corresponds to a conjunction analysis in the sense of a logical "AND." Maximum of the resulting map of z values is again located in the vicinity of the inferior frontal junction. (C) Results of the meta-analysis of studies investigating Stroop (Str) and Switch (Sw) tasks with functional magnetic resonance imaging (fMRI) transformed into the MNI space using the unified segmentation approach (Ov overlap, Derrfuss et al., 2005, Hum Brain Mapp, 25, 22–34). (D) Results of our previous study with exactly the same cohort investigating the neural correlates of behavioural disorders in dementia—correlation between reduced glucose metabolism and apathy (Ap), disinhibition (Dis) and eating disorders (Ea) (Schoeter et al., 2011).
Congress, Workshops, and Symposia

2010


2011


Appointments

Kiebel, S. W2 Professorship (Computational Neuroscience). University Clinic, Friedrich Schiller University Jena, Germany.

Pleger, B. W2 Professorship (Neuroscientific Imaging). Ruhr University Bochum, Germany (declined).

Pleger, B. W2 Professorship (secundo loco) (Cognitive Neuroscience). Heinrich Heine University Düsseldorf, Germany (declined).

Schroeter, M. L. APL Professorship. University of Leipzig, Germany.

Awards

Hoyer, J. Werner Straub Award (for excellent achievements during scientific qualification). Technical University of Dresden, Germany.

Margulies, D. S. Otto Hahn Medal. Max Planck Society, Germany.

Schroeter, M. L., & Vogt. B. Poster Award. German Association for Psychiatry and Psychotherapy (DGPPN), Berlin, Germany.

Taubert, M. Kurt Meinel Prize. Faculty of Sport Science, University of Leipzig, Germany.

Yildiz, I. B. Best Presentation Award. Department of Mathematics, Michigan State University, USA.

2011

2010
Yildiz, I. B. Dissertation Completion Fellowship. Graduate School, Michigan State University, USA.

Dukart, J., Müller, K., & Schroeter, M. L. Hans Heimann Prize. German Association for Psychiatry and Psychotherapy (DGPPN), Germany.


Publications

Books and Book Chapters


Journal Articles


Plasticity


Professor Dr Angela D. Friederici
Director
Language is a trait specific to humans. Its phylogenetic origins have been and still are disputed. In the face of a lack of strong phylogenetic evidence, comparative across-species data as well as ontogenetic data have recently contributed to the discussion. Together with Constance Scharff and Michael Petrides, Angela D. Friederici launched a *Frontiers* Special Research Topic on the “Neurobiology of human language and its evolution: Primate and non-primate perspectives” in the section of *Frontiers in Evolutionary Neuroscience*. The scope of the Special Research Topic is to bring together contributions by researchers from different fields, who investigate grammar processing in humans, non-human primates and songbirds, with the aim of finding answers to the question of what constitutes the neurobiological basis of grammar learning.

The research agenda of the Department of Neuropsychology on the Neurocognition of Language is to contribute to our understanding of the biological basis of language. The Neurocognition of Language Processing Group aims to specify the neural networks underlying language comprehension in adults by defining the function of the particular brain regions in the language network and, moreover, their functional and structural connectivities. The Neurocognition of Language Learning Group tries to understand the mechanisms of language learning and their underlying neural basis, both in the developing and the adult brain.

With the award of an Advanced Grant from the European Research Council (ERC) on the Neural Basis of Syntax in the Developing Brain to Angela D. Friederici, a 5-year cross-sectional, longitudinal research project on language development and brain maturation was started in autumn 2011. The goal of the project is to identify the neural basis of syntax acquisition by means of functional and structural neuroanatomical measures of language-related brain regions as well as behavioural measures of syntactic processing. We will do so at different developmental stages of syntax acquisition, using the adult language network as a model.
The current Model

The brain basis of language processing: From structure to function

Knowledge about the neural basis of the human language faculty has increased considerably over the past several years. The data available in the literature and from our own studies are reviewed in a recent paper in Physiological Reviews (Friederici, 2011). Structural and functional brain imaging from this publication are available in a 3D online version (see http://onpub.cbs.mpg.de). Based on this, we propose a model which assumes fronto-temporal networks that support different syntactic and semantic aspects during language comprehension.

Initial acoustic-phonological processes take place during the first hundred milliseconds after acoustic stimulation and, crucially, involve the primary auditory cortex (PAC) and the planum temporale (PT). From these regions, the information is transferred both to the anterior and the posterior parts of the superior temporal gyrus (STG) and sulcus (STS). The left anterior STG, together with the left frontal operculum, which is connected via a ventral pathway through the uncinate fasciculus (Ventral Pathway II, Fig. 2.1), builds the neural network for initial local phrase structure building processes.

Then semantic, grammatical, and thematic relations in a sentence are processed in parallel systems, activating separable left-lateralized temporo-frontal networks. The semantic network involves the middle and posterior STG/MTG (sometimes extending into anterior temporal regions) and BA 45/47 in the inferior frontal cortex, connected via the extreme capsule fibre system (Ventral Pathway I, Fig. 2.1).

For the processing of syntactically complex sentences, a network is proposed which consists of Broca’s area (in particular, the pars opercularis, BA 44) and the posterior temporal cortex (pSTG/STS) connected via the arcuate fascicle/superior longitudinal fascicle (Dorsal Pathway II, Fig. 2.1). Neuroanatomical findings, moreover, suggest a dorsal pathway connecting the posterior temporal cortex to the premotor cortex (Dorsal Pathway I, Fig. 2.1), supposedly supporting sensory-to-motor mappings. These two dorsal streams may have different functions, with the former subserving top-down processes and the latter supporting bottom-up processes, making rule-based and possibly context-based predictions about the incoming information. Suprasegmental prosodic information is predominantly processed by the right hemisphere. The interaction of syntactic information processed in the left hemisphere and prosodic information processed in the right hemisphere is supported by the posterior portion of the corpus callosum, the structure which connects the temporal cortices of the two hemispheres.

This model serves as a conceptual basis and research agenda for much of the work in the Department of Neuropsychology, both in the Neurocognition of Language Processing Group and as an adult template, for the developmental work in the Neurocognition of Language Learning Group.

Figure 2.1 Schematic view of two dorsal pathways and two ventral pathways. Dorsal Pathway I connects the superior temporal gyrus (STG) to the premotor cortex via the arcuate fascicle (AF) and the superior longitudinal fascicle (SLF). Dorsal Pathway II connects the STG to BA 44 via the AF/SLF. Ventral Pathway I connects BA 45 and the temporal cortex via the extreme capsule fibre system (ECFS). Ventral Pathway II connects the frontal operculum (FOP) and the anterior temporal STG/STS via the uncinate fascicle (UF).
Neurocognition of Language

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- Dr Thomas C. Gunter
- Dr Hyeon-Ae Jeon
- Dr Claudia Männel
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- Dr Jutta L. Mueller (14)
- Dr Stefanie Regel (14)

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  - Dr Marc Bangert (11)
  - Dr Douglas Davidson
  - Dr Roland Friedrich
  - Dr Anja Hahne
  - Dr Manuela Macedonia (29)
  - Dr Regine Oberecker
  - Dr Jonas Obleser
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- Katrin Cunitz (35)
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- Anja Hubert (19)
- Lisa J. Knoll
- Dana Marinos
- Julia Merrill (née Groh) (11)
- Lars Meyer
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(16) Berlin School of Mind and Brain, Humboldt University Berlin, Germany/funded by German Research Foundation (DFG)  
(19) IMPRS NeuroCom, Leipzig, Germany  
(29) The Cogito Foundation, Switzerland  
(30) University of Leipzig, Germany  
(32) Programme Beatniu de Pinos, Generalitat de Catalunya, Spain  
(35) European Union, ERC Advanced Grant, funded by European Research Council (ERC)  
(**) Left the Department during 2010/2011
2.1 Neurocognition of Language Processing
Based on the current model of The Brain Basis of Language Processing (Friederici, 2011), we aimed to further specify the neural networks of syntactic processing and its different subcomponents.

The fronto-temporal language network. The goal of the present research was to clarify the role of the prefrontal cortex, the temporal cortex as well as the relation between them. Previous research on the role of Broca’s area in the processing of syntactic hierarchies focussed on the result of the process (i.e. comprehension). In a novel study, we investigated the process of hierarchy building in language and mathematics and its prefrontal basis, including Broca’s area (2.1.1). Broca’s area has long been known to be involved in the processing of syntactically complex sentences although its nature was discussed as supporting either working memory or syntax. Here, we demonstrate that syntax is located in Broca’s area, whereas verbal working memory storage is located in the left temporo-parietal cortex (2.1.2). The processing of syntactically complex sentences during auditory comprehension clearly involves Broca’s area and the pSTS, under signal degradation; however, we observed a shift in the activation pattern towards brain areas which are lower in the processing hierarchy (2.1.3). This and previous studies indicate that under normal processing conditions, syntactically complex sentences involve Broca’s area (pars opercularis) and the pSTG/STS. Based on the hypothesis that brain regions within a functional neural network reflect similar molecular parameters, we analyzed the neurotransmitter receptor distribution of these brain regions and found support for our hypothesis (2.1.4).

Gesture and speech. Another aspect relevant to sentence comprehension during communication is gesture. We demonstrated that beat gestures enhance the processing of syntactic aspects during language comprehension (2.1.11), but that the integration of gesture and speech is restricted to a particular time window (2.1.12).
Building hierarchies in language and mathematics

Makuuchi, M., Bahlmann, J., & Friederici, A. D.

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Language and mathematics are expressed as linear symbol sequences that have inherent hierarchical structures. We investigated the neural mechanisms for the building up of hierarchical structures in language and mathematics. To provide mathematical sequences with a comparable hierarchical structure as in language (Japanese), we presented mental arithmetic in the Reverse Polish notation, in which the integration operator is given after the two operands (Fig. 2.1.1.1). As a control condition, we added a verbal working memory task in which a se-

![Diagram](attachment:image.png)

**Figure 2.1.1.1** Two-level integration creating hierarchical structures: (A) Two-step stimuli integration. a1- a4 are elements, φ1 and φ2 are the first-level integrators, and Φ is the second-level integrator. Two-step integration results in a hierarchical structure. (B) Hierarchical structures are built in language and arithmetic and also in string operations (not depicted here).

![Diagram](attachment:image.png)

**Figure 2.1.1.2** Differential integration costs between the levels: (A) Differential integration cost (ΔCOST) between the second-level integration (INT2) and the first-level integration (INT1) was computed for language (LANG), arithmetic (ARITH), and string operation (STRING). (B) ΔCOST between INT1 and no-integration condition (LIST). Error bars show standard errors. (C) Schema for the integration operations and the supporting neural basis. The ventral premotor area (PMv, green) and dorsal pars opercularis (POd, pink) are projected onto the surface of a template brain.
neural string operation was organized to have the identical hierarchical structure. All tasks required the integration of elements on two levels, which results in an identical hierarchical structure. The goal of the present functional magnetic resonance imaging study was to investigate how the posterior lateral prefrontal cortex is organized to process hierarchically structured sequences. Specifically, we examined if integration at hierarchically higher levels is supported by more anterior regions than the regions for lower-level integration. Common to all domains, the ventral premotor cortex (PMv) supports the integration of externally given elements, while Broca’s area (BA 44) subserves the integration of internally represented elements produced in the preceding integration steps (Fig. 2.1.1.2). Notably, within the pars opercularis (BA 44), language showed a qualitatively different activation pattern from the other domains (not depicted here). These results suggest that Broca’s area and the PMv support a domain-general integration mechanism for the processing of hierarchical structures, with uniquely efficient computation for language.

Sentence processing: Linking syntax in Broca’s area to working memory in left temporo-parietal regions

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The involvement of Broca’s area in sentence processing is well documented. However, one of the most enduring issues in language neuroscience concerns whether brain activations in Broca’s area during sentence processing result from verbal working memory processes or specifically from syntactic ordering processes. To tackle this question, we scrutinized the relation between subject and object—the arguments—and the verb. Our fMRI study fully crossed sentence processing difficulty (“ordering” of sentential elements) with a working memory storage factor (i.e. the “distance” in terms of time and intermittent speech material between these elements). Note that previous studies in English were ambiguous in this respect, since English does not allow an independent manipulation of argument order and argument-verb distance.

Our results show that argument–verb distance activated deep left temporo-parietal (TP) regions, while argument order was found to focally activate the left pars opercularis in Broca’s area. Left TP activation correlated with listeners’ forward digit spans (listeners with worse spans activated TP most strongly), while Broca’s area activation did not. Furthermore, fractional anisotropy in listeners’ left arcuate fasciculus/superior longitudinal fasciculus (AF/SLF) covaried with the functional effects, but at differential sites along the tract. Functionally, this suggests that verbal working memory storage during sentence processing relies on TP regions, while Broca’s area appears as the neural correlate for syntactic ordering. Our fibre-tracking analysis is the first to show a critical role of the AF/SLF in mediating verbal working memory in left TP regions and syntactic processing in Broca’s area.
Under real-life adverse listening conditions, it is unclear how the challenge of analysing syntactic structure and that of analysing the acoustic signal itself influence each other: Where along the neural processing pathways does the potential mutual dependency of sound and syntax analysis manifest?

First, in an fMRI experiment, we tested the functional neural organization when listening to increasingly complex syntax, using three levels of argument scrambling. The left anterior and posterior superior temporal sulcus (STS) as well as the left inferior frontal cortex (IFG) were monotonically more activated with increasing syntactic complexity.

In Experiment 2, we then parametrically combined syntactic complexity with speech signal degradation (noise-band vocoding in three different numbers of bands). As syntax became more complex and signal quality improved (a “trade-off” between challenges; shown in blue, Fig. 2.1.3), the pattern of activations was replicated. However, when syntactic complexity increased while...
signal quality deteriorated (an “additivity” of challenges, shown in red, Fig. 2.1.3), the syntactic complexity effect in the IFG shifted dorsally and medially, and the activation effect in the left posterior STS shifted from posterior towards more middle sections of the sulcus. Furthermore, we devised a distribution analysis of supra- as well as subthreshold data (z-scores; Fig. 2.1.3) that further substantiated that this pattern of activity shifts in the anterior and posterior STS and within the IFG.

Results suggest a signal quality gradient within the fronto-temporal language network. More signal-bound processing areas, which are lower in the processing hierarchy, become relatively more recruited for the analysis of complex language input under more challenging acoustic conditions (“upstream delegation”). This finding provides evidence as well as a testable framework for dynamic resource assignments along the neural pathways in auditory language comprehension.

Neurotransmitter receptor distribution in Broca’s area and the posterior superior temporal gyrus

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Since Paul Broca’s first achievements in the middle of the 19th century, the question of how cognitive functions (e.g. language skills) are linked to the underlying brain structure has not been fully answered. To help resolve this issue, the densities and distribution patterns of numerous neurotransmitter receptors of particular brain re-

![Figure 2.1.4 Normalized neurotransmitter densities of four human brain regions.](image)

Figure 2.1.4 Normalized neurotransmitter densities of four human brain regions.
regions (Fig. 2.1.4E) were analyzed using the technique of quantitative autoradiography, following the hypothesis that the participation of a brain region in a neuronal network with a common function, here language, is reflected in a similar neurotransmitter receptor distribution.

Three different regions of the human language network were chosen (Fig. 2.1.4A): the left pars opercularis (LPO) in the inferior frontal gyrus, which is responsible for the processing of hierarchically structured sentences, the left inferior frontal sulcus (LIFS), where verbal working memory resides (Makuuchi, Bahlmann, Anwander, & Friederici, 2009, Proc Natl Acad Sci USA, 106, 8362–8367) and the posterior superior temporal gyrus and sulcus (pSTG/STS), which accomplish the integration of syntactic and semantic information (Friederici, Makuuchi, & Bahlmann, 2009, NeuroReport, 20, 563–568). These regions of the language network resemble each other very closely (Fig. 2.1.4B, Fig. 2.1.4D), whereas they could be clearly segregated from regions with a different function, for example the visual cortex (V1) (Fig. 2.1.4C).

Thus, receptor densities represent an organizational structure strictly correlated with specific cognitive brain functions in the human cerebral cortex. These data also provide molecular anatomical evidence of the existence of a neural network which is comprised of at least the left pars opercularis, the inferior frontal sulcus and the posterior superior temporal gyrus and sulcus. Its function is to identify grammatical dependencies in complex sentences of a natural language, such as German (Friederici, 2002, Trends Cogn Sci, 6, 78–84).

2.1.5 The role of the caudate nucleus in language processing

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The left prefrontal cortex and basal ganglia work together to mediate working memory and top-down regulation of cognition. This system regulates the balance and interactions between automatic and high-order control responses. Using ultra-high-field high-resolution functional magnetic resonance imaging (7T fMRI), the present study examined the role of subcortical structures in cognitive control during language processing. Participants were asked to judge the grammaticality of syntactically ambiguous, unambiguous and ungrammatical sentences. Half of the sentences contained subject-relative clauses and half object-relative clauses. Unambiguous sentences require an automatic response, while ambiguous and ungrammatical sentences do not fulfill the expected sentence structure, and hence create a temporal conflict. In this circumstance, automatic responding should be inhibited, and higher-order controlled responding engaged, in order to review information held in working memory, determine when processing went wrong, and find a solution. Our experimental paradigm not only created a conflict, but also manipulated its resolution by the use of ungrammaticality (incorrect, no possible resolution) and ambiguity (correct, an alternative solution). The imaging results showed that more posterior regions of the head of the caudate were active for both types of conflict situations (Fig. 2.1.5A). However, in more anterior regions, only ambiguity continued to...
activate the head of the caudate (both subject-relative and object-relative), and in most rostral regions, only the most cognitively highly demanding condition (ambiguous object-relative) engaged the head of the caudate nucleus (Fig. 2.1.5B). The results revealed a posterior-anterior axis within the head of the caudate nucleus with more anterior regions supporting higher levels of cognitive processing. This functional architecture mirrors the rostrocaudal hierarchical organization observed within the lateral prefrontal cortex.

Syntactic and auditory spatial processing in the superior temporal gyrus: An MEG study

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Syntactic processing is considered to be a cognitive function involving cortical regions outside sensory cortices. In particular, the neural sources underlying early syntax-related brain responses at around 100–200 ms for spoken sentences have been localized in anterior regions of the superior temporal gyrus (STG). Pure auditory perceptual processes, on the other hand, have been linked to activations in sensory cortices. However, recent studies using a visual sentence processing paradigm showed early modulations of visual sensory cortices in response to syntactic violations, thereby adding diverging findings to earlier studies (e.g. Dikker, Rabagliati, Farmer, & Pylkkänen, 2010, Psychol Sci, 21, 629–634).

The current magnetoencephalography study was designed to examine whether auditory sensory cortices are affected by syntactic manipulations. Specifically, the aim was to localize the cortical regions underlying early syntactic processes and those underlying perceptual processes. To this end, auditorily presented sentences were varied along the factors syntax (correct vs incorrect) and auditory space (standard vs change of interaural time difference, ITD).

The results show that both syntactic and auditory spatial anomalies led to very early activations (40–90 ms) in the STG. At around 135 ms after the onset of the violating word within the sentence, differential effects were observed for syntax and auditory space. Syntactically incorrect sentences activated the anterior STG, whereas ITD changes activated regions that are more posterior (Fig. 2.1.6). Furthermore, the results strongly indicate that the anterior and posterior STG are activated simultaneously when a double violation is encountered. These results provide evidence of a dissociation of speech-related processes in the anterior STG and the processing of auditory spatial information in the posterior STG. This is compatible with the view of there being different auditory processing streams in the temporal cortex.

Figure 2.1.6  Local activation maxima in the temporal cortex. (A) The 100 vertices in each hemisphere showing the strongest grand average activations. (B) Analysis of the local maxima (syntax violation = magenta; auditory space violation = blue; double violation = cyan; sentence onset M50 as reference to the auditory cortex – red; *PFDR ≤ 0.05; **PFDR ≤ 0.01; ***PFDR ≤ 0.001). Brain activity distribution is displayed on the inflated surface, with dark grey representing sulci and light grey representing gyri.
Disentangling prosodic and syntactic influences on the early left anterior negativity (ELAN)

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Previous studies investigating early syntactic processes reported an early left anterior negativity (ELAN) between 100–200 ms that is elicited by syntactic violations. Another early negativity has been observed for sentences comprising an unexpected change in the fundamental frequency (F₀) contour. In natural language, however, syntax and prosody (i.e., expressed as a change in F₀) are intertwined within the speech signal. In order to investigate syntactic processes independently of prosodic parameters, cross-slicing procedures are commonly applied. In this way, syntactically incorrect sentences are created by carefully deleting a word from a recorded sentence that is syntactically correct. Using this approach, previous studies strongly controlled for prosodic effects in the sentence materials. Nevertheless, this procedure can cause a slightly larger than normal change in the F₀ contour at the position of the syntactic violation. The present magnetoencephalography study aimed to disentangle the influence of these two superimposed processes. In order to estimate the contribution of prosodic incongruence to the ELAN effect, neural activations in the superior temporal cortex (STC), elicited by a syntactic word category violation, were compared to activations elicited by a prosodically incongruent change in the F₀ contour of the sentence.

The results showed stronger STC activations for each violation compared to correct sentences in the 110–160 ms time window. Importantly, the syntax violation effect was larger than the prosody violation effect and showed a left-hemispheric bias which was absent for the prosodic violation. Moreover, an additional very early effect in a preceding time window (40–80 ms) was observed only for syntactically incorrect sentences (Fig. 2.1.7). These results show that the syntax violation effect (ELAN) found in the present as well as in previous studies cannot be attributed to the processing of an unexpected F₀ contour, but rather reflects difficulties in initial syntactic parsing.

Figure 2.1.7  Activation grand average time courses for the syntax violation (magenta) and the prosody violation (blue). Grey bars highlight the time windows used for the statistical analysis. Statistical comparisons are provided for the left and right superior temporal cortex regions (n.s. – not significant; #p ≤ 0.10; *p ≤ 0.05; **p ≤ 0.01; ***p ≤ 0.001).
Prosody meets syntax: The role of the corpus callosum

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Contemporary models of auditory language comprehension propose that the two hemispheres are differently specialized in the processing of segmental and suprasegmental features of language. While segmental processing of syntactic and lexical semantic information is predominantly assigned to the left hemisphere, the right hemisphere is thought to have a primacy for the processing of suprasegmental prosodic information. A dynamic interplay between the hemispheres is assumed to allow the timely coordination of both information types. The present event-related potential study investigated whether the anterior and/or posterior portion of the corpus callosum, being the brain structure connecting the two hemispheres, provides the crucial brain basis for the online interaction of syntactic and prosodic information. Patients with lesions in the anterior two-thirds of the corpus callosum, connecting orbital and frontal structures, or the posterior third of the corpus callosum, connecting temporal, parietal and occipital areas, and matched healthy controls were tested in a paradigm that crossed syntactic and prosodic manipulations. An anterior negativity elicited by a mismatch between syntactically predicted phrase structure and prosodic intonation was analyzed as a marker for syntax–prosody interaction. Healthy controls and patients with lesions in the anterior corpus callosum showed this anterior negativity, demonstrating an intact interplay between syntax and prosody (Fig. 2.1.8A). No such effect was found in patients with lesions in the posterior corpus callosum, although they exhibited intact, prosody-independent syntactic processing comparable with healthy controls and patients with lesions in the anterior corpus callosum (Fig. 2.1.8B). These data support the interplay between the speech processing streams in the left and right hemispheres via the posterior portion of the corpus callosum, building the brain basis for the coordination and integration of local syntactic and prosodic features during auditory speech comprehension.

Figure 2.1.8 (A) Words carrying a syntax-prosody mismatch (red dotted line) compared to a match (red solid line) elicited an anterior negativity in healthy controls and the anterior corpus callosum (CC) group (see black arrows and topography maps), but not in posterior CC patients, indicating a deficient interhemispheric interaction between syntactic with prosodic information in this group. (B) Syntactically incorrect (green dotted line) compared to correct words (green solid line) elicited an ELAN and a P600 in all three experimental groups, indicating normal syntactic processing irrespective of whether participants had brain lesions or not.
Every language has the means to reverse the truth value of a sentence by using specific linguistic markers of negation. In the present study, we investigated the neural processing costs caused by the construction of meaning in German sentences containing negation in different clause types. We studied negations within and across clause boundaries as well as single and double negations. Participants read German sentences comprised of affirmations, single negations in the main or in the subordinate clause, or double negations. We found a network including the left inferior frontal gyrus (pars triangularis, BA 45) and the left inferior parietal gyrus (BA 40) is activated whenever negations in the main clause had to be processed. Additionally, we found increased functional coupling between the left pars triangularis (BA 45), left pars opercularis (BA 44), left SMA (BA 6), and left superior temporal gyrus (BA 42) during the processing of main clause negations. The study shows that in order to process negations that require semantic integration across clause boundaries, left BA 45 interacts with other areas that have been related to language processing and/or the processing of cognitive demands and logical/conditional reasoning. The results indicate that areas within the left perisylvian language network synchronize in order to resolve negations, in particular, whenever there are greater requirements to integrate meaning.

Figure 2.1.9 Psychophysiological interaction analysis of negation. Illustration of the functional coupling between the seed region pars triangularis (BA 45) and the pars opercularis (BA 44), the left STG, and the SMA. The processing of negations triggers the coupling of the hemodynamic response between the brain regions.

Conceptual and syntactic factors in sentential negation

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Negative statements take numerous forms, with different combinations of conceptual and syntactic structures resulting in a complex and multi-faceted phenomenon. The aim of the present study was to investigate how the brain contends with such complexity. Specifically, this study examined the activity in brain areas responsible for the processing of conceptual and syntactic factors of negation during sentence comprehension. Participants read various types of Japanese sentences displayed on a screen a single word at a time. In contrast to simple negation sentences (x did not believe, plus optional negation marker at the sentence-final verb), when processing conceptually complex negative sentences (only x did not believe, plus optional negation marker at the sentence-final verb), participants recruited a semantic network that comprises the left inferior frontal gyrus (BA 47)
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and angular gyrus. In cases in which negation demanded syntactic licensing (everyone except x did not believe, plus obligatory negation marker at the sentence-final verb), the left inferior frontal gyrus (BA 44) and the left insula were activated. Enhanced activation of the left inferior parietal lobule was also observed. This is likely due to the increased load on working memory required to compute the syntactic licensing across the sentence. Overall, the current data advance our understanding of the processing of negation by disentangling the different factors involved and locating the brain regions responsible for them.

**Simple beat gestures enhance syntactic language comprehension**

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Recent research suggests that the brain routinely binds together information from gesture and speech. However, most of this research has focussed on the integration of representational gestures with speech. Much less is known about how other aspects of gesture, such as emphasis, influence our interpretation of a spoken message. We tested the hypothesis that beat gestures facilitate the comprehension of syntactically more complex sentences. We measured EEG while presenting gesture-supported spoken German sentences that were temporally ambiguous in their syntactic structure. Sentences were disambiguated at the final word, either towards a less complex Subject-Object-Verb (SOV) or towards a more complex OSV structure. It is known that a disambiguation towards OSV is somewhat unexpected (i.e. non-canonical) and creates additional processing costs which can be seen in electric brain activity as a positivity peaking around 600 ms after the onset of the disambiguating word (i.e. the P600). In Experiment 1, we found that this P600 effect for OSV structures is absent when
beats accentuate the subject of a sentence, suggesting that gestures can facilitate the processing of complex syntactic structures. Moreover, the effect appears to be gesture-specific because it was not found for other stimuli that draw attention to this part of speech including prosodic emphasis (Experiment 2), or a moving visual stimulus with the same trajectory as the gesture (Experiment 3). Although prosodic cues have a communicative function, they are more variable than an isolated visual beat cue and therefore less effective. More importantly, Experiment 3 suggests that only visual emphasis produced with a communicative intention in mind (i.e. beat gestures) influences language comprehension, but a simple visual movement that lacks an apparent communicative intention does not. Our data therefore suggest that most effective communication not only involves the mouth and ears, but also the hands and their perception.
The integration of gesture and speech is typically explored either from a gesture or a language perspective. This is rather odd because it involves a cross-modal signal. In the present experiment, we took a cross-modal perspective and explored whether a time window (TW) of gesture-speech integration exists. In the cross-modal literature, the length of such a TW seems to depend on the complexity of the material used. Whereas the TW of simple material is quite small, it is much larger for complex audio-visual information, suggesting that the TW of gesture-speech integration is probably large. A disambiguation paradigm was used in which participants were presented with short video clips of an actress uttering sentences like “She was impressed by the BALL, because the GAME/DANCE...”. The ambiguous noun (BALL) was accompanied by a dynamic iconic gesture fragment containing the minimum amount of information necessary to disambiguate the noun towards its more frequent dominant or less frequent subordinate meaning.

We used four different temporal alignments between the noun and the gesture fragment: The uniqueness point of the noun was either prior to (+120 ms condition), synchronous with (0 ms condition), or lagged behind the end of the gesture fragment (–200 & –600 ms conditions). ERPs triggered to the uniqueness point of the critical noun showed significant word meaning frequency effects for the integration of the gesture fragments in the –200 ms, 0 ms and +120 ms condition, with the strongest effects in the synchronous condition. Thus, the present data suggest that there is a TW for gesture-speech integration ranging from at least –200 ms up to +120 ms. This is in the range of complex types of multimodal integration like the McGurk Effect. Because a shallow task was used, we suggest that within this TW, the integration of gesture and speech is automatic. Outside of the TW, it is controlled in nature (cf. Obermeier, Holle, & Gunter, 2011).
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The model presented in Friederici (2011) assumes two dorsal pathways: Dorsal Pathway I connecting the temporal cortex to the premotor cortex, and Dorsal Pathway II connecting the temporal cortex to Broca’s area. Dorsal Pathway I is taken to support auditory-to-motor mapping, which is crucial for early language learning (Hickok & Poeppel, 2007, Nat Rev Neurosci, 8, 393–402). Dorsal Pathway II is taken to support the processing of syntactically complex sentences (Brauer, Anwander, & Friederici, 2011). Applying this model to language development results in a number of predictions, which are seen to hold up in the studies we conducted. The neural network at birth should show Dorsal Pathway I, but not Dorsal Pathway II, and this is demonstrated in newborns (2.2.1). The maturation of the functional connectivity between Broca’s area and the posterior temporal cortex should only develop as the brain matures, and this is what we found (2.2.2).

Language learning in infants. Learning of rule-based dependencies from the auditory cortex should be present early in natural languages (Friederici, Mueller, & Oberecker, 2011) and in artificial grammars (2.2.3), and, moreover, learning in infants (Friederici, Mueller, & Oberecker, 2011; 2.2.3) should be different from adults (Citron, Oberecker, Friederici, & Mueller, 2011; 2.2.3). These predictions were verified and, in addition, it was shown that infants’ ability to successfully learn rule-based dependencies from auditory input is directly related to their auditory processing abilities (2.2.3). The learning of novel words was also demonstrated in infants as young as 6 months of age (2.2.4). Recognizing a novel recently learned word in connected speech in 6-, 9- and 12-month-old infants is dependent on two crucial parameters: frequency of occurrence and prosody. However, the two parameters are differentially effective at different stages during early development (2.2.5).

Syntax-learning in children. Syntax learning and processing occurs between 3 and 10 years with crucial developmental stages in this period. In an ERP study, it was shown that although 3-year-olds are able to detect case-marking information, only 6-year-olds are able to use this information to assign thematic roles—but still with increased effort (2.2.6). An fMRI study with 5- to 6-year-old children, on the processing of case-marking information in short subject-verb-object and object-verb-subject sentences, revealed individual differences. Only the subgroup with high grammatical performance showed the predicted activation increase for the more complex object-initial sentences (2.2.7). When looking at the function-brain structure relation, we found that 5- to 8-year-old children demonstrate a positive correlation between language function and the grey matter volume in language-relevant regions in the left hemisphere. When processing complex sentences in a study crossing the factors syntactic complexity and semantic plausibility, children at the age of 9 to 10 still differ from adults. While both children and adults show increased activation for syntactic complexity in Broca’s area, only children show an effect of semantic plausibility (2.2.9).
The ability to learn language is a human trait. In adults and children, brain imaging studies have shown that auditory language activates a bilateral frontotemporal network with a left hemispheric dominance. It is an open question whether these activations represent the complete neural basis for language that is present at birth or not. Here, we demonstrate that in 2-day-old infants, the language-related neural substrate is fully active in both hemispheres, and involves the inferior frontal and temporal cortices with a preponderance in the right auditory cortex. Functional and structural connectivities within this neural network, however, are immature. In contrast to adults, who show strong functional intra-hemispheric connectivities in the left hemisphere, newborns
only show clear connectivities between the two hemispheres. Structurally, both newborns and adults demonstrate a strong ventral connection between the frontal and the temporal cortex. However, while the dorsal connection is twofold in the adults, with one pathway connecting the temporal cortex to the premotor cortex and another one connecting the temporal cortex to Broca's area, newborns only show the pathway connecting to the premotor cortex. Thus, although the brain already responds to spoken language at birth, thereby providing a strong biological basis for language acquisition, progressive maturation of intra-hemispheric functional connectivity occurs as a result of language exposure as the brain develops.

Maturation of the language network: From inter- to intrahemispheric connectivities

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Language development must go hand in hand with brain maturation. However, little is known about how the brain develops to serve language processing, and in particular, the processing of complex syntax, a capacity unique to humans. Behavioural reports indicate that the ability to process complex syntax is not yet adult-like by the age of seven. Here, we apply a novel method to demonstrate that the basic neural basis of language, as revealed by low frequency fluctuation stemming from functional MRI data, differs between 6-year-old children and adults in crucial aspects. Although the classical language regions are actively in place by the age of six, the functional connectivity between these regions clearly is not. In contrast to adults, who show strong connectivities between frontal and temporal language regions within the left hemisphere, children’s default language network is characterized by a strong functional inter-hemispheric connectivity, mainly between the superior temporal regions. Taking into account the data from the newborn study (Perani et al., 2011), these data indicate a very slow functional reorganization of the neural network during development towards a system that allows a close interplay between frontal and temporal regions within the left hemisphere.
2.2.3 Maturation of auditory perception predicts rule learning in 3-month-olds

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The ability to discover rule-based dependencies between speech units, as in phrases like "she smiles", is a basic requirement for language acquisition. We applied event-related potentials in a classic oddball paradigm to test whether this capacity is influenced by basic auditory processes in 3-month-old infants. Oddball stimuli induce electrophysiological mismatch responses in infants, which have been shown to develop from a positivity towards an adult-like negativity (He, Hotson, & Trainor, 2009, Neuropsychologia, 47, 218–229). In our study, standard stimuli consisted of three-syllabic spoken sequences that followed two different AXB rules for which A syllables predicted B syllables with variable X syllables. We used the two standard A..B frames fi..to and le..bu and 20 different X syllables. Interspersed among standards were pitch deviants, in which the B syllable was increased in frequency by ~12 %, and rule deviants, in which the final B syllable was incorrect (e.g. fi..bu). Infants were grouped according to the polarity of their mismatch responses to the pitch deviant, serving as an index for the maturation of auditory processing. Only infants who showed the more mature response, a negativity, for the pitch deviants showed a mismatch response to the rule deviants. Interestingly, girls showed a negativity, while boys showed a positivity, potentially indicating a more advanced developmental stage in girls' rule processing. We conclude that the ability to extract remote dependencies develops in early infancy and critically depends on functional aspects of basic auditory mechanisms. Future research needs to elucidate the impact of the observed interindividual differences in perceptual functions on other aspects of language learning and development.

Figure 2.2.3 ERPs on the electrode Cz and difference maps of girls with mature (A), boys with mature (B), mismatch response (MMR) (negativity) and girls with immature (C), and boys with immature mismatch response (MMR) (positivity) in the pitch condition (D).
Word learning in 6-month-old infants: Fast encoding – Weak retention

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There has been general consensus that initial word learning during early infancy is a slow and time-consuming process that requires very frequent exposure, whereas later in development, infants are able to quickly learn a novel word for a novel meaning. From the perspective of memory maturation, this shift in behavioural development might represent a shift from slow procedural to fast declarative memory formation. Here, we used ERPs to observe the brain activity of 6-month-old infants, when repeatedly presented with object-word pairs in a cross-modal learning paradigm (Fig. 2.2.4.1). During the training phase, we observed an infant N400 priming effect after being exposed to the word only a few times (Fig. 2.2.4.2), which provides first evidence that infants as young as six months of age are able to rapidly encode arbitrary mappings of novel words and novel meanings and to retain this newly encoded knowledge in short-term memory. During a memory test one day later, we did not find an N400 effect, but instead, three other priming effects (Fig. 2.2.4.3B), each of them already observed as a repetition-based word familiarity effect during training (Fig. 2.2.4.3A: increased P100, decreased N300–500, N400).

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{image1.png}
\caption{First to Fourth Presentations Fifth to Eighth Presentations}
\end{figure}

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{image2.png}
\caption{Semantic Priming Effect during Training}
\end{figure}

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{image3.png}
\caption{A Familiarity Effects during Training B Priming Effects during Memory Test}
\end{figure}
decreased frontal positivity). In particular, words presented in a congruous picture context were processed in this way as they would be more familiar than the same words presented in an incongruous picture context. The test phase results indicate that infants did not fully forget the newly acquired knowledge, but the missing N400 also suggests that the memory representations are considerably less stable than immediately after encoding. From the combined results, we conclude that the encoding process of word learning is already based on fast declarative memory formation at six months of age. It is, moreover, not the encoding but the rapid forgetting or the insufficient consolidation of declarative memory that limits the lexicon during early infancy.

2.2.5 Prosody and frequency govern infants' word recognition at different ages

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The early ability to segment words in continuous speech is fundamental to later stages in language acquisition (Newman, Ratner, Jusczyk, & Dow, 2006, Dev Psych, 42, 643–655), and is facilitated by phonotactic, rhythmic and statistical speech cues (e.g. Mattys, & Jusczyk, 2001, Cognition, 78, 91–121). Previous studies have shown that infants start to detect sentence-embedded words at between 7 and 10 months of age when familiarized with these words in isolation (e.g. Jusczyk, Houston, & Newsome, 1999, Cogn Psych, 39, 159–207). In the current electrophysiological study, we investigated infants’ word segmentation and subsequent recognition in a natural input situation by presenting sentences at familiarization and individual words in a test phase (Fig. 2.2.5.1). To explore the differential impact of prosody and frequency on infants’ segmentation abilities between 6 and 12 months, we used speech with or without accent on the words to be familiarized and monitored learning across repetitions.

Event-related brain potentials at familiarization revealed age-dependent dissociations between word processing driven by prosodic realization (with and without accentuation) and number of repetitions (Fig. 2.2.5.2A), with prosody being effective at 6 and 9 months, and repetition being effective at 9 and 12 months. Differences in infants’ sensitivity to both information types are reflected in their word recognition in the test phase (Fig. 2.2.5.2B). Here, brain responses indicate that even 6-month-olds recognize previously presented words (familiarity positivity), but only when words were accentuated during familiarization. At 9 and 12 months, infants showed recognition independent of prosodic realization (familiarity negativity), while 9-month-olds additionally displayed a sustained process for the prosody condition.

It follows that under specific familiarization conditions, infants show word segmentation and recognition at an earlier age than reported previously, emphasizing the crucial role of prosody in early language acquisition. While prosodic information initiates these processes, frequency becomes the relevant cue at later stages, demonstrating specific input-sensitive windows in speech segmentation.
Preschool children’s interpretation of object-initial sentences: Neural correlates of their behaviour

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The acquisition of the function of case marking is a key step in the development of sentence processing for German children, as case marking unambiguously reveals the relations between arguments. We investigated the processing of case marking and argument structures in 3-, 4.6-, and 6-year-olds, as well as in adults. Event-related potentials (ERPs) were measured in response to object-initial compared to subject-initial German transitive sentences. In addition, children’s behavioural competence was tested in a sentence-picture matching task. Adults’ performance was close to perfect and their ERPs revealed a negativity for the processing of the topicalized accusative-marked noun phrase (NP1) (Fig. 2.2.6.1D) and no effect for the second NP (NP2) in the object-initial structure (Fig. 2.2.6.2D). Children’s behavioural data showed a significant above-chance outcome in the subject-initial condition for all age groups. In the object-initial condition, however, 3-year-olds’ performance was significantly below chance level, while 4.6- and 6-year-olds still did not perform above chance. ERPs of 3-year-olds show a positivity at NP1 (Fig. 2.2.6.1A) and a negativity at NP2 (Fig. 2.2.6.2A), while 4.6-year-olds do not differ in the processing of object-initial vs subject-initial sentences at NP1 (Fig. 2.2.6.1B) and show a slight positivity at NP2 (Fig. 2.2.6.2B). This positivity at NP2, which implies syntactic integration difficulties, is more pronounced in
6-year-olds (Fig. 2.2.6.2C) but absent in adults. At NP1, however, 6-year-olds show the same negativity as adults (Fig. 2.2.6.1C). In sum, 3-year-olds detect differences in the two sentence structures without being able to use this information for comprehension, 4;6-year-olds use a word order strategy, processing NP1 in both conditions in the same manner, which leads to processing difficulties upon detecting case-marking cues at NP2. Children aged 6 are able to use case-marking cues but still show enhanced effort to correctly assign thematic roles.

Figure 2.2.1 Grand-average ERPs of 3-, 4;6-, 6-year-olds, and adults for the selected electrodes FC3/FC4, object-initial versus subject-initial, relative to the onset of NP1. The subject-initial condition (blue line) is plotted against the object-initial condition (red line).

Figure 2.2.2 Grand-average ERPs of 3-, 4;6-, 6-year-olds, and adults for the selected electrode CZ, object-initial versus subject-initial, relative to the onset of NP2. The subject-initial condition (blue line) is plotted against the object-initial condition (red line).

### 2.2.7 Individual differences in sentence processing in preschool children reflected in the prefrontal cortex

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The study investigated the acquisition of case-marking cues for argument interpretation in the developing brain of children aged 5 to 6 using fMRI. Short sentences, consisting of a transitive verb and two arguments with subject-initial or object-initial word order, were presented auditorily.

FMRI results revealed mainly left-hemispheric activation comprising the dorsolateral prefrontal cortex (DLPFC), the inferior parietal cortex (IPC), and the anterior cingulate cortex (ACC) for object-initial compared to subject-initial sentences. Contrary to our predictions, an ROI focusing on the left IFG did not show a significant word order effect. However, post-hoc analysis revealed two distinct activation patterns within the overall group. One subgroup showed increased activation for object-initial compared to subject-initial sentences, as predicted. However, the other subgroup showed the opposite effect, with stronger activation for subject-initial sentences. To investigate the interactions between group and word order, ROI analyses were performed in the IFG, DLPFC, ACC and IPC, respectively. These were significant only in the prefrontal areas. Whereas the first group showed no differences in activation intensity between the two conditions, greater activation for the object-initial sentences was found in the prefrontal areas in the second group. Importantly, these groups differed significantly in their performance in a language development test (TROG-D). The results suggest a broad heterogeneity within children related to sentence processing. Irrespective of age, only the group with generally higher grammatical
knowledge showed an adult-like pattern of activation (larger activation for object-initial compared to subject-initial sentences). Furthermore, only high performing children showed a significant decrease for subject-initial sentences in left prefrontal areas. Moreover, the IFG, in particular, comes into play when children are challenged by the sentence structure.

![Diagram](image)

Figure 2.2.7 fMRI study results. (A) Observed activations for object-initial vs subject-initial sentences in all children are shown. (B) Anatomically defined IFG ROI is shown. (C) Diagrams show percent signal changes (PSC) for all children and the two subgroups (normal and high performing children). Dark blue bars refer to subject-initial condition and light blue bars to object-initial condition. Illustrated are four regions of interest (ROIs).

**Abbreviations:** IPC, inferior parietal cortex; DLPFC, dorsolateral prefrontal cortex; ACC, anterior cingulate cortex; IFG, inferior frontal gyrus.

**Language- and memory-related grey matter volume correlates:**

A VBM study

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Little is known about how age-related structural changes in the brain map onto children’s language comprehension. However, structural MRI studies mapping brain development have shown that areas that are known to be part of the adult language network undergo structural changes in grey matter volume during maturation. In the present study, we aim to investigate in which areas grey matter volume correlates with child language comprehension. To this aim, we quantified children’s language comprehension skills using a German version of the Test for Reception of Grammar. Since sentence processing also involves domain-general mechanisms, such as verbal working memory, we additionally quantified children’s verbal working memory capacities using the number recall subtest of the Kaufman Assessment Battery for Children. A voxel-based morphometry analysis was run on T1-weighted images of 46 five-to-eight year-old children. To overcome the problem of multicollinearity, we converted the behavioural data into principal components. Subsequently, we ran a voxel-wise multiple regression analysis on the grey matter volume, factoring out age, sex and intracranial volume and including the principle components of the TROG scores and the scores of the number recall test as main regressors. Positive correlations of grey matter volume with language comprehension scores were found bilaterally in the pars opercularis and caudate nucleus. The grey matter volume of the left superior frontal gyrus and inferior temporal gyrus as well as the right superior parietal lobe and precuneus was found to be positively correlated with the verbal working memory scores. While all these areas are known to be involved in language- and memory-related processes in adults, their structural alteration in relation to language and memory development has not be shown so far.
Neurocognition of Language

Functional segregation of syntax and semantics in the developing brain

Skeide, M. A., Friederici, A. D., & Brauer, J.

Although there is a tight functional interrelation between syntactic and semantic computation, these language components are represented in segregated brain systems in adults (Newman, Ikuta, & Burns, 2010, Brain Lang, 113, 51–58). However, a previous fMRI study with 5- to 6-year-old children (Brauer, & Friederici, 2007, J Cogn Neurosci, 19, 1609–1623) revealed an activation overlap for both domains, indicating that the neural networks responsible are not yet fully specialized.

Using fMRI, we investigated whether 9- to 10-year-old children already show distinct activation patterns for processing each type of linguistic information. Adult
and child participants performed a picture-selection task while listening to either semantically plausible or implausible German object and subject relative clauses.

Interestingly, adults and children show an analogous behavioural pattern; as both perform slightly better and faster on subject than on object relative clauses and on plausible versus implausible semantics.

FMRI results for both groups revealed an increased BOLD response for syntactic complexity in the pars opercularis in the left inferior frontal gyrus but children’s activation also extended into the dorsal pars triangularis. In contrast to adults, who showed no semantic plausibility effect, children showed increased activation in the pars orbitalis in the inferior frontal gyrus and the anterior temporal lobe for semantic implausibility. In both groups, no interaction effects occurred.

Results indicate that 9- to 10-year-old children still recruit a broader neural network than adults for the processing of complex syntax. Increased activation for semantically implausible information in children suggests that even of the ages of 9 and 10, they still rely more on semantic cues than adults. Data suggest that although sentence processing is adult-like at the behavioural level, the underlying brain specialization for both domains is still in progress.

**Figure 2.2.9.1** Main BOLD effect of syntactic complexity in the adult group (red) and in the child group (green) (whole brain analyses). A group comparison revealed no significant difference between adults and children for processing syntactic complexity.

**Figure 2.2.9.2** Main BOLD effect of semantic implausibility in the child group (green) (whole brain analysis). A significant group difference between children and adults for semantic implausibility at $p < 0.01$ (unc.) was found in the anterior superior temporal sulcus activation cluster. No main effect of semantic implausibility was observed in the adult group.
Conferences, Workshops, and Symposia

2010

2011
- Männel, C. (July). Neural Correlates of Lexical Segmentation in Infancy: Crosslinguistic ERP and NIRS Data. Symposium. 12th International Congress for the Study of Child Language (IASCL), Université du Québec à Montréal (UQAM), Montréal, Canada.

Degrees

PhD Theses

2011
- Obermeier, C. Exploring the significance of task, timing and background noise on gesture-speech integration. University of Leipzig, Germany.
**Awards**

Friederici, A. D. *Johannes-Gutenberg-Stiftungsprofessur [Johannes Gutenberg Professorship]*. Johannes Gutenberg University Mainz, Germany.


Friederici, A. D. *Carl-Friedrich-Gauß-Medaille [Carl Friedrich Gauss Medal]*. Braunschweigische Wissenschaftliche Gesellschaft (BWG), Germany.

Friederici, A. D. *Ehrendoktorwürde der Universität Mons [Doctor Honoris Causa of the University of Mons]*. University of Mons, Belgium.

Friederici, A. D. *ERC Advanced Grant*. European Research Council (ERC), Brussels, Belgium.

Grossmann, T. *SRCD Early Career Research Award*. Society for Research in Child Development, USA.

**Publications**

**Books and Book Chapters**


**Published Papers**


Figure 2.1
Figure adapted from Friederici, A. D. (2011). The brain basis of language processing: From structure to function. *Physiological Reviews*, 91(4), 1357–1392.

Figure 2.1.3

Figure 2.1.6

Figure 2.1.7

Figure 2.1.8

Figure 2.1.9

Figure 2.2.1.1, Figure 2.2.1.2

Figure 2.2.2

Figure 2.2.4.1, Figure 2.2.4.2, Figure 2.2.4.3

Figure 2.2.6.1, Figure 2.2.6.2
Professor Dr Tania Singer
Director
The scientific focus of the newly created Department of Social Neuroscience is on understanding the foundations of human social behaviour. More specifically, we aim to investigate the influence of the environment on social behaviour and to uncover the underlying cognitive processes sub-served by neuronal circuits and ultimately by neurotransmitters. The role of hormones and genes on social behaviour is a further area of study. Through an interdisciplinary and multi-method approach, we study the neuronal, hormonal, developmental, and evolutionary foundations of human social cognition and social emotions, such as empathy, compassion, revenge and Schadenfreude, as well as our sense of fairness and envy, in children, adults, and our nearest relatives, the great apes. Furthermore, we are interested in how these social emotions influence social and economic decision making and how they can be regulated and trained to achieve better well-being and health.

To allow for such a multidisciplinary research programme, we have been recruiting scientists from a variety of backgrounds, including: social, cognitive, developmental and bio-psychology, cognitive neurosciences, evolutionary anthropology, biology, and economics. In addition, in the last year notable infrastructural advances have been made, including the set-up of new experimental laboratories supporting our multi-methodological research programme. The research programme includes five major interconnected research foci.

1. **Foundations of Social Cognition**

Previous decades of social neuroscience research have revealed different neuronal routes underlying our capacity to understand others; be it their actions, thoughts, or emotions. Early research associated with the discovery of the so-called "mirror neurons" in monkeys, identified a neural network under-
lying the representation of others’ motor actions and intentions comprising the inferior parietal lobule (IPL), the ventral premotor cortex, and the caudal part of the inferior frontal gyrus (IFG) corresponding to pars opercularis. This research was then expanded to the area of emotions and empathy. In contrast to mirror-neuron networks implicated in the domain of motor actions, sharing sensations and feelings with others such as pain, disgust or touch mostly engages somatosensory cortices, as well as the insula and anterior cingulate cortex (ACC). In addition to this affective route to the understanding of others, researchers have distinguished yet another cognitive route helping to understand the beliefs, thoughts and desires of other people. This “mentalizing” or “Theory of Mind” network typically comprises areas in the medial prefrontal cortex (mPFC), precuneus, superior temporal sulcus (STS), and right temporo-parietal junction (rTPJ). Our goal is to develop integrated models of social cognition and to gain a more differentiated understanding of the interaction between these different routes of social cognition; including their role in social decision making and the exact functions and computations sub-served by the identified brain regions. Moreover, we are interested in understanding the generation of self- and other-related thoughts and how the content of our inner thoughts modulates brain activity and bodily responses. Similarly, we are investigating how mind-wandering relates to the so-called “default-network” and the above mentioned “mentalizing” or “Theory of Mind” network, as both engage similar brain regions, such as the mPFC and precuneus.

2. Developmental Social Neuroscience

Even though developmental psychology has a long tradition of studying the ontogeny of social abilities, such as perspective taking, empathy, and emotion regulation, developmental social neuroscience is still in its infancy. In the last few years, we have started to investigate the development of the social brain in children (5–12 years of age) and are now expanding our focus to even younger children and adolescents. We are particularly interested in the neural mechanisms underlying the developmental changes in children’s ability to take other people’s perspectives. We also focussed on how this is related to their ability to reflect on themselves and grasp their own feelings and those of others, as well as control their own emotions and behaviour. One key component of this endeavour is to understand how age-related changes in functional and structural brain parameters predict changes in social emotions, social cognition, and social behaviour, and to identify critical periods for the acquisition of these socio-affective skills. Methodologically, we have adapted paradigms developed in, for example, experimental economics, that allow for the investigation of social behaviour in an ecologically valid setting.

3. Plasticity of the Social Brain

Here we focus on micro-genetic within-subject changes elicited by a variety of mental training programmes. To investigate the plasticity and trainability of socio-affective functions, we are conducting small- and large-scale longitudinal studies in search for evidence for the malleability of competences such as empathy, compassion, affect regulation, cognitive perspective taking, mindfulness, attention, and memory. More specifically, we are researching whether training can significantly induce functional and long-lasting structural neuronal, as well as hormonal, health-related, and behavioural changes by means of a multi-disciplinary and multi-method approach. In addition to short-term training studies, the Department has begun planning a large-scale longitudinal study, which will train large numbers of subjects in Leipzig and Berlin in different socio-affective skills over a duration of several months to one year. This study is partly funded by a grant from the European Research Council (ERC) awarded to Tania Singer prior to her arrival at the Max Planck Institute.

4. Psychopathology of the Social Brain

In order to understand the underlying mechanisms that produce inadequacies in social behaviour, we study populations with affective and social deficits, such as people with mild autistic spectrum disorder (e.g. Asperger’s syndrome), alexithymia, narcissistic personality disorder, borderline disorder, and depression. The main goal of this research focus is to gain a more differentiated understanding of the specific subcomponents which might explain the observed social and affective deficits. For instance, we look at whether people with Asperger’s syndrome are equally deficient in empathic and cognitive perspective taking routes or merely in the latter. In the same population, we pursue the question of whether these individuals display a heightened bias towards themselves (e.g. egocentricity bias), when making inferences about the emotional states of others. We also consider whether such an enhanced egocentricity bias may be caused by malfunctioning of brain regions involved in the self-other distinction and perspective taking, such as
the rTPJ or the rSMG, rather than originating in deficient empathy-relevant regions, such as the insula and ACC. The rTPJ is known to be a crucial part of the “Theory of Mind” network, which has been shown to be deficient in autism. In contrast, we expect populations with psychopathic traits to be unimpaired in cognitive perspective taking but to show deficits in empathy associated with hypoactivation in emotion- and empathy-relevant circuitries involving the insula, amygdala, ACC, and others. Similarly, we are extending this work to people with strong narcissistic traits, depressed people, and people with borderline personality disorder to see whether these populations have preserved or impaired empathy, cognitive perspective taking, self-other distinction, and emotion-regulation capacities. Furthermore, we are interested in studying which of these social deficits comes with an enhanced egocentric bias, whether this is related to the inability to disengage from one’s own current emotional experience in order to accurately infer that of someone else, and whether this emotional egocentricity is biased towards a specific affective valence (e.g. negative in depressed, positive in narcissists). Finally, another project plans to investigate the influence of early life adversity in children (e.g. abuse and neglect) on affective brain responses (especially amygdala functions) and how these relate to functioning of the HPA-axis when these children are exposed to psychological stressors (TSST) and to pro- and antisocial behaviour measured in social exchange paradigms.

5. Evolutionary Basis of the Social Brain

We are collaborating with Michael Tomasello and Josep Call in the Department of Developmental and Comparative Psychology at the Max Planck Institute for Evolutionary Anthropology in Leipzig, to investigate the evolutionary and ontogenetic origins of social emotions in great apes and very young children. While there is promising research asking whether our nearest relatives share social capacities with us, such as Theory of Mind and cognitive perspective taking, the study of other social emotions, such as envy, Schadenfreude, empathic concern, and shame have so far been neglected in great apes. This is probably due, in part, to the methodological challenges associated with measuring emotions in our nearest relatives. Thus, this research focus also aims to develop new methods allowing for the non-invasive study of autonomic changes in great apes and small children, such as thermal imaging. The implementation of the same behavioural paradigms in great apes, in very young children, in children over 5 years of age, and in adults will be complemented by brain imaging data for the two latter age groups and should give us a better understanding of the evolutionary foundations of such social competencies.
Recruitment of the team and construction of the Department

Tania Singer was appointed as full Director of the Department of Social Neuroscience in September 2010. Since then, she has recruited new members for the research and support team of her Department. Currently, her group consists of three senior researchers, five post-doctoral fellows, six PhD students and project team members, nine support team members, and one external member.
Moreover, Tania Singer has been working on developing the necessary infrastructure for a multi-methodological and interdisciplinary investigation of social behaviour. In concert with her appointment, the Institute purchased a new state-of-the-art Siemens MAGNETOM Verio 3T scanner which allows scientists to conduct structural and functional neuroimaging studies and is also set up for the implementation of real-time fMRI. An entirely new building had to be constructed to host the scanner, provide space for MRI quality control, for participant testing and pre-training, post-processing and analysis, as well as additional equipment and a pharmacological laboratory.

A separate laboratory space was created to enable subjects to enter virtual worlds in which social dynamics, or so-called "proxemics," can be manipulated and measured. This lab provides a powerful tool for studying social phenomena within highly controlled, but relatively naturalistic, environments. It allows us to design experimental paradigms that manipulate context, social identity, and behaviour in ways that would be difficult in the physical world. We are further able to record what the participant sees and how the participant moves during an experiment.

The newly constructed psychobiology laboratory allows for the testing of physiological responses to standardized psycho-social stressors of participants, for example the Trier Social Stress Test (TSST), and the change of such responses following training or during certain social paradigms. The TSST induces stress by simulating an evaluated job interview followed by a difficult mathematical task. The laboratory has space for a mock interview panel and has an observation room with a one-way mirror to test for stress contagion in third-party observers.
Another technological accomplishment has been the design and set-up of two interactive multi-computer laboratories, one in Leipzig and one in Berlin, with 18 and 14 interconnected computers, respectively. Among other behavioural studies, we plan to apply a variety of new and innovative methods using multi-player computer-based social games. The resulting data from participants can be complemented with physiological measurements.

As we plan to recruit many subjects for a large-scale longitudinal study and for patient studies in Berlin, we are renting a satellite laboratory ("Haus 5"), with additional testing space, from the Humboldt University in Berlin. The building had to be completely restored over the past 1.5 years. The official opening of the laboratory took place in July 2011. It is equipped with the previously mentioned multi-computer laboratory, a neuro-pharmacological laboratory, additional office space, and a big seminar and mental-training room.

Figure 3.5 The multi-computer laboratories in Leipzig (A) and Berlin (B).

Figure 3.6 Pictures of "Haus 5" and the timeline for its reconstruction during 2010 and 2011.
**Director: Professor Dr Tania Singer**

### Senior Researchers and PostDocs
- Boris C. Bernhardt, PhD
- Dr Annette Brose (*)
- Dr Veronika Engert
- Joshua Grant, PhD
- Cade McCall, PhD
- Dr Natacha Rodrigues Mendes Fritz
- Jonathan Smallwood, PhD
- Dr Nikolaus Steinbeis (28)
- Anita Tusche

### PhD Students
- Haakon Engen
- Ferdinand Hoffmann
- Olga Klimecki
- Florence Ruby (20)
- Marjan Sharifi (5)

### Secretarial and Technical Staff
- Nicole Lorenz
- Matthias Bolz
- Boris Bornemann
- Henrik Grunert
- Elisabeth Murzik
- Sylvie Neubert
- Hannes Niederhausen
- Lisa Wittenburg
- Willi Zeidler
- Dr Christina Zube
- Sandra Zurborg, PhD

### Former Researcher
- Dr Annette Brose  
  Max Planck Institute for Human Development, Berlin, Germany

### Affiliated Researchers
- Dr Grit Hein  
  University of Zurich, Switzerland
- Dr Susanne Leiberg  
  University of Zurich, Switzerland

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(5) Excellence Cluster “Languages of Emotion”, Berlin, Germany
(20) Institute of Education Sciences (USA)/Max Planck Society
(28) Swiss National Science Foundation (SNSF)

(*) Left the Institute during 2010/2011
3.1 Foundations of Social Cognition
One important part of our research programme is to identify the various routes underlying our ability to understand others; we are working towards a unifying model of social cognition. As stated above, three major networks for social cognition have been identified, so far, that are essential to our ability to understand others: (a) motor actions—the so-called mirror neuron system; (b) beliefs and desires—the so-called mentalizing or Theory of Mind (ToM) system; and (c) affective states—our ability to empathize. While these different routes of social cognition seem to recruit different brain networks, some studies in the domains of ToM, empathy, or mirror neuron system research suggest that a basic mechanism exists in our brain enabling the experience of intersubjectivity. These so-called ‘shared networks’ or ‘simulation mechanism’ rely on the activation of representations underlying our own motor actions, thoughts and feelings to understand these states in others.

However, a major question remains: If our own experience and the observation of a related experience of others are processed by the same neural networks, how does our brain make the self/other distinction? A lack of self/other distinction when empathizing with the feelings of others can, in some situations, result in self-related ‘empathic distress’, or can also lead to an ‘emotional egocentricity bias’ when judging others’ states. Egocentricity bias refers to the propensity to judge other people in terms of one’s own perspectives, attitudes, and mental states. Despite the high prevalence of egocentrism and the detrimental effects of such egocentricity bias in social interactions, its development, failure, and neural basis are still poorly understood.

A number of our projects focus on the unique private mental lives that we possess as social beings: We spend half of our lives engaged in mental activity unrelated to the events in the here and now, such as mind-wandering or daydreaming. An aim here is to explore how spontaneous thought can be understood in terms of the brain’s attempt to make predictions to navigate the complex social world within which it exists. One research stream examines the functions that mind-wandering experiences can serve, such as ensuring the continuity of a sense of self and the management of emotions. A second will examine how the mind-wandering state differs in states of psychopathology, such as narcissism, depression, autism, and borderline personality disorder. To achieve these goals, the content and underlying neural substrates of the mind-wandering state will be characterized in a three-dimensional space. One dimension of this space represents the temporal focus of the experience (thoughts related to events in the past or imagined possible events in the future). The second dimension describes the affective nature of the cognitive experience (positive or negative). Finally, the third dimension represents the referent to which the thoughts are directed (to the individual himself/herself or to another person). Using this multi-dimensional approach, we will examine the neural basis and functions of these different types of mind-wandering.
Empathy for pleasant and unpleasant touch

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Most empathy studies in social neuroscience have been performed in the domain of primary or secondary negative emotions such as pain, disgust, social exclusion, or embarrassment, and have pointed to the anterior insula (AI) and anterior cingulate cortex (ACC) having a crucial role in the processing of vicarious emotions (for an overview see Bernhard & Singer, in press). Another line of fMRI studies focussed on vicarious touch (e.g. Keysers et al., 2010, Nat Rev Neurosci, 11, 417–428) and identified somatosensory cortices elicited by both, first-hand and second-hand experience of neutral touch. Even though these touch studies revealed shared empathic activations in brain regions other than in AI and ACC, they did not directly test for emotions, as the experience of touch was neutral.

To fill these research gaps, we developed a new paradigm for testing empathy for pleasant and unpleasant touch. Two participants, present in the same room, were touched sequentially by either pleasant, neutral, or unpleasant stimuli on their hands, and were asked to rate how either they (self condition) or the other person (other condition) would feel about being touched in the different conditions. Touch was accompanied by pictures, which matched the touch experience, allowing for other-related rating in the absence of any somatosensory stimulation.

Behavioural analyses of the affective ratings confirmed that the newly developed affective touch paradigm was indeed able to elicit equally strong negative and positive feelings when participants were being touched with pleasant or unpleasant stimuli. Analysis of the fMRI data of the individual/self condition revealed that while activation in the bilateral medial orbitofrontal cortex increased during pleasant touch, activation in a network that includes the right amygdala, bilateral anterior insula, and medial and anterior cingulate cortex increased during unpleasant touch. Conjunction analyses further revealed that different “shared neural networks” are recruited in empathy for pleasant and unpleasant touch. Both experiencing pleasant touch oneself and observing others experiencing it, resulted in activation of the medial orbitofrontal cortex (MNI coordinates x/y/z = –12/38/–18, P_SVC = 0.001). Both experiencing unpleasant touch oneself and observing others experiencing it, resulted in activation in the right anterior fronto-insular cortex (44/32/–8, P_SVC = 0.05).

In conclusion, these analyses suggest that previous findings of “shared networks” can be extended to the domain of affective touch. Furthermore, they suggest that the insula cortex is more generally activated upon vicarious experience of negative affect, while the medial OFC, an area previously associated with first-hand experience of positive affect and reward, is activated by positive touch.

Figure 3.1.1.1 Affective ratings for visuo-tactile stimulation of (A) self and (B) other in adults.
Humans tend to understand the mental states of others in relation to their own mental states. As mentioned above, social neuroscience has provided plenty of evidence for the existence of “shared empathic networks” underlying the experience of affective states in self and others. In many situations, however, such a simple projection mechanism from the self onto another can lead to an egocentricity bias, causing serious misunderstanding and interpersonal conflict.

To study emotional egocentricity bias and its neural basis, we extended the “empathy for affective touch” paradigm such that both participants were now touched simultaneously with either pleasant or unpleasant stimuli on his/her hands and the participant had to judge either his/her own emotions, or the emotions of the other person (condition simultaneous/self vs simultaneous/other). Importantly, the valence of self- and other-related stimulation was either congruent or incongruent; thereby, the emotional egocentricity bias was defined as the difference between ratings in incongruent and congruent trials when judging the other, as compared to the difference when judging one’s own feelings.

To investigate the degree of emotional egocentric bias in healthy adults and the neural mechanisms associated with it, we performed a series of experiments. First, a behavioural experiment ($N = 72$), which served to estab-
lish the baseline occurrence of emotional egocentricity bias in healthy adults. Second, an fMRI experiment ($N = 18$) served as a first step to identify the neural correlates underlying empathy for touch as well as emotional egocentricity bias. This experiment was followed by a second fMRI experiment ($N = 32$), in which we validated and extended the findings of the first fMRI experiment. The results of these three experiments revealed that adults consistently show emotional egocentricity bias and that the right supramarginal gyrus (rSMG) is specifically engaged when we need to judge emotions experienced by others that are incongruent to our own. Finally, a repetitive transcranial magnetic stimulation (rTMS) experiment, that entailed a temporary disruption of rSMG activity, revealed that this area is essential for overcoming egocentricity bias during affective judgements.

Taken together, these results provide behavioural and neural evidence for the presence of human affective egocentrism and point to a crucial role of the rSMG in overcoming it. The present paradigm may prove to be immensely useful for diagnosis and research in clinical settings, and might inspire research in developmental neuroscience as egocentrism is known to be a key feature of both the developing brain and for many socioaffective disorders.

3.1.3 Pupillometric evidence for perceptual decoupling during stimulus independent thought

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Taking a shower, queuing for coffee, or riding the bus are all everyday tasks that allow the mind to wander. These experiences illustrate that mental activity is not confined to the online processing of sensory information; it also has an offline mode which depends more on the contents of memory than it does on perception and is known as stimulus independent thought (SIT).

One hypothesis of how to discriminate between the online and offline modes of cognition is to examine the coupling between neural markers of cognitive processing and incoming perceptual information. When cognitive processes are generated in response to an external event, neural processing occurs that is coupled to the imperative stimulus, whereas when the neural processes are generated spontaneously, the correlation between the neural event and perceptual information can be reduced or abolished.

To test this decoupling hypothesis, we explored the correlation between the dynamics of pupil dilation (PD) and external events as participants performed two tasks: (1) a working memory (WM) task that required an almost continual external focus, and (2) a simple choice reaction time (CRT) task, which provided greater opportunity for participants to engage in offline thought. In the WM task,
Absorbed in thought: The impact of mind-wandering on relevant and irrelevant events in a task

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Despite the prevalence of mind-wandering (MW) in daily life, it is frequently associated with absent-minded error. This juxtaposition of an important form of social cognition with performance detriments has proved difficult to incorporate into models of cognitive science. According to one view, MW occurs because executive control of external task-relevant information has failed, allowing distracters (such as stimulus independent thought, SIT) to

the identity of non-coloured numbers must be encoded, while in the CRT task, no attention need be paid to these events. The time course of the tasks is presented in figure 3.1.3A. In Study 1, experience sampling demonstrated that the offline mode of thought was more frequent in the CRT task than in the WM task (Fig. 3.1.3B). In Study 2, we measured PD while participants performed the same tasks and examined how the tasks differed in the correlation between the PD and task events. A robust event related PD response was observed when the non-target numbers were presented in the WM task (Fig. 3.1.3C, in red), a pattern that was absent from the CRT task (Fig. 3.1.3C, in blue). These data support the hypothesis that one characteristic of SIT is the absence of neural activity that is related to the current stimulus environment.
be processed more readily. This view proposes that MW error results from the executive failure that causes the spontaneous mental events to occur in the first place. An alternative view is that the errors associated with SIT occur as a by-product of how the mind generates and maintains an internal train of thought. According to this view, known as the decoupling hypothesis, during SIT, attention is decoupled from perception and that compromises performance on the external task.

To contrast the decoupling hypothesis and the executive failure account, we conducted an event-related potential (ERP) investigation. Participants detected infrequent target events in a visual oddball task and ignored distracter events with the same frequency. The ERPs produced by this experiment are presented in Figure 3.1.4. Target events generated a potential that was maximal over posterior and parietal regions and is known as the P3. The distracter events generated a slightly earlier potential that was maximal over regions in the frontal central cortex that is known as the P3a. Critically, individuals who reported high levels of SIT showed statistically smaller ERPs to both targets and distracters. This suppression of the cortical responses to all task events confirms the prediction of the decoupling hypothesis, which is that SIT reduces attention to all stimuli regardless of task relevance. Thus, rather than being a product of executive failure, the experience of mind-wandering is a by-product of the capacity for consciousness to transcend the present moment.

**Figure 3.1.4** Scalp maps of the evoked response to the distracter and target stimuli used to examine the consequence of mind-wandering on both, task-relevant and task-irrelevant events. High levels of mind-wandering were associated with a reduction in the magnitude of the evoked response to both targets and distracters, indicating that high levels of mind-wandering are distinct from a simple state of distraction.

### 3.1.5 Self-reflection and the temporal focus of the wandering mind

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In the bestselling novel "The Time Traveler’s Wife", the male protagonist has a genetic disorder that causes him to travel physically through time to periods of the past or future which have personal significance. While the laws of physics currently prohibit time travel, we are nevertheless able to revisit the past or simulate the future using our imagination. Current accounts suggest that self-referential thought serves a pivotal function in the human ability to imagine the future during mind-wandering (MW) and this hypothesis was tested in two studies.

Using a between subjects design, Study 1 compared the effects of a brief period of self-reflection on the temporal focus of MW by examining if rating adjectives for self-relevance relative to comparing the same stimuli for rel-
evance to one's best friend, a familiar other (the UK prime minister), or a no task control condition, altered the temporal focus of stimulus independent thinking. Figure 3.1.5A represents the findings that, following a period of self-reflection, MW was focussed on the future more than for all other conditions. Study 2 used a within-subjects design to explore if individual differences in the strength of memories for self-relevant information were related to the extent of future-related thinking during MW. Figure 3.1.5B illustrates that the magnitude of the self-reference effect (SRE) was positively associated with the amount of prospective MW. Individual differences in the strength of self-memory, therefore, were associated with a greater tendency to think about the future during MW. Together, these results confirm that self-reflection is a core component of future thinking during MW and provide novel evidence that a key function of the autobiographical memory system may be to allow mental simulation of events in the future during spontaneous thought. More generally, given that a coherent sense of self is important, these studies suggest that prospective MW may be an important process in ensuring that individuals have a coherent view of who they are.

Figure 3.1.5. (A) Asking participants to determine the self-relevance of a set of adjectives increased future-focused mind-wandering compared to individuals who rated the same adjectives to their best friend, the current UK prime minister, or a no task control. (B) The frequency of future thinking during MW was positively associated with the magnitude of the memory advantage for words rated to oneself relative to a familiar referent.
3.2 Developmental Social Neuroscience
The nature of social interaction changes dramatically throughout the life-span. One of the major aims of this research focus is to describe the changes in social emotions and cognition, as well as in social behaviour, from childhood to adulthood and to explore the development of the underlying neural processes accompanying these changes.

Amongst others, we are using game-theory paradigms, initially developed in empirical economics, to study the development of social phenomena such as altruism, reciprocity, trust, and strategic social behaviour in an ecologically valid way. Via paradigms utilising primary sensory stimuli, such as affective touch, or pleasant and unpleasant tastes, we are able to induce and measure emotions with a strong degree of reliability across a large range of different ages. Here, we focus on the development of first-person and second-person affective experiences and the ability to suppress and regulate these emotions. Particularly, we will investigate the extent to which developmental changes in social emotions, such as empathy envy, Schadenfreude, or our sense of fairness can be accounted for by age-related changes in general cognitive capacities, such as executive functions. Our hypotheses are based on findings from paediatric imaging revealing differential maturational time-courses for specific brain regions. Applying a range of structural and functional markers of brain development, our ultimate goal is to use these as predictors for observed age-related changes in social behaviour and affect to achieve a better understanding of how the development of the brain shapes the emergence of specific socio-affective functions over ontogeny.
Impulse control and underlying functions of the left DLPFC mediate age-related individual differences in strategic social behaviour

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Human social exchange is often characterized by conflicts of interest requiring strategic behaviour for their resolution, but little is known about how this develops during childhood and what the underlying cognitive and neural mechanisms of this development are. We studied children’s (N = 28; age range = 6.9–13.1) decisions, as well as their brain activity by means of fMRI, while they played two types of economic exchange games with differing demands of strategic behaviour: the Ultimatum Game (UG) and the Dictator Game (DG). In the UG, two anonymous individuals—a proposer and a responder—need to negotiate the division of a set amount of money between them. The proposer can offer a split of the sum, which the responder can accept or reject. If accepted, the money is divided between the players as proposed. If the responder rejects, neither player obtains anything (Fig. 3.2.1A). The DG is different in that the responder can only accept. Thus, in the UG, the proposer needs to be able to consider the sanctioning threat and exercise increased behavioural control in order to act strategically when making the offer. The difference in the proposer’s offer size between UG and DG is considered a measure of strategic behaviour and is the focus of this study. In addition, an extensive battery of tasks, testing for impulse control, social knowledge, skills, and preferences was administered.

We demonstrated an increase in strategic behaviour with age, which was best explained by age-related differences in impulse control and not by differences in social preferences for fairness. This developmental difference was also reflected by increased activation of the left dorsolateral prefrontal cortex (lDLPFC). Specifically, the activity of the same region of the lDLPFC correlated positively with increased age (Fig. 3.2.1B, in red), strategic behaviour (Fig. 3.2.1B, in yellow), and impulse control (Fig. 3.2.1B, in blue).

Based on these findings, we conclude that selfish behaviour in younger children is not caused by a lack of understanding right from wrong but by the inability to implement behavioural control when tempted to act selfishly, which seems to rely on brain regions maturing only late in ontogeny.

Figure 3.2.1  (A) Economic games used to assess strategic behaviour in the proposer. (B) Increased activation of lDLPFC with increased age (red), strategic behaviour (yellow), and impulse control (blue).
The development of envy and *Schadenfreude*

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Comparing ourselves with others can elicit social emotions such as envy and *Schadenfreude*, which can potentially lead to highly antisocial behaviour. Nothing is known about the emergence and development of these emotions. To this end, we tested 210 children aged 7 to 13 on a task developed specifically to measure these social emotions.

Children were assigned to groups of four. Each subject simultaneously performed a speeded reaction time task with the instruction to be as fast as possible (Fig. 3.2.2A). If one was fast enough, money could be earned; whereas if one were too slow, money would be lost. Importantly, to induce an element of competition, children were also told that whoever was fastest would obtain an extra-large monetary prize. The money earned during the experiment could be traded in at the end for a present of varying cost, size, and desirability. After each task, children were informed about their performance (speed, earnings) relative to how the group had performed.

Then, children were asked to give a rating on a scale ranging from +10 to −10 on how happy or sad they felt. Our definition of envy was such that one feels worse when losing while seeing the other win, as compared to when both lose. Equally, our definition of *Schadenfreude* was such that one feels better when winning while seeing the other lose, as compared to when both win (Fig. 3.2.2B).

We found strong main effects of envy and *Schadenfreude* in our sample of children, demonstrating that our paradigm successfully induced these emotions (Fig. 3.2.2C). Moreover, we found a highly significant age-related decrease in both envy and *Schadenfreude*. These age effects remained even after controlling for the strength of the emotional response to winning and losing. In addition, we found a strong correlation between envy and *Schadenfreude* (Fig. 3.2.2D), suggesting a high interdependence of the two emotions. A future study will focus on the functional and structural development of those brain regions, related to these age-dependent changes.
Age-related changes in impulse control and not valuation mediate increased patience in intertemporal choice

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Deciding between an immediate reward or future benefits is a dilemma we face constantly (e.g. meeting a work deadline now to gain a free evening vs stopping for a chat with colleagues). Individuals tend to demonstrate a preference for receiving rewards immediately, a phenomenon also known as intertemporal discounting. This is subject to a high degree of trait- and state-dependent inter-individual variability. The importance of studying discounting behaviour is warranted by its profound implications for one’s health, the economy, and the environment.

It has been shown that discounting decreases with age during childhood (Green, Fry & Myerson, 1994, Psych Sci, 233, 33–36). However, whether this is a result of age-related changes in valuation of immediate rewards vs delayed rewards, or in increased self-control abilities in the moment of decision-making, remains an open question. We studied children ($N = 20$, age range = 6.63–12.73)

Figure 3.2.3 There were no age-related changes in how attractive single valuable options were rated as a function of (A) reward magnitude or (B) reward delay. There was (C) a significant age-related decrease in the degree of discounting, as well as (D) an association between discounting and impulse control, whereby improved impulse control implied lower discounting.
while they made decisions about two simultaneously presented reward options varying in magnitude and time of receipt. In addition, we measured how attractive each individual option appeared to the participants, as well as each individual’s self-control abilities.

We found that attractiveness ratings differed neither in reward magnitude (Fig. 3.2.3A) nor reward delay (Fig. 3.2.3B) as a function of age. More importantly, we showed that in spite of similarities in attractiveness ratings, discounting decreased with age (Fig. 3.2.3C), which in turn was associated with improved impulse control (Fig. 3.2.3D). These data suggest that age-related changes in self-control and not in valuation are the driving factors of lower intertemporal discounting and visibly greater patience in older children. Simultaneously acquired functional and structural imaging data will be able to shed light on the development of the critical neural structures, which mediate this change in behaviour. We hypothesize late-developing cortical areas (e.g., dorsolateral prefrontal cortex) as candidate regions and thereby expect to confirm results from previous studies from this Department.
Plasticity in Social Neuroscience
Recent research has greatly advanced our understanding of neural plasticity in the domains of cognitive and motor skills. However, very little is known with regard to the neural substrates underlying socio-affective plasticity and, specifically, the training of positive social affect, such as prosocial motivation or compassion. Thus, this research focus aims to investigate the subjective, behavioural, neuronal, and hormonal changes associated with mental training of socio-affective capacities ranging from empathy, prosocial motivation, and compassion to emotion-regulation and perspective taking. In order to reliably study neural, physiological, and behavioural changes induced by such mental training programs, we started developing a range of new tasks optimized for repeated measurements of socio-affective functions in longitudinal designs as well as new short-term and long-term intervention programs. The training programs are based on old and new practices derived from both, contemplative traditions in the East and different approaches from the West, all focussing on achieving better mental and physical health, and balance in life. We hope that the insights gained from these mental training studies will further advance our basic knowledge about the plasticity of the social brain and help increase subjective well-being, strengthen resilience in coping with an increasingly complex and uncertain world, reduce stress and other health-related challenges, and promote prosocial motivation and behaviour.
Short-term compassion training increases prosocial behaviour in a newly developed prosocial game

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Compassion has been suggested as a strong motivator for prosocial behaviour. While research has demonstrated that compassion training can have positive effects on mood and health, it is unknown whether it also leads to increases in prosocial behaviour. We addressed this question in two experiments. First, we introduced a new prosocial game, the Zurich Prosocial Game (ZPG), which allows for repeated, ecologically valid assessment of prosocial behaviour. In the ZPG, participants rapidly navigate a virtual character through a maze in order to reach a treasure which is paid out at the end of the experiment. Simultaneously, an ostensible other player is navigating through the maze. While both players try to reach a different treasure, obstructing gates fall onto their paths which can only be opened by a colour matching key. Thus, the participant is given the opportunity to use his/her resources (time and key) in order to help the other player reach the treasure (Fig. 3.3.1.1).

In Experiment 1 (N = 68), we showed that the ZPG is sensitive to the influence of reciprocity (implemented through trials in which the participant was helped by the other player before having the opportunity to help), helping cost (implemented through a reduced probability to reach one’s own treasure), and distress cues (auditory and visual cues that show the virtual character crying when stuck) on helping behaviour (Fig. 3.3.1.2). Furthermore, we compared the influence of short-term compassion training (N = 27) with that of short-term memory training (N = 32) on helping behaviour in the ZPG. The results revealed that helping behaviour in the ZPG increased in participants who had received short-term compassion training, but not in participants who had received short-term memory training (Fig. 3.3.1.3). Interindividual differences in practice duration were specifically related to changes in the amount of helping under no-reciprocity conditions. Our results provide first evidence of the positive impact of short-term compassion training on prosocial behaviour towards strangers in a training-unrelated task.

Figure 3.3.1.1 Labelled screenshot of the ZPG. Participants move their virtual character forward by clicking with the mouse on the area in front of it. Usage of keys in order to open the blocking gates occurs by mouse click on the key matching the gate’s colour.

Figure 3.3.1.2 Percent helping in the different conditions of the ZPG. Error bars denote standard errors of mean.

Figure 3.3.1.3 Effects of training on overall helping in the ZPG for the compassion-training and memory-training group. Error bars denote standard errors of mean. * p < 0.05, one-sided.
The Socio-Affective Video Task (SoVT): A new, fMRI-compatible measure for the repeated assessment of social affect

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Paradigms which allow the repeated measurement of social affect are rare. We, therefore, developed a new task, the Socio-affective Video Task (SoVT), which was optimized for repeated measurements in longitudinal designs (Fig. 3.3.2.1). The SoVT consists of high emotion (HE) videos, depicting people in distress and low emotion (LE) videos, presenting people performing everyday activities. Based on subjective ratings from a normative study (N = 265), we assembled three parallel video sets (A, B, and C) that were matched in terms of empathy, valence, and arousal ratings. As expected, we observed that HE and LE videos differed on all three dependent variables (empathy, valence, and arousal).

In an independent functional imaging study (N = 94), we confirmed the parallel nature of the three video sets. The difference between HE and LE videos was reflected in subjective ratings (see Fig. 3.3.2.2A–C) and underlying neural responses. HE compared to LE videos evoked stronger neural activity in an extended network comprising areas in the occipital, temporal, frontal, and parietal lobes, as well as subcortical areas, including the amygdala, paralleling previous findings (Vrticka et al., 2011, Neuropsychologia, 49, 1067–1082; Goldin et al., 2008, Biol Psychiatry, 63, 577–586). Conversely, LE compared to HE videos elicited stronger activation in the posterior insula, the medial orbitofrontal cortex, the fusiform, and the precentral gyrus. We also observed that empathy ratings in response to HE videos in the SoVT mapped to activations in the anterior insula and the anterior medial cingulate cortex (Fig. 3.3.2.2D)—the two core regions involved in empathy for others’ suffering (Lamm et al., 2011, NeuroImage, 54, 2492–2502). Taken together, these results indicate that the SoVT could be validated as a new measure of social affect that prevents repetition confounds, while at the same time allowing the dissociation of positive and negative affect in response to witnessing other people’s suffering.

Figure 3.3.2.1 In one session, participants saw 12 high emotion (HE) and 12 low emotion (LE) videos (duration 10–18 s). Each video was subsequently rated on subjectively experienced empathy, positive affect, and negative affect. Every mini-block of three HE or LE videos was followed by a fixation cross (displayed for 10 s).

Figure 3.3.2.2 Subjective emotional experiences and related neural activations evoked by the SoVT. (A–C) Average subjective ratings of positive affect, negative affect, and empathy in response to low emotion (LE) and high emotion (HE) video stimuli at pre-training (zero, no affect; ten, maximum affect). Error bars indicate standard error of mean (s.e.m.); *** p < 0.001. (D) Small volume correction (SVC) with a functional activation map from a recent meta-analysis on empathy for pain revealed that activations in the AI and the aMCC were parametrically modulated by subjectively experienced empathy for HE videos. Colour-coded activations (brighter colours indicating lower p values) were rendered on an MNI template in neurological orientation. Inset x values indicate stereotactic coordinate of the shown slice in MNI space. AI, anterior insula; aMCC, anterior medial cingulate cortex.
Evidence for neural plasticity and associated changes in positive affect after short-term compassion training

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Since almost nothing is known about neural plasticity resulting from training socio-affective capacities, we performed multiple functional imaging studies on the effects of training compassion—the emotional capacity to meet another person’s suffering with feelings of concern and the motivation to help. First, we observed that in a long-term practitioner, strong, compared to weak, feelings of compassion consistently increased activations in subcortical structures including the striatum and the ventral tegmental area/substantia nigra (VTA/SN), as well as in cortical regions including the medial orbitofrontal cortex (mOFC). Next, we derived independent regions of interest (ROIs) based on two short-term compassion training experiments (total $N = 46$). We found that in a pre-post design with the newly developed Socio-affective Video Task (described above), short-term compassion training ($N = 28$) compared to memory training ($N = 30$), induced stronger activity in response

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Figure 3.3.3.1 Effects of compassion and memory training on neural responses to HE videos. The contrast ['Compassion Δ HE > Memory Δ HE'] revealed higher activations ($p < 0.05$; SVC) in (A) the right medial orbitofrontal cortex (mOFC), (B) the right ventral tegmental area/substantia nigra (VTA/SN), (C) the right pallidum, and (D) the right putamen. Bar charts show the change in parameter estimates in the depicted independent region of interest; error bars denote s.e.m. Orange boxes show BOLD activations of an expert practitioner immersed in compassion [high > low degree]. All activations were colour-coded with brighter colours indicating lower $p$ values. Activations were rendered on an MNI template in neurological orientation. Inset x/z values indicate stereotactic coordinate of the shown slice in MNI space.
to HE videos in the mOFC, the putamen, the pallidum, and the VTA/SN within these ROIs (Fig. 3.3.3.1). Notably, these brain regions were previously associated with positive affect and affiliation. On the behavioural level, compassion, but not memory training, increased subjective ratings of empathy in response to low emotion (LE) videos and positive affect ratings in response to both, low emotion and high emotion (HE) videos (Fig. 3.3.3.2). The observed increase in activity in this brain network along with more positive affect after compassion training is remarkable, as participants were exposed to distressing social stimuli that at pre-test elicited negative responses associated with a brain network usually observed when subjects are exposed to negative stimuli. These findings suggest that the deliberate cultivation of compassion offers a new coping strategy that might foster resilience and ultimately increase prosocial behaviour.

Figure 3.3.3.2 Behavioural effects of compassion and memory training. (A) Self-reported positive affect in response to LE and HE videos increased after compassion training but not after memory training. (B) No significant changes were observed for negative affect. (C) Compassion training (not memory training) increased empathy towards people in LE videos. LE, low emotion; HE, high emotion.
3.4 Multi-Method & Multi-Disciplinary Approaches in Social Neuroscience
In this chapter we describe, in more detail, some of the novel multi-method and multi-disciplinary approaches that we use to investigate social behaviour and emotions. Applying virtual reality (VR) technology in our Department, researchers can immerse participants in ecologically valid environments (e.g. classrooms, streets, the edge of a cliff) where subjects will socially interact with avatars, while retaining a high level of experimental control. Experiments can selectively vary social identities (e.g. race, gender, body type) and the actual verbal and nonverbal behaviour of interactants. Because participants’ movements are tracked and their viewpoints rendered, experiments produce a near-continuous record of the movement and visual experience of each person during an interaction. Moreover, researchers can combine VR paradigms with physiological measurements and biophysical markers (e.g. cortisol), allowing them to place participants in perceptually rich scenarios even when they are physically confined by peripheral physiological or neuroimaging tools. The software behind these worlds is platform-general, allowing us to use components of our worlds in network gaming or neuroimaging environments.

Another method used in our Department is the measurement of adaptive responses elicited to re-establish homeostasis after an instance of stress. Both, physical and psychological health, are shaped by an individual’s lifelong stress exposure. However, not everyone who experiences significant life stress develops psychopathology. Coupling physiological measures with the paradigms of social neuroscience promises to shed light on the topic of interindividual variability in vulnerability and resilience to stress; an important topic in stress research. We will, for example, investigate how specific content of thought (e.g. negative self-related thoughts) influences stress markers such as cortisol or heart rate variability, or reversely, how stress experiences prime a certain kind of thought, which will then in turn modulate brain and bodily functions. Additionally, we will study the relationship between social phenomena, such as social rejection, and stress-related markers. In search of techniques to build resilience, we will investigate whether the training of adaptive social emotions and behaviours improves markers of physical and psychological health.

Finally, another project focuses on identifying the affective traits common and unique to great apes and humans. This approach will allow tracing back of the emergence and reconstruction of primary and higher-order emotions over evolutionary history. Great apes share with us a large number of flexible adaptations, both from the physical and social domains (e.g. problem solving, future planning, Theory of Mind, and cooperation). However, in the domain of social emotions, no comparative research has yet been conducted. Therefore, we have started to collaborate with the Max Planck Institute for Evolutionary Anthropology in Leipzig and aim to investigate the ontogenetic and the phylogenetic origins of social emotions (e.g. empathic concern, Schadenfreude with/without pro-social behaviour, shame, and embarrassment). More specifically, we propose to measure the development of these emotions in infants and older children, behaviourally and with neuroimaging paradigms, and to adapt the same paradigms to the study of social emotions in great apes.

These multi-disciplinary approaches will be extended by the development of thermal imaging as a new method to better measure the autonomic changes underlying emotions in infants, older children, and great apes in a non-invasive way.
Neural Correlates of Social Behaviour

3.4.1 Mere presence is not enough: Responsive support in a virtual world

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One might expect the presence of a trusted companion to reduce anxiety in the face of a threatening situation. However, attachment theory suggests that the mere presence of the loved one is insufficient: instead, the attachment figure must also be emotionally responsive and attentive. While this claim has been debated in the literature, evidence has been lacking, given the difficulty in experimentally manipulating the social support of a loved one during a stressful event. In this study, we used an immersive virtual environment to do so (Kane et al., in press, J Exp Soc Psy). Participants brought their close relationship partners into the lab. We then led them to believe that they would interact with each other in a shared virtual world—their nonverbal behaviours tracked and rendered on the bodies of avatars. In reality, we controlled the partner’s behaviour. During the interaction, the participant’s task was to walk along the edge of a virtual cliff without falling into a canyon. In one condition, the partner’s avatar provided nonverbal support, orienting toward the participant while nodding, waving, and occasionally clapping. In the other condition, the avatar looked away from the participant, looking out over the canyon instead.

Participants in the supportive condition reported feeling less stressed and more secure during the task. They were also more likely to report seeing expressions of social support that were not actually present, such as smiling (despite the fact that the avatars displayed no facial animations). Behaviourally, participants in the non-supportive condition were more vigilant to their partners’ behaviour, repeatedly looking toward them over the course of the task. They also stayed further away from their real partners during a subsequent interaction. These findings suggest that people monitor their social environment for signs of responsiveness and that perceived responsiveness, not mere presence, is the key modulator of emotional security.

3.4.2 Measurement and modelling of proxemic responses to fair versus unfair individuals

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During face-to-face interactions, we use our bodies to physically and symbolically approach and avoid others. We orient towards or away from a given target, stand nearer or further from them, and adopt body postures that are relatively opened or closed. These proxemic patterns are often subtle and implicit. Nevertheless, they
potentially express individual dispositions, attitudes toward other interactants, and motivations within a given interaction. While measurement in this domain has traditionally lacked precision and complexity (e.g., seat choice in a lobby or coding of video-taped interactions), digital tracking technologies provide an objective moment-to-moment account of an interaction’s proxemic dynamics. The critical challenge in using these data for psychological research is to produce meaningful summaries and statistics.

Along these lines, we staged social interactions within an immersive virtual environment to manipulate participants’ beliefs about a pair of confederates, and then to measure their proxemic responses to them. Initially, while playing an economic game, the two confederates varied in the degree to which they played fairly; one confederate reciprocated the participant’s generosity while the other did not (Singer et al., 2006, Nature, 439, 466–469). During a subsequent and ostensibly unrelated task, participants encountered both confederates in a virtual art museum. Their position and orientation were recorded while they walked around the room examining photos on the walls. Based on the frequency and range of each participant’s movement through interpersonal space, we create allocentric and egocentric proxemic maps. These images are then contrasted to compare individual traits, subjective states, and responses to the other interactants. Preliminary results suggest distinctive proxemic responses between fair players, whereby participants were more likely to physically avoid and orient away from the unfair players.

An organism’s principal metabolic peripheral effectors of the stress system are the catecholamines, which are regulated by the sympathetic nervous system (SNS), and the glucocorticoids, which are regulated by the hypothalamic-pituitary-adrenal (HPA)-axis. Because stress is a multidimensional construct, multiple stress-related sys-
tems should be assessed to accurately represent stress physiology. The goal of the current research was to explore the correlation patterns between salivary enzyme alpha-amylase (sAA), an indicator of sympathetic activation, and cortisol, the end-product of the HPA-axis. We applied cross-correlation analyses to several synchronized time series of sAA and cortisol measures obtained from forty-nine healthy males who underwent the Trier Social Stress Test (TSST). We found significant positive cross-correlations between sAA and cortisol at positive time lags (Fig. 3.4.3). Changes in sAA thus preceded same-direction changes in cortisol release by 5–24 min. Peak positive correlations ($r = 0.27, p < 0.001$) were observed at 13.5 min, which means that the average positive association of all possible pairs of sAA with cortisol was highest when cortisol followed sAA by 13.5 min. Additionally, we found significant negative cross-correlations between sAA and cortisol at negative time lags, signifying that changes in cortisol preceded opposite-direction changes in sAA release. Cortisol levels predicted sAA levels 4–28 min later, with peak negative correlations ($r = -0.16, p < 0.001$) at $-13.5$ min. Significant negative cross-correlations were also found at positive time lags. Changes in sAA levels predicted opposite-direction changes in cortisol levels 36–42 min later, with peak correlations ($r = -0.09, p = 0.017$) at 41.5 min. We suggest that sAA and cortisol stress responses are reliably associated at various time lags throughout a stressful situation.

**Looking back in anger: Investigating the relationship between mind-wandering and stress**

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Event sampling of people’s everyday experience suggests a link between mind-wandering (MW) and unhappiness (Killingsworth & Gilbert, 2010, Science, 330, 932) with negative moods being associated with more frequent mind-wandering (Smallwood & O’Connor, 2011). We hypothesized that one reason for an association with unhappiness could be because the stressful nature of daily life might increase the tendency for the mind to wander.

To test this hypothesis, we administered the Trier Social Stress Test (TSST; Kirschbaum et al., 1993, Neuropsychobiology, 28, 76–81) to 19 healthy participants. Experience sampling probes assessed three dimensions of MW in a baseline session and after the TSST: (i) time (past vs future), (ii) referent (self vs other), and (iii) emotion (positive vs negative). Participants also provided ratings of anxiety and anger throughout the testing sessions. Cluster analysis was used to determine the interrelationship between each of the MW dimensions. This preliminary analysis identified four categories of mental content that are schematically represented in the upper panel of figure 3.4.4.1. The different clusters reflect distinct categories of mental content, and broadly correspond to a state of hope and anticipation (Cluster 1), a focus on the here and now (Cluster 2), a state of reminiscence (Cluster 3), and a state of rumination (Cluster 4). The
probability of each category being reported during the baseline and TSST sessions (tested on different days) is presented in figure 3.4.4.2. The only significantly elevated category following stress was ruminative thoughts. Post-stress reminiscent thoughts negatively correlated with increases in anticipatory stress ($r = -0.44, p = 0.059$), post-stress anxiety ($r = -0.44, p = 0.059$), and anxiety ratings 30 min post-stress ($r = -0.46, p = 0.047$). Post-stress ruminative thoughts positively correlated with increases in post-stress anxiety immediately ($r = 0.14, p = 0.034$) and 30 min post-stress ($r = 0.53, p = 0.020$) (Fig. 3.4.4.3). Stress-induced changes in anger were unrelated to post-stress mental content, and there were no associations between mental content and subjective-psychological ratings in the baseline testing session. These data indicate that the difficulties we encounter in daily life lead the mind to ruminate about events in the past. This suggests that the link between MW and unhappiness (observed both, in and out of the lab) is partly a reflection of the stress we encounter in daily life.

![Cluster analysis](image)

**Figure 3.4.4.1** Cluster analysis was used to identify the interrelationship between different dimensions of mental content (time, referent, and emotion). This procedure revealed four categories of thought, each of which varied on their relative combinations of each dimension of thought. The specific interrelationship between each dimension of mental content is represented schematically in this figure. In each diagram the vertical axis represents the relative emphasis on positive and negative thinking. In each sub panel, the x-axis in the left hand panel represent the relative emphasis on the past and the future, while the diagrams on the right indicate the relative emphasis of the mental content on the self or other.

![Pie chart](image)

**Figure 3.4.4.2** (A) This figure represents the percentage of the total experience-sampling probes that were recorded across the experiment in the form of a pie chart. (B) This panel presents the frequency of each type of mind wandering recorded in the baseline and TSST sessions. It can be seen that the TSST led to a specific increase in the category of ruminative thought.
Challenging individuals with controlled stressors that produce reliable stress responses is instrumental to stress research. Two widely used laboratory paradigms are the Cold Pressor Test (CPT) and the Trier Social Stress Test (TSST). The CPT (Hines & Brown, 1932, Proc Staff Meet Mayo Clin, 7, 32) is a pain induction technique; the TSST (Kirschbaum et al., 1993, Neuropsychobiology, 28, 67–81) a psychosocial stressor. Both paradigms activate various physiological stress markers—albeit with different relative effectiveness. The knowledge of specific physiological activation patterns to CPT and TSST would allow for a more targeted application of the tests in future research. Seventeen healthy males underwent CPT and TSST in pseudo-randomized order on consecutive days. Test-specific responses were compared using high-resolution thermal infrared imaging (IRI). IRI quantifies cutaneous temperature variations, giving distinct indices of sympathetic activity (Shastri et al., 2009, IEEE Trans Biomed Eng, 56, 477–484). The advantage of this new method is its complete non-invasiveness. To validate the thermal out-
The results suggest that nose temperature during the TSST decreases gradually from baseline over anticipation to stress (indicating a gradual increase in stress). During the CPT, an increase in nose temperature from baseline to anticipation was followed by a decrease from anticipation to pain (Fig. 3.4.5A, B). Thermal responses were altogether stronger for the TSST. Cardiovascular stress indices were highly correlated with the IRI output. Our findings support the use of thermal IRI to successfully differentiate between pain and psychosocial stress in humans.

**Thermal imaging in chimpanzees: A case study assessing physiological markers of frustration**

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In humans, shame and embarrassment appear to occur as a function of social evaluation processes based on the violation of moral or social norms, respectively (Buss, 1980, *Self-Consciousness and Social Anxiety*). However, whether these emotions are internalized at all by one of our closest living relatives, the chimpanzee, is still unknown. Because it is very difficult to assess shame in humans and in chimpanzees solely through behavioural...
observation, we have begun to use a new technology, thermal infrared imaging (TII), which allows detection of emotional arousal in a non-invasive manner (Fontanella et al., 2010, Metrika, 1–23).

To test for the validity of this method in great apes, we used an experimental task known to induce distress/frustration in chimpanzees (i.e. a variation of the "unwilling" vs "unable" task; Call et al., 2004, Dev Sci, 7, 488–498). The chimpanzee was first enticed (without food) to approach the mesh that divided them and the experimenter (baseline period). Next, the experimenter offered a grape to the subject and every time it tried to reach for it, the experimenter refused to give it (frustration period). The refusal of the grape lasted for approximately 1 minute. After that, the food was handed to the chimpanzee (reward period). An infrared camera recorded the subjects’ face area during the entire manipulation (Fig. 3.4.6). Data from three facial regions were considered for analysis: (1) glabella region, the circular area over the nose and between the eyebrows, (2) nasal region, the area between the tip of the nose and a point positioned slightly lower than the glabella, and (3) perioral region, the area between the nose tip and the superior lip. Changes in temperature were analysed separately for each of the three regions across all three periods. Results showed that during the distress period, the facial skin temperature in the nasal and perioral regions decreased 0.8 ± 0.2 °C and 0.6 ± 0.2 °C (mean ± SE), respectively, compared to the baseline period. However, in the glabella an increase of 0.5 ± 0.2 °C (mean ± SE) was observed instead. During the reward period, a significant increase of 0.5 ± 0.2 °C (mean ± SE) in temperature was observed in the nasal region as compared to baseline. No significant change in temperature was shown in the other two regions as compared to the baseline period. Taken together, these findings support the use of TII to successfully measure emotional states in chimpanzees.

Figure 3.4.6  Thermogram (i.e. infrared image) of a chimpanzee during the teasing task. The colour bar on the right side of the figure indicates the correspondence between colour and temperature.
Congresses, Workshops, and Symposia


Publications

Note: This list also includes publications of members of the research team of the Department of Social Neuroscience that were published prior to their arrival. These articles are included as they are highly relevant to our research topics and speak to the unique qualifications of the team members.

**Book chapters**


**Published Papers**


Professor Dr Robert Turner
Director
Physics in Neuroscience

In the five years of its existence, the Department of Neurophysics in the Max Planck Institute for Human Cognitive and Brain Sciences has established itself as a major world centre in the rapid advance of imaging techniques for cognitive neuroscience. In the last two years, we have published 43 research papers and approximately 60 conference abstracts, most of which describe new neuroscientific findings using data originating from our 7T MRI scanner.

In summarizing the main cumulative achievements of this Department, it is now fair to claim that:

a) We can measure structure, function, and connectivity in the same living human brain at a microscopy scale well below 1 mm. It is thus feasible, for the first time in human imaging neuroscience, to reliably associate brain function with its cytoarchitectural substrate in individual brains, and to correlate this with accurately defined axonal connections as they penetrate into the cerebral cortex.

b) Our application of network analyses, related to the Google search algorithm, has substantially advanced the understanding of functional connectivity in the human brain, and we have been able to define criteria for appropriateness of network analysis methods that represent a powerful critique of a currently popular strategy.
c) In regard to MRI hardware, we have refined our techniques for modelling radiofrequency fields to the point that RF coil experts around the world regularly send us designs for simulation, testing and validation. Dr Kozlov, our RF field modeller, has been invited onto a European committee of leading experts drafting international guidelines for RF safety standards. Furthermore, we have invented a novel and simple method for attaining the valuable goal of uniform RF transmit magnetic field strength across the brain.

d) We have demonstrated the feasibility of parcellating the human cerebral cortex, in cadaver brain samples and in vivo, into distinct myeloarchitecturally defined regions, corresponding to Brodmann areas.

The work of this Department falls into four closely interconnected areas: MRI Techniques at 7T, led by Dr Robert Trampel (4.1); Neuroanatomy, led by Dr Stefan Geyer (4.2); Image Analysis, led by Dr Gabriele Lohmann (4.3) and High Field RF Technology, led by Dr Mikhail Kozlov (4.4). These subgroups work together in order to jointly optimize 7T scanner performance, image contrast and spatial resolution, image analysis, and neuroanatomical interpretation.
Director: Professor Dr Robert Turner

Research Group Leader
PD Dr Stefan Geyer

Senior Researchers and PostDocs
Dr Pierre-Louis Bazin (8)
Dr Juan Dominguez-Duque (*)
Dr Robin Heidemann
Dr Mikhail Kozlov
PD Dr Gabriele Lohmann
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Dr Eugenia Solano (*) (PhD since 08/2011)
Benjamin Stahl (19)
Johannes Stelzer
Markus N. Streicher
Barbara Strotmann (19) (*)
Carsten Stüber
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Secretarial and Technical Staff
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(8) European Union 7th Framework Programme
(19) IMPRS NeuroCom, Leipzig, Germany
(*) Left the Institute during 2010/2011
(**) Left the Department during 2010/2011
4.1 MRI Techniques at 7T
At 7T we can now rapidly localize brain function, for a wide range of tasks, to an isotropic resolution of 0.65 mm, using appropriate developments of EPI. With a wide range of high-resolution anatomical techniques, we can identify the structural substrate of functionally specific brain activity on a scale of less than half a millimetre. Most of the studies described below use the Siemens 7T MRI scanner, either with a single-channel transmit, 24-channel receive RF coil (NOVA), or a less sensitive but easier access 8-channel transmit/receive RF coil (RAPID). In understanding brain function, the connectivity of the brain is at least as important as its segregation into functionally and anatomically distinct areas. Besides state-of-the-art white matter tractography with unprecedentedly high resolution, we also explore diffusion in grey matter. Using DW-MRI at 7T, we characterize nerve fibre directions in the brain with sub-millimetre precision. Diffusion in brain tissue is more complicated than in pure liquids, having at least two components. In a collaborative project with the University of Leipzig, we are gaining deeper understanding of the physical basis of this phenomenon. We use the powerful magnetic field gradients (up to 35T/m) available on the University’s NMR spectrometers, together with MRI techniques and novel analysis methods. Space precludes summaries of our successful studies concerning the biophysics of water mobility in white matter, modelling of orientation-associated contrast in white matter, in vivo MR thermometry with a temperature resolution of 0.1 degrees, localization and segmentation of the human habenula in vivo, and susceptibility mapping in a Parkinson’s Disease patient group.
Parcellation of human amygdala in vivo using ultra high-field structural MRI

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Histological studies show that the human amygdala is subdivided into several nuclei with specific connections to other brain areas. Combining high resolution, high contrast 7T structural images with two different MRI contrasts, and using cutting-edge image analysis, we show robust clustering of three such subregions. A comparison of different probabilistic parcellations of the amygdala is shown in Figure 4.1.1. In the first row, histologically derived maps are depicted. In the middle row, maps based on in vivo 3T DTI are displayed. The bottom row shows the in vivo 7T structural maps derived in this study. All probabilistic maps are in MNI space. The laterobasal and superficial nuclei show similar spatial locations in all probabilistic maps. The centromedial nucleus from the present study extends more laterally and anteriorly than the histological parcellation suggests.

4.1.2 k-space and q-space: Combining ultra-high spatial and angular resolution in diffusion imaging using ZOOPPA at 7T

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Single-shot EPI is the method of choice for diffusion-weighted imaging (DWI), but at high magnetic field, it can suffer from geometric distortions, and its spatial resolution is limited by a short $T_2^*$. Our new powerful gradient coils and an MRI sequence that combines zoomed and parallel imaging, ZOOPPA DW-EPI, enable DWI data to be acquired in vivo with an unprecedented isotropic resolution of 1 mm and 800 μm, using 60 diffusion direc-
tions with a b-value of 1000 s/mm². For each voxel, multiple fibre orientations were modelled using constrained spherical deconvolution, followed by fibre tracking using MRtrix. The high resolution allows the fibre trajectory to be followed into the cortex (see 6.1.4 in Cortical Networks and Cognitive Functions), where it shows the expected radial anisotropy. Figure 4.1.2.1 shows the radial cortical anisotropy in the trans-occipital sulcus in two different participants with two different methods at the same nominal resolution of 1 mm isotropic. (A) Anatomical reference showing the coronal slice (Talairach y = –73) with the depicted region. (B) Myeloarchitecture of human cortex (Weigert stain, from Braithen 1962) showing radial anisotropy. (C) Diffusion directions computed by a multiple compartment model (ball and two sticks). (D) Fiber orientation density functions computed by spherical deconvolution. In all examples, a clear radial asymmetry in the cortex is observed. Figure 4.1.2.2 shows fibre reconstructions in a coronal section at 800 µm isotropic resolution. The ultra-high spatial resolution allows the reconstruction of a massive bundle connecting the amygdala with the hypothalamus (HYPO). Crossing of the transcallosal fibre tract with the cortico-spinal tract (CST) and crossings within the amygdala (AMYG) can be resolved.

High resolution functional mapping of primary motor cortex and primary somatosensory cortex in humans at 7T


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The primary motor cortex (M1) and somatosensory cortex (S1) have been studied using functional magnetic resonance imaging (fMRI) for nearly two decades. High resolution MRI at 7T allows a more precise look at these areas. Functional BOLD fMRI images were acquired with 0.75 mm isotropic voxels. The paradigm comprised imagined finger movement, “classical” finger tapping, and movement of the fingers without touching the finger tips. We predicted that laminar profiles of activity within M1 would depend on the task, even though input and output projections anatomically share several layers within M1. Imagined movement presumably involves no motor output. The primary motor cortex was automatically parcellated using the MIPAV software package into a layer adjacent to the white matter (deep layer), two layers in the middle of the cortex (middle layers 1 and 2), and a layer adjacent to the pial surface (superficial layer). The signal time courses of voxels in each of four separate layers within the M1 cortex were averaged across subjects. In each of the ten human subjects, imagined finger movement activated the hand knob area of M1. As an example, the activation maps of six representative subjects are shown in Figure 4.1.3.1.
M1 cortex was activated when finger tapping with and without touch was performed. As expected, with touch S1 was more extensively activated. Additionally, the activation profile across the cortex was task dependent. During finger tapping, middle layer 1 showed relatively stronger activation than during motor imagery, after normalization (Fig. 4.1.3.2, scaled to deep layer activation). Middle layer 1 corresponds roughly to cortical layer V, which provides the main output to the cortico-spinal tract. It is likely that pyramidal cells in this layer are more active during actual motor performance than during pure motor imagery. Our study demonstrates the feasibility of functional mapping of the M1/S1 complex with isotropic voxels of 0.75 mm, enabling the non-invasive detection of intra-cortical activity profiles in humans in vivo, and potentially the assignment of neural causality.

**4.1.4 Slab-selective, BOLD-corrected VASO (SS-VASO) in human brain at 7T**

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Functional changes in cerebral blood volume (CBV) may localize changes in neural activity better than other MRI-accessible physiological variables. Vascular space occupancy (VASO) measures CBV changes non-invasively, through extravascular tissue signal change. The contrast relies on the difference in $T_1$ between tissue and blood. Because the $T_1$ relaxation times of blood and grey matter converge at high magnetic field strengths, the contrast-
to-noise-ratio (CNR) for VASO becomes disappointingly small. However, VASO CNR at the blood nulling time can be dramatically improved by applying a slab-selective gradient during inversion, such that proton spins in stationary tissue are in steadystate, while flowing blood is inverted only once. Ten subjects were scanned with this new slab-selective, BOLD-corrected pulse sequence during visual stimulation with a resolution of 1.5 mm isotropic. Slab-selective VASO provides a much larger grey matter signal than traditional VASO (Fig. 4.1.4.1). This signal increase results from the longer nulling time (TI) for once-inverted blood, compared with steady-state blood. Figure 4.1.4.2 shows the ΔCBV maps for all ten subjects. In cortical surface voxels, the BOLD signal change is larger than the mean. By contrast, in the SS-VASO signal from surface voxels, signal change is significantly smaller than the mean, suggesting that SS-VASO provides better layer-dependent localization of neural activity.

Mapping of $\text{CMRO}_2$ changes in visual cortex during a visual motion paradigm at 7T

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Regional changes in the cerebral metabolic rate of oxygen ($\text{CMRO}_2$), which are associated with neural activation, can be estimated using MRI, from both cerebral blood flow (CBF) and blood oxygenation level dependent (BOLD) responses when the “resting-state” BOLD signal has been calibrated using an iso-metabolic change in the local deoxyhemoglobin (dHb) concentration. To establish the feasibility of calibrated BOLD at 7T, which should provide greatly improved SNR compared with lower field strengths, we used a visual motion paradigm, with calibration using carbogen breathing. A PASL sequence with GRE EPI readout was used for simultaneous CBF and BOLD measurements in six healthy volunteers. During scanning, subjects had to attend to block-design visual tasks: flickering checkerboards and moving star fields. CBF and BOLD time courses were calculated from the PASL time series using sequential image subtraction and addition, respectively, and were used for computing, voxel-wise, the stimulus-induced signal changes. $T_1$ maps of the imaged region for anatomical reference were obtained using inversion recovery GRE EPI scans. The visual motion area V5/MT showed a smaller $\text{CMRO}_2$ increase than V1 ($p < 0.001$) in the moving vs blank condition. By comparison, V1 showed the same mean $\text{CMRO}_2$ increase between the blank screen and moving or static star field conditions (Fig. 4.1.5).
Embedded tracking system for prospective motion correction in MR imaging

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In high-resolution MR brain imaging, even sub-millimetre motions compromise image quality. Prospective motion correction, using existing optical tracking systems outside the bore, exhibit sub-optimal positioning and long latencies. We have designed an embedded optical tracking system, with excellent performance, for high-resolution MRI of the human brain at 7T (Fig. 4.1.6.1). The system consists of three tracking cameras with integrated micro-controllers that accelerate tracking speed. Each camera tracks the position of one of three rigidly mounted optical markers, with a spatial accuracy below 20 µm, and latency between motion and its correction.
of about 20 ms. The tracking system is positioned on the patient table of our 7T MR system, and plastic spectacle frames are used to attach the markers to the volunteer. The tracking data are sent to the MR scanner via a network connection, and the slice position is updated according to the motion. For the acquisition of the Turbo Spin-Echo images displayed in Figure 4.1.6.2, the volunteer attempted to lie still during the scan of both the uncorrected (top) and the corrected (bottom) data set. The corrected data set allows much more reliable identification of small structures such as the Stria of Gennari (arrows), paving the way to in vivo imaging with a level of detail comparable to post-mortem studies.
4.2 Neuroanatomy
Current human functional imaging studies, at best, correlate activations only with the brain’s macroanatomy, associating them with an individual subject’s gyral and sulcal anatomy. Invasive electrophysiological studies in nonhuman primates show dramatic functional changes across cytoarchitectonic borders that are topographically variable across brains, making questionable structural-functional correlations based solely on macroanatomy. Worse still, currently widespread methods that use spatial normalization to a standard template brain and extensive spatial smoothing to align homologous functional areas have resulted in regrettably imprecise spatial localization, and sacrifice experimental power that might be gained using anatomically appropriate regions of interest, based on native maps of individual brains. However, in recent years, in vivo MRI scanning of the human brain has been dramatically improved by increasing the magnetic field to 7T and by using much more sensitive RF receiver coil arrays. Relatively routine acquisitions of whole-brain images can be performed in 10 minutes, with a spatial resolution of better than 500 μm, easily showing significant features of intracortical microstructure, primarily based on myeloarchitecture. We have therefore defined a pragmatic approach to an individual-specific microstructural map of the in vivo human brain. In this we (i) define a cortical area based on myelo- and cytoarchitecture in histological sections from post-mortem brains, (ii) extract the “MR fingerprint” of this area ex vivo, and (iii) transfer this “fingerprint” to living brains and define this area in vivo. This strategy, which we describe as “in vivo Brodmann mapping,” has enormous potential to make direct correlations between microstructure and function in living human brains.
High-field magnetic resonance mapping of the border between primary motor (area 4) and somatosensory (area 3a) cortex in ex vivo and in vivo human brains

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Using the “triple jump” approach, which allows: (i) definition of a cortical area based on myelo- and cytoarchitecture in histological sections from post-mortem brains; (ii) extraction of the “MR fingerprint” of the same area ex vivo; and (iii) transfer of this “fingerprint” to living brains and definition the same area in vivo, we mapped the functionally important and histologically well-characterized border between primary motor and somatosensory cortex; firstly ex vivo, validated with cyto- and myeloarchitecture, and then in vivo.

For ex vivo analysis, we cut out tissue blocks including the pre- and postcentral gyrus of post-mortem normal human brains, fixed the blocks in 4% formalin, and scanned them with a 7T Siemens whole-body MR scanner with a MP2RAGE sequence (voxel size 330 µm isotropic). For histological validation, we sectioned the blocks at 30 µm with a freezing microtome, stained the sections of cell bodies or myelin, analyzed the cyto- and myeloarchitectonic pattern, and correlated the histology-based laminar contrast with the MRI-based contrast in the same block. For in vivo mapping, we scanned young healthy volunteers at 7T with the same MP2RAGE sequence (voxel size 600 µm isotropic). We correlated the in vivo MRI contrast in the central sulcus region with the ex vivo contrast in the same region of the tissue blocks (Fig. 4.2.1).

This is the first step towards an individual-specific microanatomical brain map, with great potential to make direct correlations between microstructure and function in living human brains.

Figure 4.2.1  (A) Ex vivo quantitative T₁ map of the central sulcus region. The arrow indicates a sharp change in T₁ contrast at the base of the precentral gyrus. (B) Section from a corresponding position of the same block, immunostained for myelin basic protein. The drop in T₁ values coincides with an increase in myelin basic protein. (C) In vivo quantitative T₁ map of the central sulcus region. Arrows mark a drop in T₁ values at the base of the precentral gyrus (cf. insets). The border matches the corresponding border in the post-mortem tissue block between area 3a and area 4. CS = central sulcus, PoG = postcentral gyrus, PrG = precentral gyrus.
Iron and myelin: Cortical distribution and MRI tissue contrast

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MRI at ultra-high field strength can detect microscopically small features in the human brain, such as cortical structure. MR contrast depends on the “magnetic architecture” of the underlying tissue, which includes contributions from myelin and iron. Thus, it is important to know the “anatomical architecture” of the sample. However, the relative importance of iron and its independent role in MR tissue contrast remains poorly understood, due to the unreliability of the histological Perls iron stain. To improve our quantitative understanding, we used proton-induced X-ray emission (PIXE) to measure the iron distribution directly within brain tissue. The Lipsion microscope, based at the Faculty of Physics and Earth Sciences at the University of Leipzig, provides a tightly focussed proton beam that scans a thin section sample. Each element in the sample emits a characteristic X-ray spectrum, allowing determination of elemental content and its distribution.

We studied tissue blocks from human primary visual cortex, containing the myelin-rich Stria of Gennari, and the pre-and post-central gyri, containing primary motor (M1) and somatosensory (S1) cortex. In both blocks, iron showed a higher concentration within grey matter and a lower concentration in white matter. Furthermore, confirming previous findings, we observed that intracortical iron content is highly correlated with cortical myelin (Fig. 4.2.2A, B). The tissue blocks were scanned using two different MRI sequences, MP2RAGE and 3D-FLASH, before they were sliced, stained, and analyzed using PIXE. Thus, we obtained $T_1$ maps and $T_2^*$-weighted images, respectively (Fig. 4.2.2C, D). Using deferoxamine, we extracted iron from one scanned block of the visual cortex, and scanned it again to investigate the independent role of iron in MR tissue contrast (Fig. 4.2.2E–H). Iron obviously affects MRI contrast of the $T_2^*$-weighted images, but it also affects $T_1$ maps, as shown in the MR images of the iron-depleted tissue.

Figure 4.2.2 (A, B) Myeloarchitecture (myelin basic protein immunohistochemistry, A) and iron distribution (PIXE technique, B) in the primary visual cortex. (C–H) Primary visual cortex scanned with an MP2RAGE (C and E) and a FLASH3D (D and F) sequence before (C and D) and after (E and F) iron extraction with deferoxamine. The Stria of Gennari is no longer visible after extraction of iron. Myeloarchitecture (myelin basic protein immunohistochemistry, G) and iron distribution (PIXE technique, H) post-extraction: Myelin is essentially unchanged, whereas iron has been completely removed. GM = grey matter, SoG = Stria of Gennari, WM = white matter.
Mapping Brain Structures Using MRI Techniques

4.2.3 Visualization of the 3D fibre architecture within the human Stria of Gennari with high-resolution diffusion-weighted imaging

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The Stria of Gennari (SoG) is a layer of myelinated axons defining primary visual cortex (V1). It can be seen with the naked eye in cadaver brain sections and has been studied extensively with histological techniques. However, 3D structures are difficult to observe in 2D histological sections. With high-field MRI, the SoG is relatively easy to observe in vivo, because its proton density, $T_1$, $T_2^*$, and phase values differ from neighbouring tissue. While isotropic MRI enables 3D visualization of the SoG, its orientational structure in 3D space is not yet well understood. Diffusion-weighted imaging (DWI) below 7T has insufficient sensitivity and spatial resolution to detect intracortical anisotropy reliably. In this cadaver brain study, we have shown fibre architecture in 3D within the SoG for the first time, using a 9.4T MRI system (Bruker Avance) with a microimaging insert with 1.5 T/m gradient strength. We used a high-angular, high-spatial resolution DWI scan to explore the preferred diffusion directions within adjacent cortical layers. From the DW data, we calculated the fibre orientation distribution functions (fODFs) for each voxel. Based on the fODFs, we differentiated four distinct layers in V1, based on different diffusion properties (Fig. 4.2.3A). As expected, diffusion is much more tangential at the cortical surface and in the region containing the SoG. After streamline fibre-tracking was performed on the fODF data, it can be seen that in layer c (Fig. 4.2.3C) many more fibre tracts run tangentially along the cortex than in layers b and d (Fig. 4.2.3B & D), which are more radial. Correlating layers a through d with cortical microanatomy when the block is processed for histology shows that layer c indeed contains the SoG, as defined by classical cyto- and myeloarchitecture. This approach complements the $T_1$ map-based approach towards “in vivo Brodmann mapping” of the human cortex.

Figure 4.2.3  9.4T MRI scan of the V1 cadaver brain sample with each voxel’s fODFs superimposed.

4.2.4 MRI-based multimodal in vivo mapping of hypothalamic substructures

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The hypothalamus, part of the limbic system, is affected in neuropsychiatric diseases, and disease-related changes in its structure and/or volume have been suspected. Unfortunately, to date, parcellating the hypothalamus into subnuclei has been feasible only in histological preparations of post-mortem brains, based on microscopic differences in structure or neurochemistry. Recently, however, high-field diffusion-weighted magnetic resonance imaging (DW-MRI) has enabled parcellation of deep brain nuclei into substructures in vivo, as demonstrated for the thalamus and amygdala. Accordingly, we hypothesized that individual hypothalamic subnuclei could be detected with DW-MRI.
We scanned ten healthy young subjects with a Siemens 3T TIM-Trio MR scanner, acquired diffusion- and $T_1$-weighted scans, and interactively traced one hypothalamus region of interest (ROI) in each subject’s left and right hemisphere, based on pre-defined anatomical landmarks. In order to assess intra-observer reliability, the same investigator traced each ROI twice, in separate sessions, under identical conditions. We computed the similarity of fibre orientations in each ROI, clustered the matrix in three regions with a k-means algorithm, rendered the clusters in 3D, and compared their topography with data from the literature in order to assess each cluster’s neuroanatomical validity.

Significant test-retest reliability and voxel overlap confirmed the reliability of the ROI definition. In each hypothalamus, we found reproducible clusters with consistent orientations across subjects: anterior (blue), posteromedial (green), and lateral (red) subdivisions (Fig. 4.2.4A–C). These provide a plausible comparison with the known anterior, medial, and lateral nuclear cell groups of the hypothalamus. This is the first noninvasive study of the human hypothalamus to show its fine-grained microstructural organization, which may greatly assist our understanding of affective disorders when applied to the pathophysiology of patients.

Figure 4.2.4. (A) Left rostro-dorsal view of the hypothalamic target region (enlarged in B and C). (B, C) 3D rendering of the parcellation into an anterior (blue), posteromedial (green), and lateral (red) subdivision in two individual subjects (both hemispheres are depicted).
4.3 Image Analysis
Analysis and Interpretation of Structural MRI Data

Image analysis is fundamental to extracting information about brain structure from MRI data. To obtain a better understanding of its fine structure, the cortex must be segmented from other brain tissues, such as white matter, non-cortical grey matter, dura, vasculature and cerebral spinal fluid (CSF). Because MRI contrast in brain images is largely determined by myelin content, which varies considerably within grey matter, segmentation is a nontrivial problem. Commonly used methods such as those implemented in the analysis packages SPM and FSL have problems in some regions, notably in primary motor cortex, where proximal pyramidal cell axons are normally heavily myelinated. We address this problem by comparing cyto- and myelin-stained sections of cadaver brain with MRI data. Once the cortex is segmented and represented in a surface-based model, a primary goal is to subdivide it into discrete areas based on very high-resolution 7T MRI data.

Analysis and Interpretation of Functional MRI Data

A dominant methodology in functional magnetic resonance imaging (fMRI) is the univariate detection of activation areas in the human brain. However, while such maps show us which brain voxels are differentially involved in a cognitive task, they do not reveal interdependencies between these voxels. We are developing new methods for this purpose. Since current methods typically explain only about 10% of the overall signal variance, there is a very good chance that the information we seek is buried somewhere in the remaining 90%.

Another research aim is to further our understanding of human sulcal patterning. The folding pattern of the cerebral cortex and its relation to functional areas is notoriously variable. The mapping of structure to function would be greatly assisted if we could identify 3D topographical cortical features that bear a consistent relationship to functional areas. Based on our previous work, we hypothesize that the deepest parts of the sulcal fundi might be the most likely to satisfy these requirements. One of our research aims is to investigate this hypothesis.

A prerequisite for all of the above research is a high-precision geometric alignment between data sets of different types.
Towards an observer-independent myeloarchitectonic parcellation of the living human brain

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Our goal is to identify cortical areas in a fully automated fashion in individual living brains, thus enabling direct correlations between structure and function. In pursuing this goal, we have developed methods and tools enabling exploratory investigation and parcellation of high-resolution 7T MRI data.

Most architectonic maps of the cerebral cortex are based on cytoarchitecture. MR images of the cortex, however, appear mainly to reflect myeloarchitecture. Although the precise concordance between maps based on cytoarchitecture and myeloarchitecture remains to be investigated, striking similarities suggest that both modalities actually reflect one microstructural map of the cortex.

The potential of MRI to reveal myeloarchitectonic areas in vivo has recently been shown in marmosets. To accomplish similar results in humans, and gain insight into MR contrast variation across the cortex, we applied level-set-based analysis tools to construct cortical surfaces and profiles orthogonal to the cortical layers, using 7T MP2RAGE data acquired in young healthy human subjects. Quantitative $T_1$ values provided by this sequence, reflecting intra-cortical myelin density, were averaged along the middle 50% of each individual profile, and mapped onto an intermediate cortical surface.

In individual living brains, we found that major primary functional areas (primary motor (M1), somatosensory (S1), auditory (A1), and visual (V1) cortex) were all characterized by a decreased $T_1$ (Fig. 4.3.1A), with a striking similarity to the classical maps of Hopf that were based on myeloarchitectonic studies in post-mortem brains (Fig. 4.3.1B). This helps to confirm that quantitative $T_1$ maps give a good indication of myelin density and demonstrates the wide potential of an MR-based myeloarchitectonic parcellation of the human cortex in vivo.

Eigenvector centrality mapping (ECM)

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Functional magnetic resonance data acquired in a task-absent condition ("resting-state") require new data analysis techniques that do not depend on an activation model. Standard methods use either correlations with pre-specified seed regions or independent component analysis, both of which require assumptions about the source (seed-based) or validity (independent component analysis, ICA) of a network. In this work, we have introduced an alternative assumption and parameter-free method, based on a particular form of node centrality...
called “eigenvector centrality”. Eigenvector centrality attributes a value to each voxel in the brain, such that a voxel receives a large value if it is strongly correlated with many other nodes that are themselves central within the network. Google’s PageRank algorithm is a variant of eigenvector centrality. Eigenvector centrality is computationally much more efficient than other centrality measures, and does not require thresholding of similarity values, so that it can be applied to thousands of voxels in a region of interest covering the entire cerebrum.

In a recent study, we analyzed rs-fMRI data of 22 normal volunteers in a hungry versus a sated state, and found a change in centrality in ventral striatum (Fig. 4.3.2). ECM can be used on a variety of different similarity metrics including spectral coherence, and has now become a widely used tool in our institute, instrumental in numerous studies. Examples are: motor training, visuo-spatial sequence processing, a pharmacological study, and CMR02 mapping. Several other studies are underway.

Connectivity concordance mapping (CCM)

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A new analysis method called “Connectivity concordance mapping” (CCM) for fMRI data is proposed. A weight is assigned to each voxel, based on the inter-subject reproducibility of its whole-brain pattern of connectivity. Voxels whose correlation pattern is consistent across subjects receive high values. The result of a CCM analysis is thus a voxel-wise map of concordance values, in which regions of high inter-subject concordance may be of interest for further analysis. We test the CCM algorithm on a “resting-state” fMRI experiment with “eyes open” versus “eyes closed” conditions. In this study, 3T fMRI data were acquired from seven normal volunteers. Four blocks of 7.6 minutes each were acquired in a resting-state condition. In two of the four blocks, subjects were asked to keep their eyes open, in the other two conditions, eyes were closed. The order of the four blocks was randomized across subjects. After standard preprocessing, we applied the CCM algorithm using Kendall’s W as a measure of concordance. The results are shown in Figure 4.3.3. Further studies using CCM are currently underway. Of particular interest are clinical applications such as recovery after stroke.

Figure 4.3.2. Changes in eigenvector centrality associated with satiety.

CCM eyes open

CCM eyes closed

Figure 4.3.3 Connectivity concordance maps in two resting-state conditions (eyes open versus eyes closed). Higher values indicate higher inter-subject concordance. Note that motor areas show higher concordance values during the eyes closed condition.
4.3.4 Seed-based correlation analysis based on fMRI low-frequency fluctuations

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Low-frequency fluctuations (LFFs) are a major source of variation in resting- and task-driven fMRI data. Here, we investigate LFFs in a task-dependent setting, with task blocks long enough to allow frequency analysis. After fitting a general linear model to the data, our method analyzes the band-passed residuals which are specific to the overall task domain without being time-locked to stimulus onsets. A seed voxel or seed region is selected and correlation maps are computed. Statistical tests contrasting correlation maps between different experimental conditions present in different runs, may reveal cognitive networks that are specific to overall task domains. This strategy differs from "resting-state" fMRI in that we allow overt experimental stimulation. We found a network apparently specific to the language domain, which may be called a "default language network." Two further studies employed this method to investigate LFFs in newborns and in children between 6 and 7 years of age.

4.3.5 Image restoration in ultra-high resolution imaging

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Good spatial resolution is essential to identify small structures in magnetic resonance images, but costs signal-to-noise ratio (SNR), which can only be restored by averaging multiple acquisitions. This may require intolerably long scan times. We have developed a new highly effective two-stage image restoration algorithm that can be applied to the raw data prior to averaging. The stages consist of a Wiener wavelet filter followed by an anisotropic diffusion filter. The method, which does not impair spatial resolution, has become a standard preprocessing routine in our Institute. A particularly nice application is found in noise cleaning of high-resolution diffusion weighted imaging at 7T (Fig. 4.3.5). The data were acquired with a 24 element phased array head coil, isotropic resolution 1.0 mm³, DWI with b = 1000 s/mm², 60 directions. Six repeated acquisitions were taken, and a 2-average and a 6-average image computed from these. The total acquisition time was 69 minutes. We compared the results of our new algorithm with averaged multiple measurements of the same subject. It was found that the effect of the image restoration procedure roughly corresponds to averaging across three repeated measurements.

Figure 4.3.5 Effect of noise cleaning. The left image shows a 2-average without noise cleaning, the central image shows a 2-average after noise cleaning was applied to the two single images that were used for averaging, and the right image shows a 6-average without noise cleaning. Note that the noise-cleaned 2-average is comparable in image quality with the uncleaned 6-average.
Software package “Lipsia” for fMRI/MRI data analysis

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Eigenvector centrality mapping (ECM), connectivity concordance mapping (CCM), noise cleaning, and seed-based low-frequency correlation mapping are part of a larger software package called “Lipsia”. Lipsia is an in-house software package for MRI/fMRI data analysis developed since 1999, and made publicly available since 2007. The original reference has now been cited 213 times (source www.scopus.com, Nov 2011). Lipsia has a strong focus on exploratory algorithms for the analysis of “resting-state” fMRI data, a very fast fMRI preprocessing pipeline and an advanced image viewer. It also contains efficient software for standard GLM analysis. One of the hallmarks of Lipsia is its computational speed, now vitally important due to the dramatic increase in the amount of data acquired. Furthermore, new analysis techniques such as ECM and CCM operate on very large connectivity matrices and therefore require highly efficient “number crunching” procedures.

Critical comments on dynamic causal modelling

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Dynamic causal modelling (DCM) is a technique designed to investigate the influence between brain areas using time-series data obtained by EEG/MEG or functional magnetic resonance imaging (fMRI). The basic idea is to fit various models to time-series data, and to select one of those models using Bayesian model comparison. We have recently published a critical evaluation of DCM, challenging this method on several grounds, including the combinatorial explosion, the validity of the model selection procedure, and problems with respect to model validation. A key point in our argumentation is based on 8000 randomly generated models, which showed that many implausible models received higher ratings than plausible ones. This result casts doubt on the validity of the model selection procedure. Also, we argue that an independent model validation is needed but is currently lacking.

Contrary to the view put forth recently by Stephan and co-authors (2010, NeuroImage, 49, 3099–3109), we argue that Bayes factors are not sufficient because the assumptions underlying the computation of Bayes factors are the same as those used in the selection procedure itself. Therefore, they cannot be used for validation purposes. Finally, we present an example where DCM showed an extremely poor model fit, but was ranked top by DCM. Even though model fit alone is not sufficient for assessing the adequacy of a model, we strongly favour the view that models should explain the data, at least to some degree. An almost complete absence of model fit is an indication of model failure, and should trigger further investigation.
Segmentation tools for 7T ultra-high resolution MP2RAGE images of the human brain

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With 7T MR imaging come new challenges for image processing. Ultra-high resolution images test the limits of the software developed for 3T data, and new 7T contrasts have different characteristics requiring an adaptation of the image processing tools. Our laboratory has recently adopted MP2RAGE, which provides ultra-high resolution (400 µm) quantitative images of the human brain with little distortion. This entails an increase in data by a factor of 15, in comparison with the accepted standard of 1 mm isotropic resolution. In order to automatically parcellate in vivo micro-anatomical regions of the cerebral cortex, we developed a series of image processing algorithms to process MP2RAGE data sets at ultra-high resolution with the maximum possible accuracy and speed. We have created fully automated tools for the following tasks: skull stripping, partial volume estimation, and full brain segmentation. These tools build upon successful methods for brain segmentation of 3T data and incorporate new algorithmic developments in topology-preserving, multi-object geometric deformable models. The tools are integrated into a user-friendly processing pipeline based on the MIPAV software platform. The end result is a full anatomical segmentation of the brain into cortical and sub-cortical structures, currently identifying 28 different regions (Fig. 4.3.8). Topology constraints ensure that the extracted regions respect anatomical relationships and provide the mathematical equivalences needed for cortical mapping and shape analysis.

Figure 4.3.8  3D rendering of various deep brain structures, and cortical segmentation using MIPAV tools.
4.4 High Field RF Technology
Research in RF technology for MRI at 7T has two main objectives: to optimize transmit and receive coil performance, and to ensure subject safety. For both purposes, given the electromagnetic field regime at 300 MHz between near-field and far-field, high quality field and circuit simulations are vital for continued progress. We have developed dramatically improved methods for such simulations, based on techniques published earlier by Kozlov based on 3D electromagnetic and RF circuit co-simulation. Furthermore, we have set up an RF coil construction facility and have built efficient RF coils that are already in use for cadaver brain imaging at 7T. In addition, we are building prototype RF coils based on Kozlov designs that show great promise to simplify the problem of generating spatially uniform transmit RF fields.
RF circuit 3D EM co-simulation

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In brief, the co-simulation approach entails substitution of all tune/match/decouple networks by ports during the 3D-EM simulation, and their reconnection during circuit simulation, followed by a simple computation (weighted sum of already calculated quantities) of the final 3D electromagnetic field distribution. Because the decoupling network influences the value of distributed capacitors, for maximal flexibility, all distributed capacitors are also substituted by lumped ports. The values of distributed capacitors are then obtained by RF circuit optimization. For an 8 element coil with 8 capacitors in the radiative loop and two connections for decoupling circuits, there are 80 ports in total.

The values of fixed and adjustable lumped elements required for a multi-channel transmit RF array are obtained by a numerical domain RF circuit tuning, matching and decoupling procedure that is very close that used in real life. The critical objective is the minimization of reflected power by the entire array, which ensures maximal coil efficiency, and also minimal dependence on coil loading. This strategy eliminates the need to calculate combined 3D EM fields for each step during coil performance investigation, a feature that additionally reduces the investigation time.

The magnetic field generated by each coil element is defined by the current distributed within it at 300 MHz. By monitoring these currents and the power reflected by the entire coil, capacitor value adjustments can be made to optimize this current distribution and/or to minimize this power for the given geometry and tune/match/decouple conditions.

Multi-row arrays

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We investigated arrays in a range of configurations, tuned, matched and decoupled using suitably placed inductors.

Exploring the transmit field properties of such arrays without going to the lengths of \( B_1 \) shimming, we swept the phase shift of all elements in the upper row by values in the range from \(-180^\circ\) to \(+180^\circ\), with \(10^\circ\) increments. In doing so, we made the remarkable discovery that for double row arrays, a \(+90^\circ\) phase shift between rows improves \( B_1^+ \) homogeneity for the entire human brain by

![Figure 4.4.2.1](image1)

**Figure 4.4.2.1** \( B_1^+ \) at central coronal plane. (A) Single row, (B) Dual row, (C) Triple row.

![Figure 4.4.2.2](image2)

**Figure 4.4.2.2** SAR in central coronal and transverse planes. (A) and (B) Single row, (C) and (D) Dual row, +90° phase shift.
a factor of (typically) two. For a triple row array, phase shifts of $-45^\circ$ for the bottom row and $+90^\circ$ for the top row gained a further 25 % improvement of $B_{1+}$ homogeneity for the brain VOI (Fig. 4.4.2.1). As expected, static transmit shimming significantly affects the specific absorption rate (SAR), in both peak value and peak location, as shown in Figure 4.4.2.2. Load independence is significantly improved using reflected power minimization, and omitting the dedicated decoupling network relative to fully decoupled and matched arrays.

**Improving UHF transmit efficiency with Mix-Mode baluns**

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Common-mode currents contribute to radiation loss, and thereby reduce the effective power of transmit coils (percentage of total power delivered to the load). As radiation losses increase with the fourth power of the frequency, the losses are more dramatic at 7T. In transmit arrays, the potential losses due to common-mode currents increase due to the increased number of feed ports. Baluns convert the unbalanced signal from a coaxial line to the balanced load of a loop-type coil element, in order to minimize common mode currents. Transmit-power limitations restrict the available MR techniques at ultra-high field (UHF) strengths, and baluns can improve transmit efficiency for UHF. Baluns serve to improve safety for the subjects by placing a virtual ground along the centerline of a loop coil, and also by reducing the highly variable coupling of currents to the environment surrounding the coil. Mixed-mode propagation along coaxial lines is assumed to be negligible in coil design and safety simulations, and therefore must be properly handled by coil engineers. Due to the increased importance of robust baluns for UHF MR, simply touching a cable as a test to determine balun efficiency is no longer sufficient, and thus quantitative methods are necessary. We have adopted Mix-Mode scattering parameter measurements for quantifying and fine-tuning baluns. Baluns can improve transmit power efficiency by 50 %.
Congress, Workshops and Symposia

2010  

2011  

Degrees

PhD Thesis

2011  
- Solano, E. In vivo anatomical segmentation of the human amygdala and parcellation of emotional processing. University of Leipzig, Germany.

Awards

2010  
- Turner, R. Outstanding Alumni Award for Professional Achievement. Simon Fraser University, Canada.

2011  
Appendix

Publications

Book Chapter


Published Papers


Siegert, T., Schulz, J., Turner, R. & Reimer, E. (subm.). Within bore embedded tracking system for motion correction in MRI. MI 1302-4183-BC-ZE.

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(Commenced January 2007)
Audition poses a particular challenge to cognitive neuroscience: First, the “bottom-up” processes of acoustically decoding and neurally encoding the auditory signal along the central auditory pathways are not well understood. Second, humans cope surprisingly well with various sorts of occlusions, deletions, and degradations in their auditory input—in phone lines and at noisy parties, in chronic hearing damage, or, most drastically, when living with a cochlear implant.

As illustrated in Figure 5.1, our group is interested in the following main questions: First, how does the human brain analyse, categorise, and interpret meaningful sounds such as speech, particularly under substantial degradation? Second, how do contextual cues facilitate this process: Semantic context (e.g. in speech; 5.1.1), and also simple temporal or spectral regularities of sound (5.1.3) can shape the neural processing as well as facilitate the integration of information. Third, how can cognitive mechanisms effortfully compensate for degraded sound: Executive functions like working memory and cognitive control clearly support successful coping with degradation; their neural interfacing with auditory processes is unclear, however, and of particular relevance to our work.

These key questions touch on speech and hearing, psychology and neuroscience alike. We pursue them using listening and learning experiments and various methods of brain imaging: First, we ask which brain areas within the auditory cortex, and beyond, contribute critically to the emergence of meaningful auditory and speech percepts, and how do they interact? This is investigated mainly using fMRI. Second, we study the oscillatory brain dynamics (e.g. 5.1.2) using M/EEG to infer brain states that precede and accompany successful speech comprehension. In short, what are good indicators of facilitation and compensation in the time–frequency domain? Third, we aim to isolate individual markers of auditory skills, cognitive ability, and brain structure that can help us predict the extent to which listeners will be able to cope with adverse listening situations.

Answers to these questions will further our knowledge on the listening brain as well as on the human faculty of speech comprehension. They will also eventually be useful in developing new approaches to the treatment of hearing disorders.

Figure 5.1 Scheme illustrating the working perspectives of the “Auditory Cognition” group.
Brain dynamics in degraded speech: Initial neural effort versus late facilitation

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When listening to speech under adverse listening conditions, expectancies resulting from semantic context can strongly influence comprehension. This leads to the question of how minimal variations in semantic context affect the unfolding comprehension of acoustically degraded speech. Two main results were observed in the brain electric response of 28 normal-hearing subjects. First, auditory evoked responses to the onset of a degraded sentence (N100) correlated with participants’ comprehension scores, but were generally more vigorous for more degraded sentences. Second, during highly predictable sentence-final words, a late Gamma-power enhancement (~40–70 Hz) reflecting top-down-facilitated integration was observed. This Gamma-band effect also varied parametrically with signal quality. Notably, these two effects exhibited a negative correlation (Fig. 5.1.1C), suggesting that they reflect two partly distinct neural strategies and potential individual differences when dealing with moderately degraded speech; a more “bottom-up”, resource-allocating and effortful strategy (reflected in a comparably stronger early N100) versus a more “top-down”, associative and facilitatory strategy (reflected in stronger Gamma bursts).

Suppressed alpha oscillations predict intelligibility of speech and its acoustic details

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Modulations of alpha oscillations (8–13 Hz) accompany many cognitive processes in the human brain, but their functional role in auditory perception has proven elusive: Do alpha oscillatory dynamics reflect acoustic details of the speech signal, and are they indicative of comprehension success? Spoken words were degraded spectrally
and temporally and presented in an orthogonal design, and EEG responses in the frequency domain were analysed in 24 participants, who rated word comprehensibility after each trial. First, a broad posterior cluster of alpha power decrease appeared at 600–900 ms post word onset, wherein alpha power decreased monotonically with increasing spectral detail (Fig. 5.1.2A) and with concomitantly higher comprehension rates. Second, source localisation of the relevant time–frequency effects yielded superior parietal, prefrontal, as well as right anterior temporal brain areas driving the speech degradation alpha effects (Fig. 5.1.2B). Third, across conditions and channels, a significant negative relationship of alpha power and subsequent comprehension ratings was found (Fig. 5.1.2C).

Fourth, searchlight multivariate pattern classification of the power spectra across participants showed that patterns of late posterior alpha power best allow significant above-chance classification of word intelligibility (Fig. 5.1.2D).

The results suggest that both magnitude and topography of late alpha suppression in response to single words can indicate a listener’s sensitivity to acoustic features and the ability to comprehend speech under adverse listening conditions. Alpha oscillations do have predictive power in auditory and speech processes, and they are a promising parameter in populations where comparably few trials can be acquired or speech comprehension requires objective validation.

Figure 5.1.2  (A) Alpha power estimates dependent on spectral detail. (B) Beamformer localization of this alpha effect. (C) Across conditions, alpha power correlates negatively with subjective speech comprehension. (D) In machine learning, late posterior alpha power allows above-chance decoding of spectral detail.
The impact of spectral distributions on establishing auditory categories

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We studied the bases of auditory category formation using a paradigm in which listeners learned to categorize stimuli varying along two perceptual dimensions, through trial and error. Specifically, listeners categorized white noise bursts defined by two spectral filter frequencies, F₁ and F₂. Two distribution types were defined by negative versus positive F₁–F₂ correlations (“falling” vs “rising”; Fig. 5.1.3A). Critically, listeners could have adopted two strategy types: an explicit, rule-based (RB) strategy, which requires decisions based on a single stimulus dimension (e.g. F₁), or an implicit, information-integration (II) strategy, which requires the integration of both dimensions (i.e. F₁ and F₂). If human auditory perception is tuned by experience with auditory categories that are defined by a negative F₁–F₂ correlation (e.g. vowel categories), then we predicted better learning and overall performance for falling relative to rising distributions. Moreover, we anticipated that II learning would be more likely for falling distributions.

As predicted, category learning was more successful in the “falling” than in the (otherwise identical) “rising” condition (Fig. 5.1.3B), and model-based analyses confirmed that significantly more “falling” listeners used an II strategy (Fig. 5.1.3C). We conclude that human auditory category learning is overall better and more likely based on an optimal (II) strategy when categories are defined according to a preferred F₁–F₂ correlation. Subsequent studies will examine the impact of adverse listening conditions on RB vs II strategy use.

See also the Obleser et al. projects 2.1.3 in the Department of Neuropsychology and 6.2.3 in the Research and Development Unit “MEG and EEG: Signal Analysis and Modelling.”
Research Groups

Congresses, Workshops, and Symposia

2010

2011

Publications

Published Papers


5.2
Max Planck Research Group “Body and Self”

The Research Group Body and Self focusses on sensorimotor aspects of cognitive neuroscience. In particular, our research addresses questions about the “bodily self” arising from sensory and motor signals that accompany nearly every bodily activity. Our main interpretation of the bodily self is in terms of a sense of agency (the experience of being in control of one’s actions) and a sense of ownership (the sense of oneself as subject of experience). Moreover, we assume that a bodily self-representation is especially driven by interactions with the bodies of other people who surround us as, for example, governed by a mirror mechanism. Methodologically, we use techniques from both experimental psychology (e.g. reaction times, detection thresholds) and neurophysiology (e.g. EEG, fMRI, TMS). During the first two years of the group’s term of operation (2008–2009), our studies tackled questions pertaining to the nature of the bodily self as constituting consciousness of the body as a perceptual object (e.g. Hach & Schütz-Bosbach, 2010; Hach et al., 2011) or as part of the action system. We were able to demonstrate, for example, that self-attribution of actions is accomplished by monitoring motor-related signals (e.g. Weiss et al., in press; Gentsch & Schütz-Bosbach, in press). Thus, low-level, bottom-up mechanisms obviously play a fundamental role in encoding some specific components of bodily self-consciousness. In 2010 and 2011, we continued this line of research including a broader perspective. For example, we studied the extent to which automatic self-registration in action, based on a low-level sensorimotor process, is altered in pathological cases for which an aberrant sense of agency has been described (5.2.3). Another study explored whether this process can be influenced by direct interactions between individuals (5.2.4). Moreover, we investigated the neuro-cognitive relationship between self-attribution and higher-order, top-down cognition, such as reward processing (5.2.5), and finally, we extended our research focus to an embodied simulation account of aesthetic experience (5.2.6 and 5.2.7). In addition to these broader and new research foci, we have continued to pursue and provide evidence of a low-level self-representation beyond the motor system by focusing on the primary somatosensory system (5.2.2) and finally, we have sought to identify and functionally specify the neuroanatomical correlates of one's body in space (5.2.1).
Spatial integration of visual and tactile events

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The ability to recognize, localize, and quickly react to events in the environment is crucial for an organism’s protection and its interaction with the space surrounding it. The traditional view states that the right posterior parietal cortex plays a special role in integrating information about events arising from different sensory modalities and different spatial locations. An alternative account ascribes similar functions to the right temporal lobe. We determined the respective contributions of the right supramarginal gyrus (SMG) and middle superior temporal gyrus (mSTG) to the spatial and crossmodal integration of sensory events by disrupting neural activity in the target sites through theta burst stimulation (Fig. 5.2.1.2A). Behavioural effects were measured using the crossmodal congruency effect paradigm. Visual target stimuli were presented at varying distances to the body and paired with spatially congruent or incongruent tactile cues/distractions (Fig. 5.2.1.1). Consistent with the traditional view, spatially congruent tactile input facilitated responses to visual stimuli in personal and extrapersonal space follow-
Research Groups

ing stimulation of SMG (Fig. 5.2.1.2B). In line with recent suggestions, there was also facilitation of stimuli presented in contralateral personal space following stimulation of mSTG (Fig. 5.2.1.2B). These results confirm the SMG and STG to be sites of multimodal convergence. While the SMG plays a crucial role in the higher-order integration of bilateral information arising from different spatial reference frames, the mSTG supports lower-order integration of sensory events emanating from the contralateral hemibody. These findings are the first to demonstrate multimodal spatial integration in the temporal lobe of neurologically normal participants, and challenge a conceptualization of human spatial functions as arising predominantly from the right parietal cortex.

Social responsivity in the primary somatosensory cortex during observed human touch

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Observing another person being touched activates our own somatosensory system (Keysers et al. 2004, Neuron, 42, 335–346). Whether the primary somatosensory cortex (S1) is also activated during the observation of passive touch, and which subregions of S1 are responsible for self- and other-related observed touch is currently unclear (Schaefer et al. 2009, Hum Brain Map, 30, 2722–2730; Keysers et al. 2010, Nat Rev Neurosci, 11, 417–28). In our study, we first aimed to clarify whether observing passive touch without any action component can robustly increase activity in S1. Secondly, we investigated whether S1 activity only increases when touch of others is observed, thus being a social response, or whether S1 is also recruited when touch of one’s own body is observed. We were particularly interested in which subregions of S1 are responsible for either process. We used functional magnetic resonance imaging at 7T to measure S1 activity changes when participants viewed videos of passively applied touch to their own hand and another individual’s hand seen from either an egocentric or allocentric perspective (Fig. 5.2.2.1A). Our results clearly show that S1 activity does increase in response to observed passive touch, and that activity changes are localized in posterior but not in anterior parts of S1 (Fig. 5.2.2.1B; Fig. 5.2.2.2). Individual subject analyses showed that this effect is stable across participants (Fig. 5.2.2.3). Importantly, activity increases in S1 were particularly related to observing another person being touched (Fig. 5.2.2.2). Self-related observed touch, in contrast, caused no significant activity changes within S1. We therefore conclude that posterior but not anterior S1 is part of a system for sharing tactile experiences with others.

Figure 5.2.2.1 Experimental design and main effect of observed touch. (A) Video stimuli of an example pair. Different types of video sequences were varied in a 2 x 2 x 2 factorial design with the factors Touch (Observed Touch, No-Touch), Hand Identity (Self, Other), and Viewing Perspective (Ego = Egocentric, Allo = Allocentric); (B) Activity changes in S1 for the contrast Observed Touch > No-Touch across experimental conditions superimposed on the MNI reference brain (visualized at p < 0.005 (uncorrected) and masked with left S1).

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Dysfunctional forward model mechanisms and aberrant sense of agency in obsessive-compulsive disorder

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Patients with obsessive-compulsive disorder (OCD) lack the experience of action completion and agency. This subjective experience has been shown to depend on the integrity of predictions of action outcomes generated by forward models of the motor system. Motor predictions are critical for inhibitory gating of actions and their consequences, and abnormal activity in motor control circuits, including basal ganglia and premotor cortex, has been found in OCD. This is the first study explicitly investigating forward model mechanisms in OCD.

To test whether inhibitory gating based on motor predictions is physiologically altered in OCD, we used...
troencephalography to measure N1 suppression during active generation and passive observation of visual feedback in 18 OCD patients and 18 healthy control subjects. Predictability of action feedback was manipulated on the basis of action and external cues, and simultaneous agency judgements were assessed. OCD patients did not show the typical N1 suppression to actively generated feedback as compared to passively observed feedback (Fig. 5.2.3.1). Moreover, in OCD patients, the N1 was not modulated by additional predictive motor cues as observed in control subjects. If explicitly asked to report agency experience, enhanced estimations were found in patients (Fig. 5.2.3.2), which correlated with the strength of feelings of incompleteness. Our findings demonstrate that OCD patients fail to predict and suppress the sensory consequences of their own actions. The constant mismatch between expected and actual outcome caused by this forward model dysfunction may explain the persistent feeling of incompleteness even after properly executed actions and the obsessive searching for control in these patients.

![Figure 5.2.3.2](image)

Figure 5.2.3.2: Mean judgements of agency during active generation of visual effects (left) and mean causality judgements during passive observation of visual effects (right), for OCD patients (dark grey bars) and comparison subjects (light grey bars), separately for conditions of high and low contingency of the visual effect and for conditions of correct and incorrect effect anticipation. Effect anticipation was induced by congruent and incongruent priming of the effect prior to the action.

### 5.2.4 The self in social interactions: Sensory attenuation of auditory action effects is stronger in interactions with others

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The experience of oneself as an agent not only results from interactions with the inanimate environment, but often takes place in a social context. Interactions with other people have been suggested to play a key role in the construal of self-agency. In the present project, we investigated the influence of social interactions on sensory attenuation of action effects as a marker of pre-reflective self-agency. To this end, we compared the attenuation of the perceived loudness intensity of auditory action effects generated either by oneself or another person in an individual, non-interactive or interactive action context (Fig. 5.2.4.1). Participants were required to compare the loudness of a given self- or other-generated standard sound with a subsequent comparison sound of varying magnitude. The data from each condition were fitted with a logistic function in order to calculate the point of subjective equality (PSE) as an indicator of the perceived loudness intensity of the standard sound. Figure 5.2.4.2 shows the PSE values in the four experimental conditions. In line with previous research (Weiss, Herwig, & Schütz-Bosbach, 2011), the perceived loudness of self-generated sounds was attenuated compared to sounds generated by another person. Most importantly, this effect was strongly modulated by social interactions between self and other. Sensory attenuation of self- and other-generated sounds was increased in interactive as compared to the respective individual action contexts. This is the first experimental evidence suggesting that...
pre-reflective self-agency can extend to and is shaped by interactions between individuals. Follow-up studies will investigate whether this interindividual element is specific to human interactions or would also apply to similar interactions with non-human ‘agents’ like robots.

Rewarding outcomes modulate the attribution of actions in the ventral striatum

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When we execute actions to bring about changes in our environment, we usually have the feeling of control over our actions and attribute the accompanying action–effect to ourselves. The objective of the present study was to investigate whether this ‘sense of agency’ (SoA) can be modulated by the outcome value of actions. Findings from social psychology have shown that participants typically attribute positive outcomes to themselves and blame others for failures (‘self-serving bias’, SSB, Heider, 1958, The psychology of interpersonal relations). Here, we specifically aimed to investigate how, in an ambiguous situation, information about the outcome of an action (i.e. either negative or positive values) affects the agency judgement, and how regions previously found during reward processing (especially the ventral striatum, VS) contribute to the SoA.

We used a modified version of an established reward paradigm (Knutson et al., 2001 J Neurosci, 21, 1–5; Fig. 5.2.5.1A). In each trial, subjects could gain or lose money according to their reaction time to a target, in comparison to a second person outside the scanner who also reacted to the target. The potential outcome of each trial was displayed but the subjects did not receive information about their performance compared to the other person (i.e. who actually received the monetary outcome). Participants then rated to which extent they felt the monetary outcome was a consequence of their own action or produced by their interaction partner.
As predicted, we showed that monetary reward modulated the SoA according to the SSB (i.e. higher feelings of self-agency in reward trials and a decreased SoA in the loss condition). Furthermore, when subjects made self-serving attributions, we found higher activation of the VS bilaterally (Fig. 5.2.5B), reflecting the rewarding value of those decisions. These results show that the SoA is influenced by the action outcome through regions representing the intrinsic value of those action attributions.

The impact of physical ability and aesthetic experience on dance perception

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The field of neuroaesthetics attracts attention from neuroscientists and artists interested in the neural underpinnings of a perceiver’s aesthetic experience. Although less studied than the neuroaesthetics of visual art, the neuroaesthetics of dance is a particularly rich subfield to explore, as it is informed not only by research on the neurobiology of aesthetics, but also by an extensive literature on how action experience shapes perception. Moreover, it is ideally suited to explore the embodied simulation account of aesthetic experience, which posits that activation within sensorimotor areas of the brain, known as the action observation network (AON), is a critical element of one’s aesthetic response. In the present study, we investigated how observers’ aesthetic evaluation of dance is related to their perceived physical ability to reproduce the movements they watch. Dance-naïve participants underwent functional magnetic resonance imaging while evaluating how much they liked and how well they thought they could physically replicate a range of ballet and contemporary dance movements performed by professional dancers (Fig. 5.2.6A). We used parametric analyses to evaluate brain regions that tracked with degree of liking and perceived physical ability. The findings reveal strongest activation of occipitotemporal and parietal portions of the AON when participants view movements they rate as both aesthetically pleasing and difficult to reproduce (Fig. 5.2.6B). As such, these findings begin to illuminate how the embodied simulation account of aesthetic experience might apply to watching dance, and provide preliminary evidence as to why some people find enjoyment in an evening at the ballet.
Beauty on the move: Aesthetic experience selectively facilitates the motor system during passive listening to music

Ticini, L. F., Novembre, G., Schütz-Bosbach, S., Waszak, F., Repp, B. H., & Keller, P. E.

Echoing the phenomenological tradition in philosophy, recent hypotheses in the field of neuroaesthetics have proposed that the aesthetic experience is crucially grounded in the embodied simulation of the actions, emotions, and corporeal sensations represented in artworks (Freedberg & Gallese, 2007, Trends Cognit Sci 11, 197–203). For instance, it has been shown that pleasurable musical stimuli that make us feeling the urge to move, enhance activity in motor-related areas (e.g. Koelsch et al., 2006, Hum Brain Mapp, 27, 239–250). However, evidence advocating an obvious role of the motor system in aesthetics judgment has seldom been demonstrated. In a transcranial magnetic stimulation study, we investigated whether aesthetic experience is...
associated with specific motor activity in the perceiver’s brain. Since aesthetics is only partially built on objective measures, we contrasted brain responses to 60 liked (“beautiful”) versus disliked (“not beautiful”) variations of the same melody (Fig. 5.2.7.1) as judged by each of 16 participants (8 musicians). The analysis of TMS-induced motor evoked potentials (MEP) surprisingly revealed that preferred performances facilitated the motor representation of the forearm (ECR) muscle (extensor and abductor of the wrist, usually involved in music production) in both musicians and non-musicians (Fig. 5.2.7.2). The results indicate that our motor system is boosted by the music we like, and advocate a universal involvement of motor resonance mechanism in aesthetic experience.

Figure 5.2.7.2 Mean MEP amplitudes (z scores) recorded from the index finger (FDI) and forearm (ECR) muscles during passive listening to variations of the Chopin’s Etude rated as “beautiful” and “not beautiful”. Repeated measures ANOVA revealed a significant interaction between muscle and aesthetic judgment, $F(1,14) = 8.8; p = .010$. Pairwise post-hoc comparison indicated that aesthetics differently modulated the MEP in the ECR muscle, with preferred variations facilitating its motor representation ($p = .01$, Bonferroni corrected). Error bars indicate standard errors.
Congresses, Workshops, and Symposia


Degrees


Appointments

Cross, E. S. (2010). *Associate Professor, Behavioural Science Institute*. Donders Institute for Brain, Cognition and Behaviour, Radboud University, Nijmegen, The Netherlands.

Awards

Schütz-Bosbach, S. *Member of AcademiaNet – Internetportal for Excellent Female Scientists*. Robert Bosch Foundation & Spektrum Verlag, Germany.

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Figure 5.2.4
5.3

Minerva Research Group
“Brain Modes”

The brain is a highly adaptive, self-organizing complex system, which has evolved such that neuronal responses and related behaviour are continuously optimized with respect to the external and internal context. This capability is achieved by the modulation of neuronal interactions depending on the history of previously processed information. Such meaningful connectivity changes, together with stochastic processes, influence ongoing neuronal dynamics. The resulting state-dependent fluctuations may be one of the fundamental computational properties of the brain, being pervasively present in human behaviour and leaving a distinctive fingerprint in neuroscience data. By combining advanced multimodal neuroimaging and computational modelling we aim to identify generative mechanisms of ongoing neuronal dynamics, and to elucidate principles of interaction between ongoing dynamics and incoming events or tasks. We have developed a technique that allows real-time analysis of EEG signatures during simultaneous EEG-fMRI acquisitions. With this technique, we investigate how fMRI responses to stimulation depend on ongoing EEG rhythms (5.3.1). A fundamental neuronal coding principle is thought to rely on the nesting of spatial and temporal scales in neuronal dynamics. We developed a new way to systematically analyze spatiotemporal nesting taking advantage of our multimodal functional data, in particular, the high temporal resolution provided by EEG and the high spatial resolution provided by fMRI (5.3.2).

An improvement in perceptual abilities can be induced by simple passive sensory stimulation. Based on coherence analysis of EEG rhythms, we show that even short-term stimulation in the order of minutes leads to changes in resting-state connectivity (5.3.3). Using the same passive sensory stimulation paradigm, we demonstrate the state-dependency of perceptual learning by relating ongoing EEG rhythms before sensory stimulation to the behavioural learning outcome. This allows us to account for the variability of the learning success (5.3.4). By advancing an existing neural field model, we demonstrate possible generative mechanisms for different states of multistable rhythms (5.3.5). Additionally, we provide a canonical model for dynamical switching within biological systems in general (5.3.6). Also, by means of a neural field model, we investigate which mechanisms underlie the well-known inverse relation between the EEG alpha rhythm and the cortical fMRI BOLD signal (5.3.7).
How ongoing neuronal oscillations account for evoked fMRI variability

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It is a feature of large-scale brain signals recorded by fMRI that there is variability of evoked single-trial responses despite input or task being constant. Fluctuating coherent background fMRI activity, constituting resting-state networks, has been shown to linearly superimpose evoked responses (Fox et al., 2006, Nat Neurosci 9, 23–25), explaining much of the trial-by-trial variance. Yet, the underlying intrinsic neuronal sources have not been previously substantiated. We addressed this issue using simultaneous EEG and fMRI (Ritter & Villringer, 2006, Neurosci Biobehav Rev 30, 823–838) and real-time classification of ongoing alpha rhythm states triggering visual stimulation in human subjects. We investigated whether spontaneous neuronal oscillations, as reflected in the posterior alpha rhythm, account for variability of evoked fMRI responses. We observed that spontaneous alpharhythm power fluctuations largely explain evoked fMRI response variance in extrastriate, thalamic, and cerebellar areas (Fig. 5.3.1). For extrastriate areas, we confirmed the linear superposition hypothesis, which states that alpha-related fMRI baseline modulations add linearly to a fixed visually evoked fMRI response. We hence linked evoked fMRI response variability to the power fluctuations of an intrinsic rhythm. These findings contribute to our conceptual understanding of how brain rhythms can account for trial-by-trial variability in stimulus processing.

Figure 5.3.1 fMRI results of conjunction analysis. (A, B) Clusters deactivating during high alpha activity \((t > 2.9; p < 0.04, \text{FDR-corrected (pFDR)})\) (purple). (C) Observed difference (red) in evoked fMRI responses due to high alpha stimulation (grey) and state-independent stimulation (black) is explained by the modulation of the fMRI baseline due to high alpha during nonstimulation periods (blue). Error bars indicate SEM across subjects.
5.3.2 Exploiting the potential of three dimensional spatial wavelet analysis to explore the nesting of oscillations and spatial variance in simultaneous EEG-fMRI data

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Synchronization of the activity in neural networks is a fundamental mechanism of brain function, putatively serving the integration of computations on multiple spatial and temporal scales. Timescales are thought to be nested within distinct spatial scales, so that, whereas fast oscillations may integrate local networks, slow oscillations might integrate computations across distributed brain areas. We demonstrate the feasibility and important caveats of a novel wavelet-based means of relating time series of three-dimensional spatial variance of fMRI data to time series of temporal variance of EEG. The spatial variance of fMRI data was determined by employing the three-dimensional dual-tree complex wavelet transform. The temporal variance of EEG data was estimated using traditional continuous complex wavelets. We tested our algorithm on artificial signals with known signal-to-noise ratios and on empirical “resting-state” EEG-fMRI data obtained from four healthy human subjects. By employing the human posterior alpha rhythm as an exemplar, we demonstrated face validity of the approach. We believe that the proposed method can serve as a suitable tool for future research on the spatiotemporal properties of brain dynamics, hence moving beyond analyses based exclusively in one domain or the other.

5.3.3 Interplay between ongoing oscillations and perceptual learning: State dependency and state modulation

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Perceptual learning refers to the ability to systematically improve perceptual performance as a function of repeated sensory experience (Seitz & Dinse, 2007, Curr Opin Neurobiol 17, 148–153). However, the same amount of repeated sensory experience does not necessarily lead to the same improvement in behaviour. It is a common observation that learning rates vary greatly across subjects, and subpopulations of subjects often show little or no learning. We investigated whether ongoing brain states account for the variability of perceptual learning outcomes. We characterized the relationship between ongoing neuronal oscillatory activity as measured by EEG and exposure-based, tactile perceptual learning in human subjects (Pleger et al. 2001, Proc Natl Acad Sci USA 98, 12255–12260). Thirty minutes of passive high-frequency finger stimulation led to an overall enhancement of tactile discrimination acuity, yet with considerable behavioural variability across individuals. This variability can be attributed to individual differences of ongoing activity in the alpha frequency band derived from somatosensory cortex (i.e. the human mu-rhythm). The intrinsic mu-rhythm power before sensory stimulation along with the stimulation-induced event-related desynchronization (ERD) predicted the individual learning outcome (Fig. 5.3.3). For the first time, individual mu-rhythm states are linked to perceptual learning. Our
findings support two theories of the role of local alpha rhythms: Mu "idling" during the "resting-state" increases the readiness to process incoming information, and ERD goes along with increased neuronal excitatory activity—hence facilitating synaptic plasticity.

Figure 5.3.3  Relationship between perceptual learning and EEG signatures of ongoing activity. Left column (A1, B1, C1): Alpha-band baseline power before learning; right column (A2, B2, C2): Alpha-band ERD during learning. (A) Correlation coefficients between two-point discrimination (2PD) change and EEG signature; Black dots: Channels within significant cluster. (B) Scalp distribution of corresponding p-values. (C) Scatterplot of single-subject values of one channel (grey diamond). Successful learners in green (n = 20), other subjects in red.

### 5.3.4 Repetitive sensory stimulation leads to changes in alpha-band "resting-state" functional connectivity: Implications for treatment of sensorimotor decline

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Many neurological events can lead to a decline of sensory and perceptual abilities. The conventional therapeutic approach to counteract this sensory decline comprises intensive training and practising. However, passive repetitive somatosensory stimulation (RSS) has recently gained increasing attention as an alternative by improving perceptual abilities without the need for active participation. One particularly effective type of high-frequency RSS, based on Hebbian principles, improves perceptual acuity as well as sensorimotor functions (Kalisch et al., 2008, Clin Interv Aging 3, 673–690), and has been successfully applied to treat chronic stroke patients (Smith et al., 2009, Arch Phys Med Rehabil 90, 2108–2111) and elderly subjects (Dinse et al., 2006, Ann Neurol 60, 88–94). It induces local plastic changes of the somatosensory cortex, but its impact on the brain's ongoing network activity and long-range connectivity has not been investigated so far. We applied high-frequency RSS in healthy...
human subjects and analyzed “resting-state” functional connectivity patterns before and after RSS by means of EEG imaginary coherency (ImCoh). Thirty minutes of passive high-frequency RSS lead to significant long-range ImCoh-changes of the resting-state mu-rhythm in the individual upper alpha frequency band within sensorimotor cortical areas (Fig. 5.3.4). Our data show that in addition to local plastic reorganization, high-frequency RSS also induces more distributed connectivity changes, which might underlie the improvement of tactile, haptic and sensorimotor abilities.

5.3.5 Biophysical mechanisms of multistability in “resting-state” cortical rhythms


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Fluctuations of the human alpha rhythm have traditionally been perceived as “waxing and waning”, akin to the fluctuating behaviour of a random signal with a Gaussian amplitude distribution. Contrary to this prevailing notion, we recently demonstrated that spontaneous alpha activity switches between two distinct modes of activity (Freyer et al., 2009, J Neurosci 29, 8512–8524). Here, we establish a mechanism for this multistable phenomenon in “resting-state” cortical recordings by characterizing the complex dynamics of a biophysical model of macroscopic corticothalamic activity. We studied the predicted activity of cortical and thalamic neuronal populations in this model as a function of its dynamic stability, and the role of non-specific synaptic noise. We find that fluctuating noisy inputs into thalamic neurons elicit spontaneous bursts between low and high amplitude alpha oscillations when the system is near a particular type of dynamical instability—subcritical Hopf bifurcation. When the postsynaptic potentials associated with these noisy inputs are modulated by cortical feedback, the standard deviation of power within each of these modes scales in proportion to the mean, showing remarkable concordance with empirical data (Fig. 5.3.5). Our state-dependent corticothalamic model hence exhibits multistability and scale-invariant fluctuations—key features of resting-state cortical activity and of human perception, cognition and behaviour—thus providing a unified account of these apparently divergent phenomena.
Multistable dynamics with multiplicative fluctuations: A canonical model of switching in biological systems

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Multistable dynamics and scale-invariant fluctuations are two complex dynamical processes whose presence in a wide variety of biological organisms suggests their fundamental roles. The former enables switching amongst a wide variety of dynamical scenarios, whereas the latter ensures sensitivity to environmental fluctuations, even if their background ambient intensity scales across several orders of magnitude. Here, we elucidate the underlying fundamental dynamical mechanisms in a canonical model of nonlinear bifurcations under stochastic fluctuations. We exploit a simple algebraic model of multistable oscillations and find that the co-occurrence of multistability and scale-invariant fluctuations mandate two important dynamical properties: A subcritical Hopf bifurcation is required for multistability, and multiplicative (state-dependent) noise ensures that as the system jumps between attractors, fluctuations remain in constant proportion to their mean and their temporal statistics become long-tailed. The algebraic construction of this model affords a systematic analysis of the contribution of stochastic and nonlinear processes to cortical rhythms and allows a “proof-of-principle” model inversion from EEG data (Fig. 5.3.6). Similar dynamics also occur in a kinetic model of gene regulation (Hasty et al., 2000, Proc Natl Acad Sci USA 97, 2075–2080), suggesting universality across a broad class of biological phenomena.
Congress, Workshops, and Symposia

2010

2011

Awards

2011
- Ritter, P. Charité Branding Competition, Winner, Charité Foundation, Charité University Medicine Berlin, Germany.

Degrees

Habilitation Thesis

2010
- Ritter, P. Spatio-temporal dynamics of spontaneous and evoked large-scale signals in the human brain. Charité University Medicine Berlin, Germany.

PhD Theses

2010
- Freyer, F. Electroencephalography-based characterization of human cortical population spikes and ongoing rhythms during functional magnetic resonance imaging. Charité University Medicine Berlin, Germany.
- Becker, R. A spatiotemporal characterization of the relationship between ongoing and evoked activity in the human brain: Interaction between ongoing and evoked neurodynamics. Charité University Medicine Berlin, Germany.
Publications

Books and Book Chapters


Published Papers


Infancy is the time of life during which enormous changes take place: The “helpless” newborn seems almost a different creature from the inquisitive, walking and talking 2-year-old. But modern infancy research is fundamentally changing our understanding of the first years of life, revealing that, even at very young ages, infants learn and understand more than we had ever imagined. Critically, during this formative life period, infants develop in an intensely social world filled with other people. Relating socially to others has been shown to not only have profound effects on what infants feel, think, and do, but to also be essential for their healthy development throughout life. Therefore, developing skills that help them to interact with others and understand others’ social behavior is one of the most important tasks that infants face in learning about the world.

In the Early Social Development Group, we strive to gain new insights into the early development of these social and affective competencies by studying the infant brain at work. In order to gather information about ongoing brain activity while infants are engaged in social tasks, electroencephalography (EEG) and event-related potential (ERP) methods will be used to provide precise information on the timing of brain processes, while functional near-infrared spectroscopy (fNIRS) will be employed to localize brain activation. In addition, we will record infants’ looking patterns during social perceptual and interactive tasks by using modern eye-tracking technology. By using these methods, we will be able to examine what changes in infant brain function occur while important social developmental milestones are achieved.

We plan to study these developmental processes across a range of situations in which infants can glean social and emotional information from various different sources such as faces, voices, or motion. Moreover, we will examine the important question of how the development of these brain processes varies across individuals and what genetic and environmental factors give rise to individual differences in social development. This research programme represents an integrated multi-method approach to the study of the developing social mind. By cutting across disciplines, this project will, for the first time, allow us to pool neural, genetic, and behavioral data concerning early social development, providing a unique window into the infant mind.
The Research Group “Infant Cognition and Action” is an offshoot of the former Department of Psychology headed by Professor Wolfgang Prinz. The overarching aim of the research group is to address the roots of action perception, and interpretation early in life. The understanding of others’ actions is one of the most fundamental skills in our everyday social life. It is crucial for any engagement in cooperative and communicative activities. In our research, we aim to explore the development of the (neuro-)cognitive mechanisms underlying action perception. The general theme of our research can be subdivided into three lines of research.

The first and major line of research focusses on the mechanisms of action perception in infants. Action perception relies on different information depending on when an observed action is processed. The processing timeline of infants’ action perception includes a number of component processes operating at different processing stages: shifts of covert attention in the direction of the agent’s goal (5.5.1), shifts of overt attention to the action goal (5.5.3, 5.5.4, and 5.5.5), and the post-hoc evaluation of the outcome of the action with the respect to a previously built expectation (5.5.3). Prior research has encountered surprising dissociations between these mechanisms and our aim is not only to examine the development of the singular processes, but also how they are related to each other, and to uncover the cognitive bases of potential dissociations and associations (5.5.3). Additionally, we are interested in uncovering the neural bases of early action perception, and the extent to which it is already similar to that of adults (5.5.2).

The second line of research addresses the interrelation of action and language. Much is known about the onset and development of language. However, little is known about how this emerging symbolic system interacts with the previously developed embodied system of action perception. The aim of this line of research is to chart the ways in which the onset of an explicit symbolic system for social cognition (i.e. language) impacts on the early understanding of social events (5.5.4, and 5.5.5).

The third line of research focusses on the selective implementation of observed behaviour into self-performed actions via imitation. Infants selectively imitate actions according to observed intentions and situational constraints. We explore how socially relevant characteristics such as age, competence, and cultural background, as well as low-level attentional characteristics, impact on the likelihood of an action being imitated (5.5.6).

The research conducted in the research group investigates the aspects of action perception outlined above and their interplay with action control by means of different paradigms and methods such as measuring looking time and heart rate, the analysis of infants’ eye movements using a Tobii Eye Tracking system, and the analysis of infants’ imitation of observed actions. In collaboration projects, we examine infants’ action perception using neurophysiological measures such as EEG and NIRS. The research group is involved in a number of
collaborations with other Departments and groups of the Max Planck Institute for Human Cognitive and Brain Sciences and with the wider scientific community. At the MPI, this includes collaborations with the Departments of Neuropsychology and Neurology, and the Research Groups “Neurocognition of Rhythm in Communication”, “Auditory Cognition”, and “Body and Self”. Furthermore, we have ongoing collaborative projects with the Universities of Uppsala (Sweden), Oslo (Norway), Zürich (Switzerland), Birkbeck, London (UK), Bangor (Wales), Chicago and Maryland (both USA), Saarbrücken, Potsdam and Greifswald (all Germany), and the MPI for Evolutionary Anthropology (Leipzig).

5.5.1 Cognitive mechanisms: Covert attention

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When presented with a cueing stimulus that contains directional information (e.g. an arrow), adults shift their covert attention in the direction indicated by the cue (Posner, 1980, Q J Exp Psychol, 32, 3–25). Observing pictures of referential gestures like pointing and grasping results in the same effect (Daum & Gredebäck, in press). We adapted the spatial cueing paradigm for use in research with infants as it provides a method for identifying cognitive processes that occur very early in the timeline of action perception.

Recent research has shown that the directional information contained in the static picture of a grasping hand (Fig. 5.5.1) already elicits shifts of covert attention towards a possible action goal in 7-month-olds (Daum & Gredebäck, 2011). In a follow-up study we explored the extent to which the presentation of a complete action, rather than just a static image, may help infants to perceive a grasping action as goal-directed at an earlier age. We presented infants with cues (grasping hand, geometrical object) that moved from the periphery toward the centre of the screen and disappeared, followed by the presentation of a target stimulus at a peripheral location congruent or incongruent to the motion direction of the cue. Saccadic reaction times (SRT) upon the appearance of the target were assessed via eye tracking. Observing a natural grasping movement yielded a congruency effect (i.e. shorter SRTs on congruent than incongruent targets) in infants as young as 5 months old. A geometrical object that moved on the same motion path as the grasping hand—thus containing some of its biological motion information—caused a congruency effect only in 7-month-olds. No congruency effect was observed when the same object moved in a linear way. Additional motion information thus helps infants as young as 5 months to identify agents that behave in a goal-directed way. Two processes may have helped infants to identify the goal-directedness of the cues: (1) low-level visual analysis of motion properties, and (2) high-level identification of hands as agents. At the age of 7 months, infants can use both processes in separation, while at the age of 5 months, they need both together.

![Figure 5.5.1 General paradigm of the studies measuring infants' shifts of covert attention.](image-url)
Neurophysiological basis of covert attention

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Despite the wealth of studies that focus on infants’ perception and production of goal-directed actions on a behavioural level, little is known about the development of the neurophysiological basis of action perception. In a series of recent studies, we examined the neural correlates of infants’ perception of pointing and grasping gestures. Using a spatial cueing paradigm, infants were presented with a target briefly flashed at the periphery of a computer screen, followed by a cue directed towards (congruent trials) or away from (incongruent trials) the target’s previous location (Fig. 5.5.2.1). The cue was either a pointing or a grasping hand. The results showed that when 8-month-old infants and adults were tested with a pointing cue, brain responses already showed differential activation to congruent and incongruent gestures in infancy, with an enhanced P400 in infants (Fig. 5.5.2.2), and an enhanced N200 in adults over posterior temporal sites including STS. The functional similarity of these components suggests that both might have a common source. When presented with grasping gestures, 6-month-olds showed an increased P400 over similar areas as the 8-month-olds in the pointing study (Gredebäck et al., 2010), but 4-month-olds did not. An intermediate group of 5-month-olds showed a significant correlation of the differences in amplitude between congruent and incongruent trials and the infants’ own reaching experience. These results suggest that the neural correlates of action perception in older infants are already comparable to those of adults. Interestingly, the processing of grasping actions is closely related to the infant’s own grasping skills, while the processing of pointing actions precedes the infant’s own pointing behaviour.

Figure 5.5.2.1 Example of stimulus sequence in the pointing study. (A) Congruent condition and (B) Incongruent condition.

Figure 5.5.2.2 Grand-average ERP for left and right posterior temporal channel groups (black solid circles in channel map). Broken lines represent the incongruent condition; solid lines represent the congruent condition. Grey solid circles represent included channels (the five grey exterior channels with a dark grey border provide support only and do not record EEG). Significant differences are marked with triangles, ▽ = P400. (From Gredebäck, Melinder, & Daum, 2010).
5.5.3 Interrelation of mechanisms: Retrospective and prospective attention

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Previous research revealed that different measures used to investigate infants’ perception of goal-directed actions are dissociated. In a recently completed study, it was shown that when action perception is measured post-hoc (via looking times), 9-month-old infants already encode the action goal based on its identity. In contrast, when action perception is measured online (via predictive gaze), the same-aged infants predict the agent’s goal based on its previous location (Daum et al., submitted). Identity-related predictions were not found before the age of three. In two follow-up experiments, we tested whether reducing the saliency of the goal location helps to predict an agent’s behaviour based on goal identity.

In Experiment 1, infants first saw an agent moving to one of two goal objects (Fig. 5.5.3.1). In the test phase, both goal objects were placed at a new location. In line with our previous findings, 9-month-olds did encode the goal post-hoc based on goal identity. In contrast to our previous findings, identity-related predictions were already demonstrated at the age of two. Thus, reducing the saliency of the goal location helps 2-year-olds to predict an agent’s goal-directed behaviour.

In Experiment 2, the saliency of the location was reduced by introducing a second agent that moved to the other goal during familiarization (Fig. 5.5.3.2). Here, the results showed that 3-year-olds and adults learned...
the agent–goal association, but only adults used this knowledge to predict the goals of both agents in the test phase. However, 2-year-olds already looked longer to the respective goal object in the test phase. Although the additional agent did not help them to predict the agent’s behaviour at an earlier age, post-hoc measures again reflected identity-related expectations earlier than online measures. In sum, we replicated the dissociation between post-hoc and online measures as found previously.

Cognitive mechanisms: Overt attention during the observation of everyday interactions

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Any social interaction requires rapid and accurate perception of a partner’s action and anticipation of the upcoming events in the flow of social interchange. The measurement of eye movements allows us to explore how we process ongoing actions and draw conclusions about how we perceive others’ actions. In this study, we investigated the development of infants’ and toddlers’ perception of natural, dyadic conversations and the role of semantics and intonation on the ability to anticipate turns in conversations. Children from four different age groups (6-, 12-, 24-, and 36-month-olds) and adults were presented with videos of a conversation between two women (Fig. 5.5.4.1); one with normal intonation and one with flattened (i.e. reduced) intonation. Their eye movements were recorded and we calculated the frequency of anticipated turns (i.e. how often gaze was shifted to the next speaker before she started speaking). The frequency of anticipated turns increased with age (Fig. 5.5.4.2). Only 3-year-old children showed a difference between normal and flattened conditions; they anticipated more turns when intonation was present. In all other age groups, the lack of intonation did not result in fewer anticipatory eye movements. Our results show that intonation is of particular importance for 3-year-olds in the context of conversations. Younger children do not yet use intonation to facilitate the anticipation of turns, whereas adults are probably able to compensate for the lack of intonation by focusing on semantics. Overall, our results indicate that there are fundamental differences in the comprehension of conversations between age groups, which need to be further investigated.

![Figure 5.5.4.1 Screenshot of a conversation between two women.](image)

![Figure 5.5.4.2 Mean frequency of anticipated turns in normal and flattened conversations for all age groups (with standard errors).](image)
Interrelation of action and language: Evidence of embodied language comprehension in 2-year-old children

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Previous research has shown that, in adults, language about actions is part of a common representational system including action perception and production. However, it is not known whether and how the onset of language production has an impact on infants’ action perception; in other words, whether a child’s action representation is altered once the child acquires knowledge about how the action is labelled. We investigated this question by adapting the paradigm introduced by Springer & Prinz (2010, Q J Exp Psychol 63, 2141–2158) for research with children aged from 12 to 30 months. The children watched a series of multistep actions that were either labelled beforehand or not. The children’s eye movements were analyzed in terms of anticipation times. In Experiment 1, we showed complex, familiar and novel actions, in Experiment 2, we presented simple two-step actions with verbs that are acquired early and late. The results of Experiment 1 showed that the labeling of an action interfered with action anticipation at 24 and 30 months. This indicates that the facilitating connection between language and action present in adults does not exist at this age. In Experiment 2, “early” verbs similarly interfered with 12-month-olds’ anticipation. However, beginning at 18 months of age, action labelling facilitates action perception, as indicated by faster anticipation times compared to the control condition (Fig. 5.5.5). This facilitation effect was not found for the “late” verbs. These findings support an embodied account of language comprehension stating that language representations are connected to perceptual representations of action. The results further suggest that this embodied language comprehension starts early on and develops gradually.

Rethinking ‘rational imitation’ in 14-month-old infants: An attentional competition approach

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Fourteen-month-old infants imitate an unusual action (i.e. illuminating a lamp using the head) only if the model freely chose to perform this action and not if the action could be ascribed to external constraints. This selective imitation was attributed to the infant’s understanding of the principle of rational action (Gergely, Bekkering, & Király, 2002, Nature, 415, 755). In the present project, we present evidence that a simpler approach of attentional competition may be more appropriate to explain these results: Seeing a model being wrapped in a blanket might distract the infants’ attention away from the target action resulting in a lower likelihood of imitation. We tested this idea with two conditions: 1) We reduced attentional competition by familiarizing the infants to the sight of the model being wrapped in a blanket (hands-occupied-familiarization; HO-Fam). 2) We enhanced attentional competition by adding two big smileys next to the model (hands-free-competition; HF-Comp) – see
Fig. 5.5.6.1. In addition, we conducted the two original conditions (hands-free; HF; hands-occupied; HO). The two accounts make opposing predictions for the two new conditions. The rational-imitation account predicts that the likelihood of infants imitating the head touch would be low in the HO-Fam condition and high in HF-Comp. In contrast, the attentional-competition account predicts a high likelihood of imitation in HO-Fam (because infants are familiarized to the unusual sight of the model). In HF-Comp, the smileys compete with the infants’ attention to the target action which reduces the likelihood of imitation. Our study replicated the original findings. Infants imitated the head touch in the HF but not in the HO condition (Fig. 5.5.6.2). More notably, in HO-Fam, the head touch was imitated as often as in the original HF condition. In HF-Comp, the likelihood of imitation was intermediate compared to the two original ditions, \( d = .32; p < .05 \) (Somer’s \( d \) coefficient). Thus, likelihood of imitation increases when infants are familiarized with an unusual sight of a model, and is reduced when infants’ attention is distracted. Selective imitation in 14-month-old infants does not require a demanding understanding of rationality, but can be explained more simply with attentional competition.

Figure 5.5.6.2  Percentage of infants performing a head touch in each of the four experimental conditions. The original conditions are represented by the first (hands-free) and the third (hands-occupied) column (from Beisert et al., in press).
Congress, Workshops, and Symposia

2010

Degrees

Habilitation Thesis

2011
- Daum, M. M. *Mechanisms in the early development of action understanding*. University of Leipzig, Germany
Publications

Books and Book Chapters


Published Papers


5.6
Max Planck Research Group “Music Cognition and Action”

When one observes how humans make music around the globe, it becomes apparent that interpersonal coordination during musical activity is characterized by remarkable temporal precision and flexibility. However, it is also clear that, even within a particular culture and genre, there are marked individual differences in the degree of precision and flexibility that is achieved.

The research agenda of the Music Cognition and Action (MCA) group focusses on the cognitive and motor processes—and the underlying neural mechanisms—that allow multiple performers to coordinate their actions with one another in musical contexts, such as instrumental ensembles and dance.

Our investigations centre on three core cognitive/motor “ensemble” skills. The first relates to anticipatory mechanisms, such as musical imagery and covert action simulation, which are involved in planning one’s own actions and predicting others’ actions. A second ensemble skill is based upon adaptive timing mechanisms that allow performers to react to variations in each others’ action timing. The third skill concerns the process of dividing attention between one’s own actions and those of others while monitoring the overall, integrated ensemble output.

One of our most ambitious, but promising, research strategies is to examine the relationship between an individual’s performance in controlled laboratory tasks assessing these three core ensemble skills, and the ability of the same individual to coordinate with other individuals under naturalistic performance conditions.

The group’s overarching aim is to understand how the three skills interact with one another to determine the quality of ensemble coordination. Furthermore, we are interested in relationships between the three skills and social factors such as empathy, emotional intelligence, and feelings of interpersonal affiliation.

The project descriptions that follow showcase the on-going research activities of the MCA group. First, we present studies on how one’s own and other’s parts are represented in the brains of co-performers in musical ensembles. Then we describe a collection of studies on how real-time coordination is mediated by temporal prediction and adaptive error correction in audio- and visuomotor synchronization tasks designed to capture the varying demands of interpersonal timing in ensembles. Finally, a cluster of projects on the role of body movements in social communication in music performance and dance is presented.
Knowing too much or too little: The effects of familiarity of a co-performer’s part on interpersonal coordination in piano duos

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Ensemble musicians perform under conditions of varying familiarity with each others’ parts. Such familiarity may affect the ability to predict, and therefore to synchronize with, co-performers’ actions. Specifically, the operation of internal models that guide processes related to action simulation and anticipatory musical imagery may be affected by knowledge of (1) the musical structure of a co-performer’s part (e.g. in terms of its rhythm and phrase structure) and/or (2) the co-performer’s idiosyncratic playing style (e.g. expressive micro-timing variations).

To test the effects of familiarity, seven pairs of previously unacquainted pianists were invited to play duets on two digital pianos under two conditions. In one condition, the individual pianists had learnt both parts of each of several duet pieces prior to the test session, while, in the other condition, they had learnt only one part from a set of pieces. In the test session, the paired pianists performed six consecutive “takes” of each piece. Interpersonal coordination was quantified by measuring asynchronies between pianists’ keystroke timing and the correlation of their body sway movements (which were recorded by a motion capture system; Fig. 5.6.1.1).

Results point to a dissociation between interpersonal coordination at the level of keystrokes and body sway (Fig. 5.6.1.2). Keystroke asynchronies decreased across the six takes, and were generally lower in the unfamiliar condition than the familiar condition. This indicates that coordination started out better, and remained so, when pianists had not rehearsed their co-performer’s part. Body sway coordination, by contrast, was high throughout the takes in the familiar condition, while it was initially low and improved across takes in the unfamiliar condition. These findings suggest that familiarity affects interpersonal coordination in ensembles by influencing predictions at different timescales. Familiarity with a co-performer’s part, but not their playing style, may engender predictions about expressive micro-timing variations that are instead based upon one’s own personal playing style, leading to a mismatch between predictions and actual events at short timescales. Predictions at longer timescales—that is, those related to musical measures and phrases, and reflected in body sway movements—are, however, facilitated by familiarity with the structure of a co-performer’s part.

Figure 5.6.1.1 Illustration of the experimental procedure. Individual pianists practised either one part or both parts of duet pieces at home. The pianists then came to the laboratory in pairs and recorded six takes of the pieces. Interpersonal keystroke asynchronies and body sway movements (which were recorded by a motion capture system; Fig. 5.6.1.1).

Figure 5.6.1.2 Variance of keystroke asynchronies (top panel) and body sway coordination (quantified by computing “mutual information”, an information-theoretic measure of dependency) (bottom panel) between duo pianists across six takes under conditions where the co-performer’s part was familiar (red squares) or unfamiliar (blue diamonds).
Co-performers in musical ensembles presumably integrate information about their own and others’ actions in order to monitor the overall ensemble sound. The present study employed transcranial magnetic stimulation (TMS) to investigate how the brain achieves the distinction between motor representations underpinning the self and others under such circumstances. Amateur pianists performed the right-hand part of piano pieces, previously learned bimanually, while the complementary left-hand part was either not executed or (believed to be) performed by another pianist (Fig. 5.6.2.1). This experimental setting was intended to induce a co-representation of the left-hand part reflecting either the self (Self condition) or the co-performer (Joint condition). Single-pulse TMS was applied to the right primary motor cortex and Motor Evoked Potentials (MEPs) were recorded from the resting left forearm. Results indicate that corticomotor excitability was modulated by whether the representation of the left hand was associated with the self or the other, with MEP amplitude being low in the Self condition and high in the Joint condition (Fig. 5.6.2.2, panel A). These different patterns of activation might reflect corticomotor suppression and facilitation, respectively. This result remained unchanged in a separate (mute) session where the participant could neither see nor hear the other, but was led to believe that he was performing in silence. Thus, the sociality of the context in which one acts modulates action attribution at the level of the motor control system. This interpretation is supported by the additional finding that corticomotor excitability in the Joint condition was positively correlated with pianists’ self-reported empathy (Fig. 5.6.2.2, panel B).
The role of temporal prediction in sensorimotor synchronization

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Musical ensemble performance is characterized by precise action coordination that necessitates anticipatory timing mechanisms. Previous studies on synchronized finger tapping with tempo-changing pacing signals revealed that individuals differ in temporal prediction abilities, indexed by cross-correlations between tap timing and pacing events.

A recent study investigated the influence of individual differences in prediction tendencies on dyadic sensorimotor synchronization (SMS) (Pecenka & Keller, 2011). Forty-four participants with high or low prediction tendencies tapped in synchrony with individuals who displayed similar or different tendencies. Dyads composed of high-predicting individuals tapped with higher accuracy and less variability than low-predicting dyads, while mixed dyads were intermediate (Fig. 5.6.3.1). This suggests that individual differences in temporal prediction ability may mediate the interaction of cognitive, motor, and social processes underlying musical coordination.

A subsequent fMRI study investigated the neural correlates of auditory temporal predictions. Eighteen musicians tapped in synchrony with an auditory pacing signal, while their prediction capacities were taxed by a concurrent visual task that increased working memory load (Fig. 5.6.3.2). Parametric analyses revealed that higher temporal prediction was related to increased brain activation in a wide network of cortical and subcortical areas (Fig. 5.6.3.3) involved in basic auditory as well as higher cognitive processes.

This work is being followed up by (1) a study that employs an SMS task to investigate how accurately pianists can predict upcoming events in recordings of their own playing compared to other pianists’ interpretations, and (2) a project that aims to develop a virtual synchronization partner that can anticipate, as well as adapt to, a human’s timing in a synchronized drumming task.

Figure 5.6.3.1  Boxplots depicting median values (crossbar) for two measures of dyadic synchronization performance separately for the three dyad types. Lower values in panel A indicate lower asynchrony (i.e. higher SMS accuracy). Dyads comprising two high-predicting individuals synchronized their finger taps with higher accuracy (i.e. lower asynchrony) than dyads including two low-predicting individuals. Mixed dyads were intermediate and only marginally less accurate than high-predicting dyads. Panel B depicts dyadic synchronization variability. High-predicting and mixed dyads synchronized their taps with lower variability than low-predicting dyads.

Figure 5.6.3.2  Observed prediction ratios during SMS with increasing working memory load: (1) SMS and object observation (Tap), (2) SMS and 1-back object comparisons (Tap1B), (3) SMS and 2-back object comparisons (Tap2B). The degree of prediction was found to decrease significantly with increasing working memory demands ($p < .001$).
Interacting with a virtual synchronization partner

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Cooperation is intrinsic to our ability to work together towards a common goal, such as music making. With three functional MRI studies, we present an approach for investigating the neural correlates of cooperation between a human and a virtual partner (VP), a variably adaptive auditory pacing signal. The paced finger tapping task requires participants to synchronize with the VP, programmed to adapt its timing so as to reduce asynchronies (ΔT) between human taps and computer tones (Repp & Keller, 2008, Hum Movement Sci, 27, 423–456).

By varying a single error-correction parameter, the VP’s level of adaptivity was modulated to investigate its impact upon the interaction and related brain activity. In Study 1, the level of computer phase correction was varied to explore the range of give and take between cooperating partners. We identified two distinct neural networks that were selectively activated during easy, automatic entrainment (midline areas) with a minimally adaptive VP or during more cognitively challenging interactions when interacting with a highly adaptive VP.
(right lateralized areas) (Fig. 5.6.4A). In study 2, the extent to which the human could lead and dictate the overall period was varied, and it was shown that right lateralized frontal areas dominate when leading. Additionally, it was found that a subgroup of individuals with a strong tendency to lead employed less error correction and showed greater activity in areas commonly associated with self-initiated action (Fig. 5.6.4B). In study 3, the level of distinction between self- and other-initiated tones was manipulated by varying auditory feedback. While right lateralized parietal activation was seen to correlate with greater self-other distinction, a more distributed network of areas varied as a function of agency attribution error (Fig. 5.6.4C). This simple cooperative model provides for a novel way to study second-person social interaction and describes a bridge between social cognition and simpler goal-directed action.

Figure 5.6.4  (A) Study 1: Degree of temporal (phase) error correction of the virtual partner (VP) was varied to manipulate the dynamic relationship between human and VP. Left: tapping with a minimally adaptive VP optimizes task performance (i.e. minimizes the variability of asynchronies - middle) correlating with activation of midline cortical structures; right: tapping with an overly adaptive and unreliable VP with correlated activity in the right inferior frontal gyrus and anterior insula. (B) Study 2: VP period correction was varied to allow the participant more or less responsibility for maintaining the overall tempo. Left: main effect of leading, with activation of the right inferior frontal gyrus and anterior insula. "Leaders" and "followers" were identified based on subjective trial-by-trial ratings of perceived influence over the tempo and task difficulty. Leaders employed less phase correction (middle) and a regression analysis showed that this was correlated with greater activation of areas involved in self-initiated action (right). (C) Study 3: manipulation of the extent to which self and other tones overlap by varying feedback sounds and VP adaptivity. Left: ROI analysis shows greater self–other distinction correlated with increased activation of the right TPJ (inset sagittal slice showing the main effect of auditory feedback). Right: Self–other blurring resulted in greater activation of a network implicated in agency error. Imaging data are presented in radiological convention, coordinates are in MNI space and associated peak voxel Z-scores are thresholded at p < .05, corrected for multiple comparisons. ** denotes significance of p < .05.
The kinematics of audio- vs visuomotor synchronization

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Previous behavioural and neuroimaging studies of sensorimotor synchronization have shown a strong modality advantage of auditory over visual stimuli for action timing. Neural activation differences were especially clear in areas implicated in timing, such as the basal ganglia and cerebellum. However, nearly all previous studies used flashing visual stimuli, and we have recently shown in behavioural studies that synchronization improves dramatically with moving visual stimuli (Hove & Keller, 2010; Hove, Spivey, & Krumhansl, 2010). This raises the question of whether the previously observed ‘modality differences’ reflect modality per se, or differences in synchronization stability.

In an fMRI experiment, participants tapped along with auditory and visual stimuli that were discrete (Beeps and Flashes) or continuous (Sirens and a Moving Bar) (Fig. 5.6.5.1). Behavioural results showed that synchronization was more stable with auditory beeps compared to visual flashes, whereas no modality difference occurred between auditory sirens and moving visual stimuli (Fig. 5.6.5.2A). This was paralleled in imaging results: For discrete stimuli, the left putamen was more active for auditory beeps compared to visual flashes, whereas no activation differences occurred between modalities for sirens vs moving visual stimuli (Fig. 5.6.5.2B; Hove, Fairhurst, Kotz, & Keller, 2011, Neurosciences and Music IV, Edinburgh, UK).

These results indicate that modality differences in synchronization, and their underlying neural processes, depend less on the modality, and more on the reliability of perceptual information. This might explain why it is easier to synchronize with a conductor’s movements than the flash of a visual metronome.

Related projects: (1) explore how musicians and non-musicians synchronize with kinematic features of conductors’ beat movements; (2) analyze differences between auditory and visual synchronization in terms of the movement kinematics of tapping and reactions to phase perturbations; and (3) examine synchronization in novices and highly trained experts (i.e. drummers from extreme metal bands).

Figure 5.6.5.1 Stimuli for the fMRI finger tapping experiment, which were discrete (auditory beeps and visual flashes) or continuous (auditory pitch sweeping ‘siren’ and a visual bar moving up and down).

Figure 5.6.5.2 (A) Behavioural results of synchronization stability by condition. (B) Activation differences between modalities for discrete and continuous stimuli (p < 0.05, corrected).
The perception of social communicative cues in the kinematics of music- and dance-related body movements

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The kinematics of a performer’s body movements can be a rich source of information during communicative acts such as music-making and dance. The Music Cognition and Action Group has been pursuing a range of projects addressing the contributions of such kinematic cues to action understanding and social cognitive processes in musical interaction. This work uses motion capture technology to record, analyze, transform, and display the movement trajectories of individuals, as well as groups of musical performers and dancers.

One exemplary project explores the role of action simulation, experience, and empathy in identifying dancers’ expressive intentions from movement kinematics shown in “point-light” displays (Sevdalis & Keller, 2010, 2011a, 2011b).

Another topic of interest concerns the perception of real-time collaboration in music and dance. This has been investigated by recording the body movements of individuals acting alone or in pairs, and then manipulating the information that is provided to observers in point-light displays. One study sought to determine the kinematic cues that observers use when judging whether a single displayed dancer is acting alone or with an invisible (occluded) partner. Another study examined the ability of observers to judge whether displays of dancing dyads contained two individuals who had actually danced together (i.e. a real pair) or two independent individuals who had been paired through splicing (i.e. a fake pair).

A related project extends this line of research to the recognition of authentic musical collaboration in improvising jazz duos (Moran & Keller, 2011, Neurosciences and Music - IV, Edinburgh, UK). The primary question concerns the ability of observers to distinguish between real and fake pairs of point-light instrumentalists (e.g. pianists, flautists, and bass players; Fig. 5.6.6) based on cues that are reminiscent of the “back-channelling” that occurs in interactions between speakers and listeners during face-to-face conversation.

Figure 5.6.6 Two real pairs of improvising jazz musicians (left) and a fake pair (right) created by cross-splicing the real pairs.
Congress, Workshops, and Symposia

**2010**

**2011**

Appointments

**2011**
- Keller, P. E. *Associate Professor, MARCS Auditory Laboratories*, University of Western Sydney, Australia.

Degrees

**PhD Thesis**

**2010**

Awards

**2010**
- Pecenka, N. *Young Researcher Award 2010*. 11th International Conference for Music Perception and Cognition (ICMPC11). University of Washington, Seattle, WA, USA.

Publications

**Books and Book Chapters**


Published Papers


5.7

Max Planck Research Group “Neural Mechanisms of Human Communication”

The aim of our research programme is to identify the sensory processes that enable us to communicate successfully with each other. Research on patients with brain lesions and neuroimaging of healthy people has offered considerable insight into mechanisms for communication. Specialized sensory cortices have been identified that are involved in processing distinct aspects of communicative signals, like auditory speech or facial expression. These findings have led to the common assumption that the communicating brain is separated into mostly non-interacting, specialized cortices, processing specific parts of the sensory input with integration occurring at a later stage by higher level brain regions.

Our two main hypotheses are that (i) the specialized regions in the human brain interact much more and at earlier stages than previously thought and that (ii) subcortical structures are already optimized for processing human communication stimuli. Findings of such cortical interactions and specialization at early subcortical levels are important because they may explain how the brain can achieve such speed, accuracy, and robustness to adverse conditions in communication. To test our hypotheses and develop novel communication models, we acquire behavioural and neuroimaging data and employ neurostimulation techniques. We also test the predictions of our models on populations with selective hereditary communication difficulties. For example, roughly 2% of the population cannot recognize others by face (prosopagnosia) and 5–10% have difficulties understanding speech in noise (e.g. dyslexics).

Our research programme will provide an integrated view on the communication abilities of our brain, and we assume that our findings will prompt a revision of conventional models. Examples of such findings and potential revisions are given in the following five abstracts. In the long term, we expect that our research will lead to two useful applications: The development of (i) neurobiologically plausible computational models, which implement novel approaches in artificial speech recognition and (ii) the identification of the underlying causes of hereditary communication deficits and the development of tailored treatment regimes (e.g. for autism spectrum disorders and dyslexia).
Direct structural connections between voice- and face-recognition areas

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Currently, there are two opposing models for how voice and face information is integrated in the human brain to recognize a person’s identity. The conventional model assumes that voice and face information is only combined at a supramodal stage (Bruce & Young, 1986, Br J Psychol, 77, 305–327; Burton, Bruce, & Johnston, 1990, Br J Psychol, 81, 361–380; Ellis, Jones, & Mosdell, 1997, Br J Psychol, 88, 143–156). An alternative model posits that areas encoding voice and face information also interact directly, and that this direct interaction is behaviourally relevant for optimizing person recognition (von Kriegstein, Kleinschmidt, Sterzer, & Giraud, 2005, J Cogn Neurosci, 17, 367–376; von Kriegstein & Giraud, 2006, PLoS Biol, 4, e326). To disambiguate between the two different models, we tested for evidence of direct structural connections between voice and face processing cortical areas by combining functional and diffusion magnetic resonance imaging (fMRI and dMRI). At the individual subject level, we localized three voice-sensitive areas in the anterior, middle, and posterior superior temporal sulcus (STS) and face-sensitive areas in the fusiform gyrus (fusiform face area, FFA). Using probabilistic tractography, we showed evidence that the FFA is structurally connected with voice-sensitive areas in the STS (Fig. 5.7.1). In particular, our results suggest that the FFA is more strongly connected to middle and anterior than to posterior areas of the voice-sensitive STS. This specific structural connectivity pattern indicates that direct links between face- and voice-recognition areas could be used to optimize human person recognition.

Figure 5.7.1  Structural connections between voice- and face-sensitive areas as found with probabilistic fibre tracking. Results of a single, representative participant’s dMRI are shown as connectivity distribution. Probabilistic tractography was done in both directions: from the visual FFA as seed region to the three target regions in the STS, and vice versa, from the three seed regions in the STS to the FFA as target region. Seed and target regions were localized with a functional localizer and are displayed as spheres with a radius of 5 mm (FFA [in yellow], anterior part of the STS [in blue], middle part of the STS [in red], and posterior part of the STS [in green]). The structural connections between FFA and STS are coloured, corresponding to their seed and target regions in the STS. The connections are displayed from different views: A, right frontal; B, top; C, right side; D, detailed view. As anatomical landmarks, the inferior longitudinal fasciculus (ILF) is shown in grey (in B, C, and D) and the posterior part of the arcuate fasciculus (pAF) is shown in black (in C and D) (Catani, Jones, & Ffytche, 2005, Ann Neurol, 57, 8–16).
Research Groups

Auditory-only speech areas are functionally connected to visual face-movement sensitive areas

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The audiovisual model of human communication assumes that speech recognition in auditory-only communication is facilitated by an internal simulation of the talking face of visually known speakers. One prediction of this model is that areas involved in auditory-only speech comprehension interact with visual face-movement sensitive areas, even under auditory-only listening conditions (von Kriegstein, K., et al., 2008, Proc Natl Acad Sci USA, 105(18), 6747–6752). Here, we test this hypothesis by using connectivity analyses of functional magnetic resonance imaging (fMRI) data. Participants were first familiarized with six speakers by means of a brief voice-face or voice-occupation training (< 2 min per speaker) and were then scanned while performing either an auditory speech or speaker recognition task. As hypothesized, we found that, during speech recognition, familiarity with the speaker’s face increased the functional connectivity between face-movement sensitive posterior superior temporal sulcus (STS) and auditory speech areas in the anterior STS (p < 0.05, FWE corrected for auditory speech area) (Fig. 5.7.2). In contrast, during speaker recognition, we replicated the previous finding that prior face learning leads to stronger functional connections between face-identity-sensitive (fusiform face area) and voice-sensitive areas in the right STS (p < 0.05, FWE corrected for auditory voice areas). Our results indicate that the interaction between facial and auditory areas is a general principle in human auditory-only communication.

Figure 5.7.2 Functional connectivity of left face-movement sensitive posterior STS. (A) Increased functional connectivity (interaction learning type x task: Speech task/voices learned with face > speech task/voices learned with occupation > speaker task/voices learned with face > speaker task/ voices learned with occupation) is shown in red on an axial and sagittal brain slice. The auditory region of interest in the anterior left STS (intelligible > unintelligible speech) is visualized by a yellow sphere taken from published coordinates (Friederici et al., 2010, Human brain mapping, 31(3), 448–57, see chapter 2 of this report). On the axial slice, the blue sphere schematically illustrates the posterior STS region around which individual seed regions were determined. (B) Whole brain functional connectivity results are displayed in the glass brain view (p < 0.001 uncorrected).
Visual face-movement sensitive cortex is relevant for auditory-only speech recognition

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There are currently two opposing views about the role of visual face-sensitive cortices during auditory-only communication. In the conventional view (the “auditory-only” model), the recruitment of visual areas during audition is not relevant for performing the auditory task. In another view (the “auditory-visual” model), the recruitment of visual face areas optimizes auditory task performance (for a review, see von Kriegstein, 2011). One specific prediction of the auditory-visual model is that after brief (< 2 min) visual exposure to a speaker, the visual face-movement sensitive posterior superior temporal sulcus (pSTS) is causally involved in auditory-only speech recognition for that specific speaker. To test this hypothesis, we performed transcranial direct current stimulation (tDCS) on the pSTS while testing (i) auditory-only speech recognition and (ii) visual-only lip-reading. All participants were familiarized with three speakers by means of audio-visual videos of the speaker’s face (“voice-face learning”) and with three others by showing a symbol of an occupation, instead of the face (“voice-occupation learning”). In subsequent auditory-only speech recognition, tDCS was administered to the pSTS in one group (N = 17), whilst a control group received either BA6 stimulation (N = 17) or Sham stimulation (N = 17). The visual-only lip-reading test was performed first without tDCS and then with tDCS. As predicted, cathodal tDCS to the pSTS interfered with performance in auditory-only speech recognition after voice-face learning compared to voice-occupation learning (Fig. 5.7.3A). In addition, stimulation affected visual-only lip-reading performance. While the controls significantly improved in performance from the first lip-reading test to the second, this was not the case for the pSTS group (Fig. 5.7.3B). These results provide evidence that the visual face-movement sensitive pSTS optimizes speech recognition even in auditory-only conditions as predicted by the auditory-visual model.

Visual influences on auditory-only speech and speaker recognition in high-functioning autism spectrum disorder

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Successful human interaction is based on the fast and accurate online perception of audio-visual communication signals, such as the face and the voice. Recent research suggests that (i) the brain exploits previously encoded audio-visual correlations to improve behavioural performance in auditory-only perceptual tasks and that (ii) this improvement relies on the ability to perceive information from the face (auditory-visual model) (von Kriegstein et al., 2008, P Natl Acad Sci USA, 105, 6747–6752). Here, we test the predictions of the auditory-visual model.
model in a group of individuals with a high-functioning Autism Spectrum Disorder (ASD), a condition that is associated with impaired face processing. We trained 14 individuals with ASD and 14 typically-developed matched-controls to identify six speakers by name and voice. Three speakers were learned by a video showing their talking face (voice-face learning). The other three speakers were paired with a symbol representing their occupation (voice-occupation learning). During subsequent auditory-only testing, sentences spoken by the same six speakers were presented. Participants decided whether the voice matched a visually presented name (speaker task) or if the spoken sentence contained a visually presented word (speech task). An additionally performed visual-only speech recognition (i.e. lip-reading) and face recognition experiment showed that the ASD group was impaired on facial movement processing, but not significantly different from controls on face identity processing (Fig. 5.7.4A/B). This pattern of impairment was paralleled by the performance in auditory tasks: Auditory-only speech recognition was improved by prior voice-face learning, compared with voice-occupation learning in controls, but not in the ASD group (group x learning interaction in speech task; Fig. 5.7.4C). Conversely, for the speaker task, there was no significant group x learning interaction (Fig. 5.7.4D). In agreement with the predictions of the auditory-visual model, the results suggest that in ASD, speaker-specific dynamic visual information is not available to optimize auditory-only speech recognition.

Figure 5.7.4 Total performance accuracy for the visual-only experiments (A, B) and the difference between performances after voice-face vs voice-occupation learning in the auditory-only experiment (C, D). (A) The ASD group was significantly impaired in visual-only speech recognition in contrast to the control group (t_{26} = 2.38, p = .025), while (B) performance in face identity recognition was not significantly different between the groups (t_{26} = 1.52, p = .141). (C, D) There was a significant group x learning interaction (F_{1,26} = 10.41, p = .003), indicating that learning affects the performance in the two groups differently. This interaction is mainly based on a learning x group interaction in the speech task: In this task, the control group benefitted from prior voice-face learning (in contrast to voice-occupation learning, t_{13} = 2.47, p = .028), while the ASD group did not (speech task: learning x group interaction, F_{1,26} = 14.33, p = .001). In the speaker task (D), there was no significant difference between the groups (learning x group interaction, F_{1,26} = 2.88, p = .102).


*p < .05; **p < .001; ns not significant.
Dysfunction of the medial geniculate body during speech perception in developmental dyslexia

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The neural origin of dyslexia is hotly debated: The phonological deficit hypothesis claims that dyslexia is a phonological deficit rooted in a cortical malfunction (Ramus, 2003, Curr Opin Neurobiol, 13, 212–218; Shaywitz, 1998, New Engl J Med, 338, 307–312), whereas the magnocellular theory proposes that dyslexia is a sensory deficit caused by a dysfunction of the sensory thalamus (Galaburda, 1993, Curr Opin Neurobiol, 3, 237–242; Stein & Walsh, 1997, Trends Neurosci, 20, 147–152). Here, we combine these two influential theories to test the hypothesis that dyslexia stems from a dysfunction of the auditory thalamus (medial geniculate body, MGB) that specifically impacts phonological processing.

Dyslexic adults (N = 14) and matched controls (N = 14) performed two tasks while blood oxygen level dependent (BOLD) activity was assessed with a functional magnetic resonance imaging protocol, optimized for subcortical auditory structures. Participants reported, via button presses, whether each syllable within a sequence of six syllables differed in content from the previous one (phonological task) or was spoken by a different voice (speaker task).

Controls showed a significantly larger BOLD signal than dyslexics in the left MGB for the phonological, compared to the speaker task (Fig. 5.7.5A, B). In dyslexics only, this task-dependent modulation of the left MGB correlated with literacy and phonological measures (Fig. 5.7.5C). These results show that dysfunction of the MGB plays a key role in phonological processing skills in dyslexia, and are in line with the recent view of the sensory thalamus as a dynamic gatekeeper tuned by cortical areas to optimize sensory processing. Based on this, and theoretical models of brain function (Kiebel, von Kriegstein, Daunizeau, & Friston, 2009, Plos Comput Biol, 5, e1000464), we propose that phonological deficits in dyslexia are caused by a difficulty in fine-tuning speech processing at the level of the MGB.
Research Groups

Congress, Workshops, Symposia

2010


2011


Awards

2011
Mathias, S. K. M. Scott PhD Prize. University of York, United Kingdom.

Publications

Books and Book Chapters


Published Papers


A renewed interest in understanding the human connectome offers a novel platform to investigate the relationship between brain organization and behaviour. While much has already been learned about the organization of the brain in non-human species by looking at connectivity between neurons, the non-invasive tools to make this fruitful area of research possible in humans have only widely emerged in the past decade. The research group “Neuroanatomy & Connectivity” aims to make a unique contribution to this research endeavour by applying non-invasive connectivity mapping techniques to describing the organization of the prefrontal cortex in humans.

Numerous subdivisions within the prefrontal cortex have been described in the macaque monkey based on unique patterns of connectivity. Nonetheless, their translation to understanding the organization of the human brain remains speculative. In collaboration with Michael Petrides, an expert in cross-species prefrontal anatomy from the Montréal Neurological Institute, we will map these same areas in the human brain using hypotheses generated from the broad tract-tracing literature from the macaque monkey. Specifically, we will focus on functional connectivity using correlations of intrinsic brain activity as measured with fMRI during the “resting-state”. Intrinsic functional connectivity, which is based on the spontaneous synchronization of activity between regions, has been found to accurately characterize widespread functionally congruous brain systems. In previous work, we have demonstrated that intrinsic functional connectivity can be a powerful tool for mapping subdivisions in cortical areas (Margulies, Kelly, Uddin, Biswal, Castellanos, & Milham, 2007, Neuroimage, 37, 579–588), can be demonstrated as well in macaque monkeys, and largely reflects predictions from the tract-tracing literature (Margulies, Vincent, Kelly, Lohmann, Uddin, Biswal, Villringer, et al., 2009, PNAS, 106, 20069–20074). Furthermore, the patterns are reliable (Shehzad Kelly, Reiss, Gee, Gotimer, Uddin, Lee, et al., 2009, Cereb. cortex, 19, 2209–2229), and detectable on the individual level (Margulies, Taubert, Ragert, Kelly, Biswal, Castellanos, Milham, M. P., et al., 2011, 17th Annual Meeting of the Organization for Human Brain Mapping). In addition, this initial aim of mapping functional connectivity-based subdivisions within the prefrontal cortex will integrate complementary approaches from anatomical connectivity measures such as probabilistic tractography (based on diffusion tensor imaging data) as well as meta-analyses of task studies (thereby aiming to ascribe putative functional roles to regions and networks described through the above methods).

The second main line of research will focus on the variability in prefrontal anatomy across individuals. How do differences in structure contribute to differences in individual behavior and cognition? Using large-scale datasets of brain and phenotypic information, we will investigate these correspondences, as they relate to the aforementioned subdivisions.

Finally, the malleability of prefrontal networks will be the topic of our third line of research. As our surroundings play a significant role in determining our individual behavior: how do environmental influences and recent experiences impact on functional brain architecture? To address this question, we will assess the impact of contextual priming and learning on prefrontal organization.
In this initial phase, we will begin data collection for the brain-phenotypic studies, as well data collection for a small cohort of highly characterized subjects for anatomical studies. The group members for this initial phase will include post-doctoral fellows with expertise in computational visualistics and surface-based and anatomical connectivity methodologies.

By providing a comprehensive connectivity-based map of the human prefrontal cortex, the research group "Neuroanatomy & Connectivity" aims to develop a wider framework with which to assess its relationship to phenotypic variability across individuals, and to investigate the impact of environmental contexts on the plasticity of these networks.
Human communication necessitates coherent and temporal integration of verbal and non-verbal (e.g. vocal, facial, gestural, body expressions) information. Such a complex process requires the dynamic formation of percepts that are updated in a given situational context and concurrently by an individual’s fluctuating internal state. However, the dynamic formation of percepts is costly, prone to conflict, and individual processing resources are limited. Therefore, mechanisms to efficiently allocate attention and to predict future input are necessary to reduce processing costs and conflict. We differentiate between agency-driven predictions that lead to the anticipation of percepts based on one’s own state and action and stimulus-driven predictions based on temporal, verbal, and non-verbal information. The primary goals of the group are (1) to specify the impact of prediction on sensory, multisensory, and integrative cognitive processes exemplified in human communication, (2) to define the neural networks supporting these processes, and (3) to understand the consequences of system breakdowns on mechanisms to predict future input in communication. We utilize behavioural, electrophysiological (event-related potentials and time-frequency analysis) measures and functional magnetic resonance imaging in this research with healthy young and aging populations and also with patients.

In a series of experiments, we have investigated the role of the cerebellum in sensorimotor-to-auditory forward predictions (5.9.1) to test whether forward predictions are domain-general. We further explored how temporal predictions (i.e. temporal regularity vs non-regularity) influence the perception of tone sequences in pre-attentive and attentive processing (5.9.2) to understand the contribution of a dedicated temporal processing system to temporal adaptation. The impact of prediction on the integration of multisensory non-verbal emotional information was tested to elucidate the precedence of visual over auditory communicative signals (5.9.3). In a complementary study, we tested the integration of verbal and non-verbal (vocal) emotional information in Parkinson’s disease patients with different motor symptom asymmetries to illuminate the specific contribution of a right lateralized cortico-subcortico-cortical system in the early integration of verbal and non-verbal emotional information (5.9.4). In the verbal domain, we investigated how predictive temporal cues such as metrical stress (the alternation of stressed and unstressed syllables) affect semantic expectancy and report that metric regularity facilitates the integration of words into a sentence context in a fronto-temporal network (5.9.5). Lastly, we explored whether listeners entrain to the metric structure of poems reflected by activation changes in sensorimotor networks involving the insula, basal ganglia and cerebellum, in limbic reward areas such as the anterior cingulate cortex and sustained attention networks (i.e. fronto-parietal interface) (5.9.6).
The cerebellum generates sensorimotor-to-auditory predictions: ERP lesion evidence

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Forward predictions are crucial in motor action (e.g. catching a ball, being tickled) but may also apply to sensory or cognitive processes (e.g. listening to distorted speech or a foreign accent). According to the “internal forward model”, the cerebellum generates motor-to-sensomotor sensory predictions of motor acts by applying a forward model (Wolpert, Miall, & Kawato, 1998, Trends Cogn Sci, 2, 338–347). These predictions simulate motor processes and prepare respective cortical areas for an upcoming motor event. Currently, there is very little evidence that a cerebellar forward model also applies to other domains, such as the sensory domain. Due to the reciprocal connections of the cerebellum to the auditory cortex, we hypothesized that the cerebellum also generates sensorimotor-to-auditory predictions relevant in auditory processing (Huang, Liu, & Huang, 1982, Brain Res, 244, 1–8; Storace, Higgins, & Read, 2011, J Comp Neurol, 519, 177–193). Utilizing the N100 suppression paradigm (Baess, Jacobsen, & Schröger, 2008, Int J Psychophysiol, 70, 137–143), we compared event-related potential (ERP) responses in the N100 to self-initiated and externally produced sounds. As sensory consequences of a self-initiated sound can be precisely predicted, self-initiated sounds should elicit a suppressed N100 response compared to externally produced sounds. If the cerebellum generates a sensorimotor-to-auditory forward prediction, patients with focal cerebellar lesions should not display a N100 suppression effect. Our results revealed that the N100 suppression effect was largely attenuated in cerebellar patients (Fig. 5.9.1). The finding suggests that the cerebellum forms sensorimotor-to-auditory predictions based on self-generated sounds, which extends cerebellar forward models to the sensorimotor domain.

Figure 5.9.1: ERP responses. (A) Direct comparison of healthy controls (black) and cerebellar patients (red). ERPs elicited in auditory-only condition (AOC; black solid line) and auditory-motor-corrected condition (ACC; black dotted line). (B) Group average of healthy controls (N = 11). ERPs elicited in auditory-only condition (AOC; black solid line) and auditory-motor-corrected condition (ACC; black dotted line). (C) Group average of patients (N = 11). ERPs elicited in auditory-only condition (AOC; red solid line) and auditory-motor-corrected condition (ACC; red dotted line).
The impact of temporal regularity on deviance detection

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In order to cope with dynamic changes in the environment, individuals have to adopt mechanisms responsible for the encoding, decoding, and evaluation of temporal structure. Such mechanisms may engage distinct automatic, or pre-attentive, as well as attention-dependent systems, involving cerebello-cortical and cortico-striato-thalamo-cortical circuits, respectively (Buhusi, & Meck, 2005, Nat Rev Neurosci, 6, 755–765). We used the high temporal resolution of the Electroencephalogram to explore a possible distinction between pre-attentive and attention-dependent temporal processing. In a first session, participants directed attention towards a muted video clip while they heard task-irrelevant oddball sequences consisting of equidurational frequent standard (600 Hz) and infrequent deviant (660 Hz) tones. In a second session, participants were asked to attend to the same oddball sequences, but to count the deviant tones. Two sequences differing in temporal structure were used, one isochronous, with tones separated by inter-stimulus-intervals of 600 ms, the other random, with tones separated by intervals chosen from a range between 200 and 1000 ms. This manipulation had no significant impact on a set of event-related potentials associated with pre-attentive processing of deviance, namely mismatch negativity (MMN), P3a, and reorienting negativity (RON). However, it did affect the amplitude of the P3b component associated with attentive processing of deviance, which was larger for isochronous relative to random temporal structure. These findings support the distinction of pre-attentive mechanisms involved in the encoding of temporal structure, and attention-dependent mechanisms involved in the evaluation and prospective use of temporal regularity to focus attention in time.

Figure 5.9.2: Attention session. Averaged EEG responses for standard (blue) and deviant (red) tones at two centro-parietal electrodes in the attentive session complemented by N2b and P3b scalp distributions for isochronous (A) and random (B) temporal structure. Difference waves and difference distributions contrast ERP effects for isochronous (blue) and random (red) temporal structure (C).
Early body–voice integration follows principles of multisensory integration

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Successful social communication draws strongly on the correct interpretation of others’ body and vocal expressions. Both can provide emotional information and often occur simultaneously. However, their interplay has hardly been studied. Using electroencephalography, we investigated the pattern underlying their neural interaction in auditory and visual perception. In particular, we tested whether this interaction qualifies as true integration following multisensory integration principles such as inverse effectiveness.

Emotional vocalizations were embedded in either low or high levels of noise and presented with or without video clips of matching emotional body expressions. In both high and low noise conditions, a reduction in auditory N100 amplitude was observed for audiovisual stimuli. However, the N100 peaked earlier in the audiovisual than the auditory condition only under high noise, suggesting facilitatory effects as predicted by the inverse effectiveness principle. Similarly, we observed earlier N100 peaks in response to emotional compared to neutral audiovisual stimuli. This was not the case in the unimodal auditory condition. Suppression of beta-band oscillations (15–25 Hz) primarily reflecting biological motion perception was modulated 200–400 ms after the vocalization. While larger differences in suppression between audiovisual and audio stimuli in high compared to low noise levels were found for emotional stimuli, no such difference was observed for neutral stimuli. This observation is in accordance with the inverse effectiveness principle and suggests a modulation of integration by emotional content. Overall, the results show that ecologically valid, complex stimuli such as concurrent body and vocal expressions are effectively integrated very early in processing. This integration process follows the principle of inverse effectiveness, and integration is modulated by emotional saliency.

Figure 5.9.3 Differential in high and low noise conditions in evoked and induced brain responses. In the top row, inter-trial coherence (left panel) and power spectrum (right panel) across all conditions one second after sound onset are depicted. In the bottom left panel, the N100 response in the high and low noise conditions is shown for audio and audiovisual stimuli. In the high noise condition only, a significant N100 peak latency reduction for audiovisual stimuli can be observed (** = p < .01, n.s. = not significant). In the bottom right panel, the difference in power change between audiovisual and audio stimuli is depicted separately for high and low noise stimuli and the different emotion conditions. Stronger difference in beta-suppression for high noise compared to low noise stimuli can be seen for anger and fear stimuli, but not for the neutral condition.
Motor symptom asymmetry matters: New evidence on emotional speech perception in Parkinson’s disease

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To date, the neural mechanisms underlying the perception of emotional speech are poorly understood and little investigated in Parkinson’s disease (PD). Furthermore, PD does not present a unitary disease profile, but can be differentiated by one of its central features, motor symptom asymmetry, with stronger dopamine depletion in the contralateral than the ipsilateral striatum. Early emotional salience detection in speech intonation is reflected in the P200 component of the event-related potential (ERP). This component is mediated by right superior temporal areas (STG/STS), with a possible bottom-up influence from subcortical structures such as the striatum. We therefore hypothesized that greater right-striatal dopamine depletion as evident in PD patients with predominantly left-sided motor symptoms may impair early emotional salience detection in speech. Therefore, we tested 22 PD patients without dementia or depression, 10 with left-dominant (LPD) and 12 with right-dominant (RPD) motor symptoms and 22 matched healthy controls in two ERP studies varying task demands (implicit/explicit). Intelligible and unintelligible speech was expressed in different emotional intonations. Results confirm that the LPD group showed P200 alterations. These were especially pronounced for disgust, but also happiness and anger in intelligible speech, while the perception of emotion in unintelligible speech proved to be largely intact. The results are corroborated by several significant correlations between the altered P200 pattern and left motor scores and asymmetry indices. Our findings suggest that PD should not be considered as a uniform disorder and support the notion that there may be a bottom-up influence from the right striatum on the right superior temporal cortex.

Regular speech rhythm facilitates semantic integration

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Speech is an inherently rhythmic phenomenon that unfolds in time. In speech comprehension, listeners exploit temporal information embedded in the speech stream to alter sublexical and lexical processing demands. In stress-timed languages, speech rhythm mainly consists of alternating stressed and unstressed syllables (called “metre”), which may result in perceptual regularity that allows the anticipation of the next speech event (Kotz & Schwarte, 2010). This anticipation may, in turn, influence the integration of spoken words into a sentence context.
We tested this possibility by investigating lexico-semantic integration as a function of semantic expectancy in metrically regular and irregular auditory sentence contexts with fMRI. Semantic expectancy modulated a classical fronto-temporal lexico-semantic network including the posterior superior temporal sulcus/middle temporal gyrus bilaterally and the left inferior frontal gyrus (IFG)/insula in the metrically irregular context. This activation pattern was reduced to left-lateralized IFG/insula activation in the metrically regular context. The latter data may result from facilitation and metric priming and provides first evidence that perceptual regularity (i.e. regular metre) influences the integration of words into a sentence context.

Figure 5.9.5 Left sagittal and axial view of the direct contrasts of semantically unexpected and expected words in sentences in the regular (blue) and irregular (orange) rhythmic context as well as a direct comparison of both contexts.

Poetic aesthetics are anchored in attentional, rhythmic, and emotional regulation systems

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Ever since early Greek antiquity, it has been believed that the metric structure of language exerts a strong, aesthetically pleasing effect on listeners and, at the same time, may also be persuasive and grab people’s attention. In the current fMRI experiment, we investigated whether the metric structure (i.e. the formalized ordering of syllable sequences) of German poetry leads to “aesthetic pleasure” and heightened attention in listeners. We did this by manipulating metric regularity and the rhyme scheme of 19th Century German poetry while partici-
participants judged the rhythmic regularity of the poems. Metric regularity enhanced activation in networks involved in sustained attention (inferior frontal gyri and parietal gyri), emotion regulation (anterior and mid cinguli) as well as rhythm processing (insulae, basal ganglia, and cerebellum), while metric irregularity led to stronger activation in the right superior temporal gyrus (rSTG). Rhyme coherence revealed stronger activation in a left cortico-subcortical network involving the inferior parietal gyrus, the basal ganglia, and the thalamus. The current results provide novel evidence that metric and rhyme features of poetry impact on attentional, rhythmic, and emotional regulation systems in listeners. In particular, regular metre seems to bind attention as observed in the activation of the “sustained attention” network. This in turn may facilitate poetry perception as discussed in “cognitive fluency” accounts (e.g. Reber, Schwartz, & Winkielman, 2004, Pers Soc Psychol Rev, 8, 364–382). According to these theories, such facilitation may be perceived as rewarding or pleasant.
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Connections between brain structures at different levels of hierarchy are a major determinant for the emergence of brain function. Therefore, studying connectivity in the brain is important for understanding the complex processes that make us think and feel.

The term “connectivity” can actually mean different things: (1) the influence functional activity in one entity (e.g. a cell, a cell population, or an entire brain area) exercises upon the activity in another entity (effective connectivity), (2) correlations between the time courses of activation in different brain areas (functional connectivity), and (3) the physical basis of the information transfer, such as axons or synapses (anatomical connectivity).

As we mainly work with the normal human brain, it is important to use methods that rely on non-invasively acquired data, such as MRI, EEG, or MEG.

In order to characterize effective connectivity, biologically inspired mathematical models for networks of neuronal populations are used. We investigate the dynamic behaviour of such models and find surprisingly complex and diverse phenomena, including chaos, which fit well to experimental data (6.1.1; Spiegler, Knösche, Schwab, Haueisen, & Atay, 2011). Moreover, we study spatially extended neural field models and find that we can mimic certain phenomena in visual perception and learning (6.1.2).

In order to bridge the gap between non-invasive electrophysiological measures (EEG and MEG) and models of intracranial activity, we use highly precise models of the human head, based on the finite element method (FEM). For EEG, modelling the skull is of particular importance. In a recent study, we systematically investigated different ways to account for the skull and derived recommendations for modelling (6.1.3; Dannhauer, Lanfer, Wolters, & Knösche, 2011).

For the non-invasive characterization of anatomical connectivity, and more specifically long-range fibre connections, diffusion-weighted MRI is the method of choice. Several research lines in our group deal with improving acquisition and analysis of such data. Here, we present achievements obtained in close collaboration with the Department of Neurophysics, based on ultra-high field and ultra-high resolution diffusion MRI. We demonstrate that it is possible to resolve complex fibre crossings, fibres entering the cortex, and fibre structures within the cortex (6.1.4; Heidemann, Anwander, Feiweier, Knösche, Turner, in press). Moreover, we demonstrate the functional relevance of such estimates of anatomical connectivity by showing that they predict behaviour (6.1.5; Forstmann, Anwander, Schäfer, Neumann, Brown, Wagenmakers, Bogacz, & Turner, 2010).
Modelling brain resonance phenomena using a neural mass model

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Stimulation with rhythmic light flicker (photic driving) plays an important role in the diagnosis of schizophrenia, mood disorder, migraine, and epilepsy. In particular, the adjustment of spontaneous brain rhythms to the stimulus frequency (entrainment) is used to assess the functional flexibility of the brain. We aim to gain deeper understanding of the mechanisms underlying this technique and to predict the effects of stimulus frequency and intensity. For this purpose, a modified Jansen and Rit neural mass model (NMM) of a cortical circuit is used. This mean field model has been designed to strike a balance between mathematical simplicity and biological plausibility. We reproduced the entrainment phenomenon observed in EEG during a photic driving experiment. More generally, we demonstrate that such a single area model can already yield very complex dynamics, including chaos, for biologically plausible parameter ranges. We chart the entire parameter space by means of characteristic Lyapunov spectra and Kaplan-Yorke dimension as well as time series and power spectra. Rhythmic and chaotic brain states were found virtually next to each other, such that small parameter changes can give rise to switching from one to the other. Strikingly, this characteristic pattern of unpredictability generated by the model was matched to the experimental data with reasonable accuracy (Fig. 6.1.1). These findings confirm the fact that the NMM is a useful model of brain dynamics during photic driving. In this context, it can be used to study the mechanisms of, for example, perception and epileptic seizure generation. In particular, it enabled us to make predictions regarding the stimulus amplitude in further experiments for improving the entrainment effect.

Dynamic switching between cortical states in visual cortex modelled using a mean-field approach

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Spontaneous switching between cortical states in the visual cortex of the cat was reported by Kenet, Bibitchkov, Tsodyks, Grinvald, & Arieli (2003, Nature, 425, 954–956). A succession of spatial activation patterns normally associated with visual input was observed even in the absence of external input. In this study, we used a
biologically realistic mean-field model together with the
heteroclinic channel theory proposed by Rabinovich,
Varona, Selverston, & Abarbanel (2006, Rev Modern Phys,
78, 1213–1265), to explain a mechanism of such a phe-
omenon.
Our model consists of Jansen & Rit (1995, Biol Cybern,
73, 357–366) neural masses distributed in 3 dimensional
space which anatomically and functionally mimic the
area V1 in the visual cortex. If we increase the strength
of inhibition, we can observe, even in the absence of ex-
ternal input, the activity patterns corresponding to the
preferred orientations (0° 22.5° etc.), which are very simi-
lar to the experimentally measured ones (Fig. 6.1.2). In
state space, the system evolves in a heteroclinic channel,
made up by the trajectories near a chain of saddle points
and associated unstable separatrixes.
We conclude that inhibitory connectivity plays the key
role as it governs the sequence of activation. Imposing
noise can introduce randomness into this sequence. Our
results demonstrate a potential mechanism for the rela-
tionship between evoked and spontaneous brain activity.

Figure 6.1.2  Activity patterns in the experimental and simulation conditions. Without any external stimulus, the simulated patterns (bottom row)
are very similar to the experimental ones (top row).

### Modelling of the human skull in EEG source analysis

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For EEG source localization and electrical impedance to-
mography, the conductivity profile of the skull is a par-
ticularly crucial model property, due to the electric blur-
ing effect, which can be related to the low conductivity
of skull tissue. It is widely known that the human skull
has a three-layered sandwich structure, where the mid-
dle layer (not equally thick everywhere) consists of soft
(spongy) bone, whereas the outer layers consist of hard
(compact) bone. We used $T_2$-weighted MR imaging and
conductivities for both types of skull tissue taken from
the literature to prepare a realistic volume conductor (reference) model of the head. In practice, this degree of
modelling accuracy is not used, and consequently, sim-
plicated skull models are applied. Thus, we evaluated the
impact of using simplifications on forward and inverse
solutions, through systematic simplification of the refer-
ence model. Local isotropic and anisotropic models (LIH,
LAH), where each skull location was modelled differen-
tly, and global models (IH, AH), where the skull was as-
sumed to be homogeneous, were compared to the refer-
ence model. In both cases, conductivity assumptions
were taken into account. Furthermore, we considered
sources in the entire brain and determined errors (RDM,
relMAG) both in the forward calculation and the recon-
structed dipole position (Fig. 6.1.3). Our results show that
accounting for the local variations over the skull surface
is important, whereas assuming isotropic or anisotropic
skull conductivity has little influence (see RDM, Fig. 6.1.3).
If local models cannot be used, simpler global models
with a considerably higher isotropic conductivity of 0.01
S/m (instead of the literature value of 0.0042 S/m) should
be used.
Benefits of 7T for tractography and connectivity analysis

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Diffusion MRI (dMRI) acquisitions for tractography and connectivity analysis are limited in the spatial and angular resolution in living humans. One possible way to increase the spatial resolution without sacrificing either image quality or angular resolution is to move to a higher magnetic field strength (7 Tesla). In the current study, we use an adapted Echo Planar Imaging (EPI) sequence with a combination of ZOOmed imaging and Partially Parallel Acquisition (ZOOPPA) together with a high performance gradient system. The method can produce high quality diffusion-weighted images with high angular resolution and very high isotropic spatial resolution of 1 mm and 800 µm. Optimized post processing using noise reduction and motion correction in combination with a complex local model using constrained spherical deconvolution allows the reconstruction of white matter fibre trajectories at ultra high spatial resolution. These data sets are particularly suitable for resolving complex and subtle fibre architectures, including fibre crossings in the white matter, anisotropy in the cortex, and fibres entering the cortex. Figure 6.1.4 shows the distribution of local fibre orientations in an axial brain section (A) with crossing fibre bundles in the white matter and radial anisotropy in the cortex. The high resolution allows streamline tractography to enter the cortex of the parietal lobe (B). The achieved spatial resolution of 800 µm shows unexpected anatomical details providing new insights into the finest anatomical structures, such as subcomponents of fibre bundles and intracortical fibres.
Cortico-striatal connections predict control over speed and accuracy in perceptual decision making


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When people make decisions they often face opposing demands for response speed and response accuracy. It is hypothesized that connections to the striatum or to the subthalamic nucleus (STN), respectively, modulate this behaviour. We conducted two experiments on perceptual decision making in which we used cues to vary the demands for speed vs accuracy. Behavioural data and mathematical model analyses confirmed that the cue selectively affected the setting of response thresholds. We used ultra high-resolution 7T structural magnetic resonance imaging (MRI) to locate the STN precisely (Fig. 6.1.5A). We then used 3T structural MRI and probabilistic tractography to quantify the connectivity between the relevant brain areas. The results showed that participants who flexibly change response thresholds have strong structural connections between the pre-supplementary motor area and striatum (Fig. 6.1.5B). In general, these findings show that individual differences in elementary cognitive tasks are partly driven by structural differences in brain connectivity. Specifically, these findings support a cortico-striatal control account of how the brain implements adaptive switches between cautious and risky behaviour.

Figure 6.1.5 Structural differences in brain connectivity predict individual differences in decision making. (A) The STN (arrows) can be localized precisely with 7T scanning. (B) Individual differences in tract strength between the right pre-SMA and right striatum are associated with flexible adjustments of the speed-accuracy tradeoff.
Cortical Networks and Cognitive Functions – Appendix

Congresses, Workshops, and Symposia


Degrees

Habilitation

Knösche, T. R. On the non-invasive reconstruction of the functional and anatomical basis for cognitive function. Technical University of Ilmenau, Germany.

PhD Thesis

Spiegler, A. Dynamics of biologically informed neural mass models of the brain. Technical University of Ilmenau, Germany.

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**Figure 6.1.1**

**Figure 6.1.3**

**Figure 6.1.5**
Recording magnetic fields from the human brain provides us with real-time fingerprints of brain activity. These magnetic fields are the direct and immediate consequence of the electrical currents resulting from neuronal or muscular activity. The methodological challenge in analyzing MEG/EEG data lies in the decomposition of the superimposed fields that are measured. In the past, we mostly concentrated on decomposition via localization using realistically shaped head models (Boundary Element Method) and source spaces (cortical layer). During recent years, we have placed additional emphasis on extending our methodological toolkit: First, time-frequency analyses have been conducted at the sensor level and at the even more attractive cortical level utilizing beamformer spatial filters. Second, we have continued using dynamic causal modelling applying SPM-DCM as a method to investigate brain networks. Third, multivariate pattern classifications were performed on the basis of sensor level and cortical level estimates taken from experiments on higher cognitive processes. All this work was done in close collaboration with colleagues from this Institute (in particular, the Department of Neuropsychology, the Cortical Networks and Cognitive Functions Unit, the Max Planck Research Group Auditory Cognition) and the University of Leipzig. As in the past, the main focus of the psychological experiments we conducted was on language processing. Utilizing the MMN design, we compared the influence of basic acoustic deviations and syntactical violations. Syntactical violations evoked brain activity which was significantly more anteriorly distributed than the activity resulting from acoustic deviations (see 2.1.6 & 2.1.7, Department of Neuropsychology). MEG sensor data from the same experiment was also analyzed using multivariate pattern classification methods and revealed that the early activity (before 200 ms) nicely generalizes across individuals (6.2.1). In a second MEG study, we investigated the maturation process of early auditory evoked responses, recording data from children at about ten years of age and young adults. We showed that the children already utilize rather mature frequency-dependent refractory effects at the N100 (6.2.2). In the third study, subjects heard a number of digits under auditorily adverse conditions. We demonstrated that alpha power increases with memory task difficulty (more digits to memorize) and with acoustic task difficulty (more adverse conditions). Furthermore, these two increases were separately assigned to different brain regions (6.2.3). The fourth study investigated attention shift between two sensory domains. Subjects had to direct their attention either to the visual or the auditory part of the stimulation. Our results support the view of modality-specific attentional resources.
Auditory perception and syntactic cognition: Brain activity-based decoding within and across subjects

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In neurocognitive research, it is an open question whether cognitive processes show a consistent functional organization across individuals similar to sensory processes. This magnetoencephalographic (MEG) study sets out to answer this question in the auditory processing domain, looking at sensory processes in auditory space and at cognitive processes (syntax) in auditory language. In particular, it was asked whether the brain states of early syntactic and auditory-perceptual processes can be decoded from single trial recordings using a multivariate pattern classification approach, and whether these early neural activation patterns reflect a functional organization which largely generalizes across individuals or is subject-specific.

On this basis, decoding was carried out within and across subjects in two classifications in which the neural patterns elicited by correct sentences were classified with patterns elicited by syntactically incorrect sentences (Syntax) or with patterns elicited by correct sentences including an unexpected interaural time difference change (Auditory space).

The results revealed highest decoding accuracies and the most significant patterns over the temporal cortex areas for both classification types (Fig. 6.2.1). Importantly, the magnitude as well as the spatial distribution of decoding accuracies for the early neural patterns were very similar for within- and across-subject decoding. At the same time, across-subject decoding suggested a hemispheric bias, with the most consistent patterns in the left hemisphere.

The present data thus show that not only auditory-perceptual processing brain states, but also cognitive brain states of syntactic rule processing can be decoded from single trial brain activations. Moreover, the findings indicate that the neural patterns evoked by syntactic cognition, on the one hand, and auditory space processing, on the other, reflect a functional organization which is highly consistent across individuals.

Figure 6.2.1 Within- and across-subject decoding grand average for the syntax and the auditory space classification. The left column of each classification shows the decoding accuracy topographies. The right column of each classification displays the Bonferroni-corrected z-score maps for the decoding accuracies at each sensor position against the overall mean of all other sensor positions (with z-scores ranging from 1.645 ($p = 0.05$) to 3.09 ($p = 0.001$)).
Obligatory auditory responses in school-age children

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In adults, simple sinusoidal tones evoke the P1-N1-P2 complex. In children, however, a large positivity at the N1 latency (≈100 ms, P1) and a later negativity (≈200 ms, N2) are observed in similar paradigms. Previous research has shown that the obligatory auditory responses specifically N1 do not reach an adult-like shape before adolescence.

The present study aimed to investigate the neural sources of obligatory responses in children (9 to 10 years of age) and compare them to adults. To this end, we measured MEG and EEG and presented an oddball and a random control block (Jacobsen & Schröger, 2001, Psychophysiology, 38, 723–727). In doing so, we were able to compare a frequently repeated sinusoidal tone of a certain frequency with an identical tone, randomly interspersed between tones of different frequencies.

Consequently, this paradigm allowed us to not only investigate obligatory responses but additionally N1 refractoriness effects. We thus investigated the hypothesis that the N1 may in fact be present before adolescence, although hidden in the strong P1 and N2.

Source analysis on the MEG data revealed rather similar source activity of the obligatory responses in children and adults. More importantly, using EEG, we detected an N1 effect in children that was similar in amplitude and latency to the effect observed in adults. This is clearly at odds with the existing literature. Consequently, we conclude that the frequency-specific component of the N1 is mature at the end of the first decade of life. This suggests that the maturation and function of the N1 need to be reconsidered.

Figure 6.2.2 Event-related responses in both age groups (adults – left; children – right). Top row: Time courses of the MEG localization in defined regions of interest (covering the primary auditory cortex and superior temporal gyrus) and grand average source localizations of age-specific obligatory responses in the right hemisphere of the random condition. Bottom row: EEG difference waves (random minus repetitive) that show the N1 effect in both age groups. The EEG topography of the N1 effect is also displayed.
Auditory memory load and signal degradation: “Joint effort” is reflected in enhanced Alpha power

Obleser, J.¹, Wöstmann, M.¹, Hellbernd, N.¹, & Maess, B.¹

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Recent assumptions suggest that cortical alpha oscillations (~8–13 Hz) are an effective means to control the timing of neuronal firing (functional inhibition; e.g. Jensen & Mazaheri, 2010, Front Hum Neurosci, 4:186). In line with these predictions, alpha power is enhanced during memory retention. But how specific to memory load is the alpha enhancement? What about additional challenges to listeners, e.g. degraded speech, and could alpha enhancement serve as a more general measure for cognitive load in audition? In an auditory Sternberg paradigm, we parametrically varied memory load (set size of 2, 4, or 6 auditorily presented digits) and signal degradation (noise-vocoding in 16, 8, or 4 bands) and measured the magnetoencephalographic response (N = 16; time-frequency analysis of gradiometer data; wavelet convolution; time–frequency–channel cluster statistics, followed by beamformer source localization).

During the retention interval, we found a significant monotonic alpha enhancement at centro-parietal sensors, in two main effects of set size (more memory load) and degradation (worse signal quality). Alpha enhancement during retention was positively correlated with the reaction time observed in response to the ensuing probe digit. Source projection of the overall alpha power during retention indicated a right-hemispheric parieto-temporal cortical origin (Fig. 6.2.3; bottom right panel). More specifically, however, parametric group statistics on the source reconstructions showed that the anterior cingulate cortex activity increased monotonically with set size, while the posterior cingulate cortex activity increased monotonically with degradation.

In sum, our results suggest a separation of load-specific from more unspecific alpha-band effects in response to the challenges in adverse listening. This bears relevance to the aging and hearing-impaired brain and provides a general measure for effortful listening.
Steady-state responses track attentional shifts towards audition and vision

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Noisy environments may require a flexible allocation of neural processing resources to input from a specific sensory modality in order to perform a given task. The mechanism mediating this allocation is termed intermodal attention. Up to now, it is not well understood how intermodal attention modulates multisensory processing within primary sensory cortices. On the one hand, findings of functional imaging studies suggest that attention to a particular modality enhances activity in corresponding cortices, reflecting facilitated processing, while activity in other sensory cortices is suppressed. This is thought to indicate redistribution of limited supramodal attentional resources. On the other hand, behavioural and physiological data suggest that attentional resources are deployed independently for each sensory modality. To provide a new perspective to this ongoing controversy, we studied the effect of shifts of intermodal attention on the amplitude of a 40 Hz auditory and a 6 Hz visual steady-state response (SSR) that were elicited by continuous stimulus streams in human MEG/EEG. After a baseline period at the beginning of each trial, participants were cued to attend to either the visual or the auditory modality to detect specific target stimuli. Attention to the auditory or the visual stream enhanced amplitude of the corresponding SSR relative to baseline. Our results demonstrate that intermodal attention facilitates processing of a stimulus that is presented in the modality currently attended to in the presence of concurrent but task-irrelevant information from another sensory modality. Moreover, the processing of unattended stimuli was not suppressed in respective corresponding primary cortices. Thus, we argue in favour of a modality-specific deployment of attentional resources.

Figure 6.2.4 Experimental paradigm and results. (A) Schematic trial time course. Auditory and visual stimulus streams were presented concurrently for 6500 ms. 40 Hz amplitude-modulated multi-speech babble served as the auditory stimulus. The visual stream of letter sets was presented with a rate of 6 Hz. In both streams, words/pseudowords were occasionally included (not shown for the auditory stream, note the presentation of the German word BAL-KEN, English BEAM, in the stream of letter sets). After a variable baseline period, participants were cued to attend to either the auditory (A) or visual (V) stream to solve a demanding task, namely to report occurrences of word stimuli (active period).

(B) Scalp topographies show distributions of attentional modulation indices (AMI, scaled in arbitrary units, a.u.). AMIs were calculated as the difference of active period and baseline SSR amplitude divided by the sum of active period and baseline SSR amplitude for both stimulation frequencies and for EEG and MEG gradiometer data, separately. A positive AMI indexes amplitude enhancement relative to baseline and, thus, facilitated stimulus processing. Negative values index suppression. Bar graphs show AMI values averaged over respective sensor clusters (indicated by black dots in scalp topographies; AMIs were averaged over all electrodes for 6 Hz EEG-VSSR amplitudes). Error bars show standard error of the mean. Black asterisks indicate significant AMI deviations from zero. Red asterisks below bars indicate significant differences between respective AMIs. General alpha level for all comparisons performed was $p < 0.05$. Grand average spectra show SSR amplitudes during the active period. Peaks correspond to the stimulation frequencies (black line = attend A, grey line = attend V).
Degrees

PhD Thesis


Publications

Book


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The development of magnetic resonance imaging (MRI) methods for the quantitative characterization of the human brain has continued to be a primary focus of our research. This is now complemented by an additional interest in aspects of image-processing and applications of brain mapping that allow the study of working memory and attention.

Work related to imaging physics includes both hardware and MRI pulse-sequence issues. At the hardware end, a simple yet efficient modification of the well-known shielded loop—an integration of a secondary floating shield—led to the design of a coil for labelling the brain-feeding arteries at 7T (6.3.1). Perfusion imaging by arterial spin labelling has been a rewarding subject for many years and was recently expanded by measurements of arterial blood volume (6.3.2). More oriented towards application was a comparison of acquisition schemes for functional MRI (fMRI) with auditory stimuli, yielding a marked sensitivity advantage of the interleaved silent steady state technique (6.3.3). With regard to fMRI applications, two projects focussed on cognition. In particular, the functional decomposition of brain regions involved in forming decisions on degraded percepts (6.3.7), and the release of information from visual short-term memory (6.3.8) were studied in detail.

Parametric tissue characterization was employed as a biophysical approach to investigate the brain’s microstructure. A thorough analysis of magnetization transfer in human white matter revealed an unexpected orientation dependence, which is explained by the dipolar lineshape of the liquid-crystalline lipid bilayers forming the myelin sheath (6.3.4). Analysis of parameters characterizing water diffusion in the corpus callosum demonstrated a correlation with body mass index, which might be associated with axonal reorganization and/or myelin changes (6.3.5). Interestingly, such effects were more pronounced in women than in men. Finally, a versatile technique for the rapid mapping of metabolic information was introduced, which utilizes centre-out spatial encoding and template-based phase correction for echo-planar-type spectroscopic imaging (6.3.6; funded through the Marie-Curie Network “FAST”).

Finally, we have enjoyed fruitful collaborations within the Institute, with Departments of the University of Leipzig, and with colleagues at Charité and from Aberdeen, Bern, Cincinnati, Lyon, Münster, Oxford, Paris, Prague, Duke, and Oregon Health and Science University.
A double-shielded label coil for continuous arterial spin labeling at 7T

Driesel, W.¹, Mildner, T.¹, Schäfer, A., Müller, R.¹, & Möller, H. E.¹

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Recently, we proposed a pair of shielded loop coils for continuous arterial spin labeling (CASL) at the human neck at 3T (Hetzer et al., 2009, JMRI, 29, 1414–1424). At frequencies above 150 MHz, this concept becomes impractical because capacitive tuning is no longer possible. This problem can be effectively addressed by adding a floating secondary shield. The coil design consists of a perpendicular pair of shielded loops made of 50 Ω, 3.6 mm-diameter semi-rigid cable with a 1 mm gap opposite the feed point. The secondary shield covering the gap was made of heat-shrink tubing and copper foil on the outside. It acts as a capacitor and shifts the impedance of the circuit towards inductive behaviour. Radiofrequency (RF) electric fields near the gap are shielded. By adjusting the phase shift between the currents in both loops, different excitation modes are obtained. Bench-top measurements yielded a low susceptibility to different loading conditions. Simulations and initial phantom experiments indicated a fairly symmetric distribution of the RF transmission field with sufficient amplitude for CASL at the expected positions of the carotid and vertebral arteries. Lowest specific absorption rates were achieved with the ‘Maxwell mode’ consistent with previous 3T results.

Figure 6.3.1 (A) Photograph of the labelling coil for the 7T CASL experiments, with two perpendicular loops (6-cm loop diameter, 7-mm thick polypropylene insulation), which are attached to the neck by a Velcro strip. (B) Schematics of a single loop of the labelling coil with a matching network consisting of a variable matching capacitor $C_M$ (3.5 pF) and tuning and termination capacitors $C_T$ (14 pF). A floating secondary shield covers the gap of the shielded loop and allows capacitive tuning at 292.2 MHz required for 7T MRI.

Absolute quantification of arterial cerebral blood volume

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Magnetic resonance imaging of inflow vascular-space-occupancy with dynamic subtraction (IVASO-DS) permits quantification of the arterial cerebral blood volume (aCBV). It is based on the acquisition of pairs of images, with and without nulling of the signal from arterial blood at the inversion time, $T_I$ (Donahue et al., 2010, JCBFM, 30, 1329–1342). In the current sequence modification, flow-weighting (FW) gradients along the $z$-axis were implemented. Without FW, hot spots of artificially increased aCBV values appear at short and disappear at long $T_I$s. This is explained by rapid inflow of non-inverted magnetization in large arteries, which partially replaces the inverted magnetization (i.e. reducing the estimated aCBV values) for long $T_I$s. Such unwanted signal contributions are eliminated by FW, which suppresses signal from arteries with vessel diameters exceeding 0.3 mm and effectively reduces spurious regional variability in the aCBV maps. The average aCBV in cortical grey matter obtained with the longest $T_I$ and FW was 0.8 ml blood/100 ml. The improved maps permit detection of subtle regional differences of the inflow characteristics (e.g. between the putamen and thalamus), which are consistent with known inter-regional differences in the cerebral perfusion pressure and arterial transit time.
Comparison of different fMRI acquisition schemes for investigating the brain response to music

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Auditory experiments with functional magnetic resonance imaging (fMRI) are limited by acoustic noise produced by the rapid switching of magnetic field gradients. Therefore, sparse temporal sampling (STS) with a long repetition time is often used to achieve stimulus presentation with minimal scanner noise. A recent development is the interleaved silent steady state (ISSS) technique, which permits the acquisition of several volumes between auditory trials while the magnetization is kept in a steady state. For further evaluation of the performance of different techniques, four different fMRI sessions of equal duration were compared including continuous axial and sagittal scanning, STS, and ISSS acquisitions. The stimulus selection comprised joyful instrumental tunes and their manipulated reversed dissonant counterparts. Significant brain activity differences between non-manipulated and manipulated music were observed in the primary auditory cortex with all schemes. Further activation was revealed bilaterally in the hippocampal region with the ISSS protocol. This activation was also observed with STS; however, at substantially reduced sensitivity due to the limited number of volumes. The ISSS approach combines advantages of sparse techniques with improved temporal sampling and appears advantageous for fMRI with auditory stimulation.

Figure 6.3.2 Quantitative maps of aCBV in ml blood/100 ml obtained in a healthy human volunteer without (A, B) and with FW (C, D) at a short inversion time (TI = 839 ms; A, C) and long inversion time (TI = 1143 ms; B, D).

Figure 6.3.3 Coronal and sagittal slices showing group results of significant differences between presentations of non-manipulated and manipulated music for all acquisition protocols. Besides consistent activations in the left and right primary auditory cortex with all protocols, ISSS acquisition yields activations in the left and right hippocampal formation, which persist after correction for multiple comparisons both on the cluster level and on the peak level (p < 0.05, FWE-corrected) (from K. Müller et al., 2011.).
Orientation effects in magnetization-transfer imaging of human white matter

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Information about macromolecular structures, such as the myelin sheath, can be obtained from magnetization transfer (MT) between highly mobile tissue water and semi-solid macromolecules (proton pools ‘a’ and ‘b’, respectively). A crucial step in quantitative MT imaging is the selection of a radiofrequency (RF) absorption lineshape for the semi-solid pool. At first glance, the widely accepted super-Lorentzian lineshape is plausible because it is attributed to liquid-crystalline lipid bilayers forming the myelin sheath. Surprisingly, the super-Lorentzian linewidth (expressed as a relaxation time $T_{2b}$) shows a distinct correlation with the polar angle, $\Theta$, of white matter fibre bundles in the external magnetic field, $B_0$. An explanation is obtained by revisiting properties of the super-Lorentzian lineshape, which results from a superposition of Gaussian lines. However, this derivation assumes an isotropic distribution of bilayers in the voxel of interest—a condition that is not met for large fibre bundles. We derived a novel lineshape for bilayers wrapped around oriented axons in a fibre bundle. It resembles features of a super-Lorentzian at $\Theta > 35^\circ$ but becomes “Gaussian-like” below this threshold. Additional consideration of a slightly imperfect fibre alignment leads to a striking consistency between our model and experimental MT data.

Gender-specific correlation between body weight and white matter microstructure

Müller, K.¹, Anwander, A.¹, Möller, H. E.¹, Horstmann, A.¹, Horstmann, J.¹, Busse, F.², Mohammadi, S.³, Schroeter, M. L.¹,²,³, Stumvoll, M.², Villringer, A.¹,²,³, & Pleger, B.¹,²

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Several studies have shown an association between obesity and brain structure. As women are more susceptible to obesity than men, it seems plausible that neural correlates also differ. Employing diffusion-weighted magnetic resonance imaging and tract-based spatial statistics, we found gender-based differences in the dependence between parameters of elevated body weight (body mass index, BMI; serum leptin level) and white matter (WM) microstructure. With increasing BMI, the axial diffusivity, a putative marker of axonal integrity, decreased in the corpus callosum in women and men, suggesting that obesity might be associated with axonal reorganization. Further changes with elevated body weight, namely, a negative correlation with the fractional anisotropy (FA)
and an increase in the radial diffusivity, suggesting myelin changes, were only found in women. Overall, similar changes in diffusion parameters are known to occur in the aging brain, which might indicate accelerated WM aging in obese subjects. Our observations also advocate the need to consider changes related to body weight in investigations of brain structure based on diffusion data. In addition, studies on obesity should account for gender-related differences.

Figure 6.3.5 Gender-specific correlation between FA and body weight using BMI (A) and serum leptin level (B). Women (top row) showed a negative correlation in the entire corpus callosum (p < 0.05, corrected), whereas no similar correlation was obtained for men (from K. Müller et al., 2011.).

Rapid metabolite mapping with “Exorcycled SCEPSIS”

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Echo-planar techniques permit the simultaneous encoding of spatial and spectral information and, hence, fast spectroscopic imaging. A novel modification is the Segmental Centre-out Echo-Planar Spectroscopic Imaging Sequence (SCEPSIS). With SCEPSIS, two or more segments of k-space are sampled along centre-out trajectories and combined after a template-based phase correction. This achieves a very short effective echo time with a robust Cartesian sampling scheme and mitigates blurring associated with the convolution of spectral and spatial information. The technique is fully compatible with efficient phase cycling schemes, such as Exorcycle, to eliminate spectral Nyquist ghosts. Spectral dwell times of less than 2 ms for 1H spectroscopic imaging at 3T are sufficient for adequate sampling of the resonances from residual water (4.7 ppm) and from methyl groups of mobile lipids (0.9 ppm) without aliasing. With a nominal voxel size of 5 ml, quantification of glutamate was achieved with Cramér-Rao lower bounds of less than 15 % within 1 min. The inherent segmentation capabilities permit a high degree of flexibility in trading temporal for spatial resolution for optimum adjustment to the specific task.

Figure 6.3.6 (A) Reference image and mosaic display of SCEPSIS data obtained in a healthy volunteer after 2.54 min. Residual fat signals visible in the left column are due to insufficient outer-volume suppression in the presence of chemical-shift displacement. (B) Results for a centre voxel (marked in blue) of the same data set after 5.37 min.
Perceptual decision making in the human brain

Cardoso-Leite, P.¹, Waszak, F.², & Lepsien, J.¹

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To disentangle contradicting assumptions about brain areas involved in perceptual decision making, we developed a paradigm asking participants whether a 9 s stimulation contained a face or a house. We hypothesized that decision-related processes show a sustained response during the task, whereas preparation-related areas yield transient responses at its beginning or end. The activation pattern at task onset is strikingly similar to that observed in previous studies, suggesting that the left dorsolateral prefrontal cortex (lDlPFC) is not involved in decision formation per se but rather in preparing the brain for the upcoming task. Participants’ individual discrimination performance predicted the response in the fusiform face areas (FFA) and parahippocampal place areas (PPA) but not in the lDlPFC and right anterior insula. Activity increased in the left FFA and right PPA when perceiving a face or a house, respectively, suggesting that these areas are part of the decision process rather than “blind” sensors transmitting signals to higher areas. Finally, the FFA and PPA showed increased functional connectivity with the right inferior parietal cortex, a region whose response could predict perceptual performance in detecting both faces and houses. We suggest that the FFA and PPA, under the top-down control of parietal and frontal areas, play an important role in forming decisions.

Neural consequences of short-term forgetting in the intraparietal sulcus

Trapp, S.¹, & Lepsien, J.¹

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Many recent fMRI studies have examined neural systems involved in active or intentional forgetting. However, little is known about neural processes underlying passive forgetting and, more specifically, the releasing of information from short-term memory that is no longer relevant. We developed a design that allows us to probe for brain areas showing reduced activity after a piece of briefly memorized information could be discarded as irrelevant. In a visual short-term memory (VSTM) task, the amount of information subjects had to memorize was varied (3, 4, or 6 items). A cue during the delay period asked subjects to select just one item for further maintenance, whereas the other items could be forgotten (Condition A). This was compared to trials where subjects were required to memorize all items (Condition B). The right intraparietal sulcus was identified as a region that not only showed increased activation according to the amount of VSTM information in condition B, but further demonstrated a significant reduction in activation in condition A. This study offers first insights into the neural consequences of the act of releasing irrelevant information from short-term memory.
Figure 6.3.8 (A) Contrast for an ordinal interaction. The right intraparietal sulcus shows both a parametric increase of activation for condition B ("No Forgetting") and a reduction in activation for condition A ("Forgetting"). The statistical maps are thresholded at $p < 0.05$ (FWE corrected). (B) Parameter estimates (with SEM) for sphere around the right intraparietal sulcus (radius: 3 mm).
Congress, Workshops, and Symposia


Degrees

PhD Theses

2010 Dukart, J. Contribution of FDG-PET and MRI to improve understanding, detection and differentiation of dementia. University of Leipzig, Germany.

Hetzer, S. Perfusionsbildgebung des menschlichen Gehirns in hoher räumlicher und zeitlicher Auflösung [Perfusion imaging of the human brain in high spatial and temporal resolution]. University of Leipzig, Germany.

Awards


Dukart, J., Müller, K., & Schroeter, M. L. Hans Heimann Prize. German Association for Psychiatry and Psychotherapy (DGPPN), Germany.

2011 Möller, H. E. Magna Cum Laude Award for his EPOS Exhibit entitled “3D imaging of pulmonary perfusion using infusion of hyperpolarized 129Xe into blood”. 28th Annual Scientific Meeting of the European Society for Magnetic Resonance in Medicine and Biology (ESMRMB), Leipzig, Germany.
Published Papers


Patents 2010/2011


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Department of Psychology: Cognition and Action

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Professor Dr Wolfgang Prinz

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Dr Pamela Baess (*)
Dr Miriam Beisert (née Lepper) (*)
Emily S. Cross, PhD (1) (*)
PD Dr Moritz M. Daum (**)
Dr Roman Liepelt (*)
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List of Employees

Max Planck Fellow Group “Attention and Awareness”

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Former Senior Researcher

Professor Dr John-Dylan Haynes
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(**) Left the Department during 2010/2011
7.1
Department of Psychology: Cognition and Action

The former Department of Psychology came to a close in September 2010 when Wolfgang Prinz retired. Accordingly, the majority of associated researchers left the Institute around that date, and most experimental projects had to be concluded. However, some research activities have continued at various places. On the one hand, former researchers have carried on their previous work in new places and positions, finishing their Leipzig projects and publishing major outcomes. On the other hand, some research activities have been continued in the Institute beyond the closing date of the Department. One major such activity pertains to the former "Baby Lab" which has now been established as a Research Group on "Infant Cognition and Action" for two years. This group is headed by Moritz Daum, with Wolfgang Prinz as a close collaborator (for report, see Chapter 5.5).

Other ongoing activities pertain to novel projects, both experimental and theoretical. Current experimental projects focus on joint action and task sharing, addressing the representational underpinnings of dyadic interactions in social interference and coordination paradigms. These studies are reported below.

Parallel to ongoing experimental work, two major theoretical projects have come to a close during the reporting period. The first project addresses a theoretical framework for understanding the social roots of agency and intentionality. This framework aims to merge cognitive science representationalism with social science constructivism (monograph authored by Wolfgang Prinz). The second project addresses major approaches to the emergent field of Action Science, providing an overview of the current theoretical and methodological landscape of that field (book with contributions by leading authorities from the field, edited by Wolfgang Prinz, Miriam Beisert and Arvid Herwig as editors).
The role of the stimulus dimension for referential coding in the go-nogo Simon task

Dolk, T.1, Hommel, B.2, Prinz, W.1, & Liepelt, R.1,3

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Many activities we perform in daily life are carried out together with other people. But how do we mentally represent other people's actions and how does this affect our own behaviour? One of the most prominent paradigms that has been developed to investigate joint action is the joint Simon paradigm in which two individuals share one task that is commonly used in the standard Simon paradigm. The typically observed stimulus-response compatibility effect in jointly interacting individuals—known as the joint Simon effect (joint cSE)—has been considered a marker of action and/or task co-representation. Recent findings, however, challenge the co-representation account, suggesting that the joint cSE may result from salient events that provide a reference for spatially coding one's own action (Dolk et al., 2011). To further clarify what the notion of saliency means, what it refers to, and how it might account for the cSE in general, we manipulated the salient nature of reference-inducing events in the response-dimension. By implementing a salient non-social “action” event (a moving object) in the alternative response dimension of an auditory go-nogo Simon task, we showed that a cSE can be induced under solo conditions (Fig. 7.1.1). We take these findings to suggest that any salient, attention-attracting event may serve as a spatial reference for the actor and/or his/her response. Accordingly, in contrast to the (social) co-representation account, we suggest that (spatial) referential coding plays an important role in the emergence of the cSE.

Figure 7.1.1  Experimental design and results. Upper panels show the within-subjects design of the “Object present” and “Object absent” conditions, which were counterbalanced across subjects. The lower panel shows the mean reaction time as a function of the implemented object (Cat present, Cat absent) and spatial stimulus–response compatibility. Error bars represent standard errors of the mean differences. * p < 0.05, *** p < 0.001.
The role of the response dimension for referential coding in the go-nogo Simon task

Dolk, T., Liepelt, R., Hommel, B., & Prinz, W.

1 Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany
2 Department of Psychology, Junior Group “Neurocognition of Joint Action”, Westphalian Wilhelm University Münster, Germany
3 Cognitive Psychology Unit, and Leiden Institute for Brain and Cognition, Leiden University, The Netherlands

Attempts to answer the question of how we mentally represent one’s own and other people’s actions have inspired a great deal of research in recent decades. However, although bottom-up and top-down manipulations of the joint go-nogo Simon effect (joint cSE) provide striking evidence of a crucial role of the response dimension, surprisingly little is known about the influence of the stimulus dimension. To this end, we developed a cross-modal go-nogo Simon task, which allowed us to manipulate the saliency of the response- and the stimulus-dimension within a single study. Participants performed an auditory-visual go-nogo Simon task by exclusively responding to their assigned modality (either auditory or visual) in the presence (joint condition) or the absence (single condition) of a co-actor. Results showed reliable cSEs in both the single and the joint condition (Fig. 7.1.2), suggesting that the cSE-inducing event does not need to share the modality with the target stimulus. We therefore conclude that the task-relevance of the reference-inducing event does not matter, provided it is sufficiently salient.

Taking both parts together, we conclude that the cSE occurs whenever agents code their own action as left or right in reference to another salient social or non-social event in the stimulus and/or response dimension. In line with the low-level feature binding framework proposed for the joint cSE recently (Liepelt, Wenke, Fischer & Prinz, 2011), the present findings suggest referential coding to be a crucial mechanism underlying the cSE.

Developmental vision determines joint action control

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3 Department of Psychology, Justus Liebig University Gießen, Germany

Vision plays a crucial role in defining external reference frames to organize and optimize action control. While recent findings showed that developmental vision fundamentally changes the default use of reference frames from anatomical – congenitally blind – to external coordinates – late blind and sighted (Röder, Kusmiercz, Spence, & Schicke, 2007, PNAS, 104, 4753–58), surprisingly little is known about the role of vision in jointly interacting
individuals. Here, we tested whether developmental vision also changes referential framing during joint action. To that end, pairs of congenitally blind, blindfolded sighted, and seeing individuals (all groups matched in terms of age, gender, and handedness) performed an auditory joint go-nogo Simon task in a crossed and uncrossed hand condition. Results showed joint go-nogo Simon effects (joint cSEs) in all groups when participants’ hands were uncrossed. Responses were significantly faster when target stimulus and assigned response corresponded as compared with when they did not. More importantly, when performing the joint go-nogo Simon task with crossed hands, the joint cSE disappeared in the congenitally blind, but not in the blindfolded or seeing groups (Fig. 7.1.3). Whereas the compatibility of stimulus-response location led to faster responses in the blindfolded sighted and seeing irrespective of hand position, this facilitation effect disappeared in congenitally blind people when hands were crossed.

Based on recent findings, we take this result to suggest that congenitally blind individuals automatically represent spatial information in an anatomical reference frame (e.g. with respect to their hand). Under crossed-hand conditions, this representation needs to be recoded in external coordinates, leading to prolonged reaction times. Sighted people, in contrast, preferably code space by using an external reference frame which is unaffected by positional changes of the effector. Extending previous findings, the present results imply that developmental vision determines the reference frames not only in individual but also in joint action control.

![Figure 7.1.3](image-url)

**Figure 7.1.3** Mean reaction time as a function of condition (“Hands uncrossed,” “Hands crossed”) and spatial stimulus–response compatibility (compatible, incompatible). (A) Congenitally blind vs sighted and (B) congenitally blind vs blindfolded individuals. Error bars represent standard errors of the mean differences. n.s. not significant, *p < 0.05, **p < 0.01, ***p < 0.001.

### Investigating characteristics of non-rhythmic interpersonal coordination

**Jung, C.¹, Holländer, A.¹, Müller, K.¹, & Prinz, W.¹**

¹ Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

In recent years, researchers have tried to understand the mechanisms of interpersonal coordination (e.g. two people dancing or pitching a tent together) in two lines of research. Some have attempted to explain spontaneous non-intentional interpersonal coordination in terms of the behavioural dynamics perspective—this means individuals are seen as neural-based behavioural oscillatory systems that are coupled by perceptual information. Researchers taking this perspective used rhythmic coordination tasks and focussed on frequencies and phase transitions. Others have explained instructed intentional interpersonal coordination in terms of joint action—this means individuals coordinate with each other to achieve a common goal. Research from this perspective used non-rhythmic everyday actions and focussed on movement parameters or brain activity. Other paradigms fall somewhere in between spontaneous and intentional coordination: In these there is no requirement to coordinate with a co-actor, although it would be natural to...
regard the task as a common task. Such a technique was used for the experiments described here. An important problem is how individuals manage to achieve extremely precise action coordination in time while performing non-intentional, non-rhythmic everyday actions. In this project, we developed a new method that was devised to quantify the strength of interpersonal coordination in a discrete, non-rhythmic task. We adopted a classic bimanual reaching paradigm to establish a dyadic version of this task in a way that each of two participants was asked to perform the task of either the left or the right hand (Fig. 7.1.4.1). The experimental procedure was as follows: An imperative stimulus informed the participants about the goal of their upcoming reaching movement and also about whose turn it was. Some trials were a "go" for one of the two participants and a "nogo" for the other; other trials were a "go" for both participants. Information about whose turn it was (who) and about the nature of the task (what) was given. In one experiment, S1 defined who and S2 what; in a second experiment, it was the reverse. In a third experiment, information about who and what was given at S1, and S2 was a simple go signal. This design allowed us to determine the conditions under which indications of interpersonal coordination emerged. Such indicators were taken from well-known strong effects found in the classical individual bimanual task like action alignment, immediate time alignment, and general time alignment. Action alignment, measured as the reaction time (RT) difference between symmetric and asymmetric movement patterns, reflects interference at the planning level if different reaching directions have to be performed. Immediate time alignment is measured as the intermanual correlation between the time series of the two hands (or participants in the dyadic version) and reflects the strength of coupling between the two effectors, which should be significant in the dyadic version if participants align their movement timing on each and every trial. General alignment is the correlation of the intermanual mean RTs over all participants (or dyads) and reflects the independence of the general speed between two effectors. We found similar, albeit significantly lower, measures in all three indicators for interpersonal coordination in the dyadic version compared to the individual task. We found significant measures of immediate and general time alignment only in the experiments where information about the upcoming task was given at the same time. If information about whose turn it was and about the movement pattern was given with a time delay, no evidence of interpersonal coordination was observed. We therefore conclude that, only if information about who has to do something and what needs to be done is
given simultaneously, do co-actors coordinate their actions with each other in time (Fig. 7.1.4.2).

In a further series of experiments, we tried to identify the time scale of interpersonal coordination. By smoothing the time series, we showed that the amount of coordination increased with increased smoothness. In general, we found more evidence that interpersonal coordination depends more upon long-term processes (e.g. monitoring the other’s performance over longer periods of time) and only very little on short-term processes (i.e. current events caused by the other’s actions).

Impact of self-construal on intra- and interpersonal coordination

Jung, C., Springer, A., & Prinz, W.

1 Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany
2 Department of Sport and Exercise Psychology, University of Potsdam, Germany

In this project, we investigated how priming of specific self-construals, which emphasize an interdependent or independent self, alters the way people coordinate their actions. The construal of the self is defined by social variables like relationships with others or one’s membership in social groups. For instance, members of western individualistic cultures are characterized as context-independent and focussed on individual characteristics, skills and attitudes (independent self) while members of eastern collectivistic cultures are described as seeing themselves as group members, context-dependent, and focussed on social contexts and social roles (interdependent self). Both types of self-related knowledge may coexist within the same individual and may thus be primed by situational cues. It has been shown that the two constructs are correlated with basic cognitive processes: Activating an independent self-concept resulted in 1) higher selective attention (focus on task-relevant information), 2) stronger inhibition (of task-irrelevant information) and 3) better task shifting as compared to when an interdependent self was activated.

An open question is whether the strength of interpersonal coordination may be altered by activating an independent or an interdependent self-construal. One hypothesis holds that after activating an independent self (IND) in both members of a dyad, indicators of interpersonal coordination are weakened relative to a condition in which interdependent self (INTER) is induced. We conducted a classical individual bimanual reaching experiment and a dyadic version of this paradigm (Fig. 7.1.4.1). Participants were either primed with an independent or an interdependent pronoun circling task. In this task, the participants are instructed to circle all the pronouns in a short story (e.g. description of a trip to a city). The two versions differ with respect to whether the pronouns were independent (I, mine) or interdependent (we, ours).

The results for the individual bimanual task indicated that INTER participants showed no RT differences between symmetric and asymmetric movements and revealed weaker immediate and general time alignment compared to IND participants. IND participants, on the other hand, showed a significant difference between symmetric and asymmetric movement preparation and higher immediate and general time alignment. A similar effect was found in the dyadic version of the task. Hence, INTER individuals and dyads demonstrated less interpersonal coordination than IND individuals and dyads (Fig. 7.1.4.2). We suggest that activating different self-concepts changed the way the coordination task was perceived and performed. Specifically, INTER individuals might integrate diverse task features whereas IND individuals disintegrate these features.
Congresses, Workshops, and Symposia

2010


Baess, P., & Lange, K. (March). *How Do Temporal Preparation and Temporal Preknowledge Influence Stimulus Processing?* Symposium. 52nd Annual German Experimental Psychology Meeting (TeaP), Saarland University, Saarbrücken, Germany.

Daum, M. M., & Aschersleben, G. (March). *Entwicklung des Verständnisses physikalischer Ereignisse vom Säugling bis zum Vorschulkind [The Development of the Understanding of the Physical World in Infants and Preschoolers]*. Symposium. 52nd Annual German Experimental Psychology Meeting (TeaP), Saarland University, Saarbrücken, Germany.


2011


Attig, M., & Daum, M. M. (September). *Die Welt aus Kinderaugen: Eyetracking als Methode zur Erforschung früher kognitiver Fähigkeiten [Seeing the World through Children’s Eyes: Eyetracking as Method to Investigate Early Cognitive Abilities]*. Symposium. 20th Developmental Psychology Section Meeting (EPSY) of the German Psychological Society (DGPs), University of Erfurt, Germany.


### Degrees

**Habilitation**

Daum, M. M. *Mechanismen der frühkindlichen Entwicklung des Handlungsverständnisses [Mechanisms in the early development of action understanding]*. University of Leipzig, Germany.

**PhD Theses**

Diefenbach, C. *Interactions between sentence comprehension and concurrent action*. University of Leipzig, Germany.

Dietrich, S. *Coordination of unimanual continuous movements with external events*. University of Leipzig, Germany.

Sparenberg, P. *Filling the gap: Temporal and motor aspects of the mental simulation of occluded actions*. University of Leipzig, Germany.

### Awards

Prinz, W. *Oswald Külpe Award*. Julius Maximilian University Würzburg, Germany.
**Publications**

**Books and Book Chapters**


Published Papers


The research group “Attention and Awareness” has focused on the neural mechanisms of visual perception and executive processing. In several projects we have employed multivariate decoding and its combination with computational modelling to study the neural mechanisms of perception and attention (Bogler, Bode, & Haynes, 2011; Cichy, Heinzle, & Haynes, 2011; Kahnt, Gruschow, Speck, & Haynes, 2011; Kalberlah et al., 2011). With postdoc Jakob Heinzle, we were able to directly map information flow between subregions of visual cortex (Heinzle, Kahnt, & Haynes, 2011). With PhD student Thorsten Kahnt, we investigated the encoding of stimulus-driven reward representations and their role in learning (Kahnt et al., 2010; Kahnt et al., 2011). In the field of executive functions we have investigated the cortical representation of intentions (Reverberi, Görgen, & Haynes, 2011) and the neural determinants of free decisions (Bode et al., 2011). Importantly, we were able to address a core question of the group by demonstrating a direct link between perception and executive functions. Specifically, we showed that low-confidence perceptual decision making and free choices share very similar brain mechanisms (Bode et al., 2012). Finally, with doctoral student Chen Yi, and postdoc Jakob Heinzle, we have developed computational methods for pattern classification and wavelet-based multiscale pattern analysis on the cortical surface (Chen et al., 2011) and for information flow (Lizier et al., 2010; Anders et al., 2011).
### 7.2.1 Perceptual learning and decision-making in human medial frontal cortex

Kahnt, T.¹, Grüschow, M.¹², & Haynes, J.-D.¹²

¹ Bernstein Center for Computational Neuroscience, Charité University Medicine Berlin, Germany  
² Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

The dominant view that perceptual learning is accompanied by changes in early sensory representations has recently been challenged. Here, we tested the idea that perceptual learning can be accounted for by reinforcement learning involving changes in higher decision-making areas. We trained subjects on an orientation discrimination task involving feedback over 4 days, acquiring fMRI data on the first and last day. Behavioural improvements were well explained by a reinforcement learning model in which learning leads to enhanced readout of sensory information, thereby establishing noise-robust representations of decision variables. Only activity patterns in the ACC tracked changes in decision variables during learning, thus providing strong evidence that perceptual learning-related involves higher order regions.

### 7.2.2 Decoding successive computational stages of saliency processing

Bogler, C.¹², Bode, S.¹, & Haynes, J.-D.¹²

¹ Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany  
² Bernstein Center for Computational Neuroscience, Charité University Medicine Berlin, Germany

An important requirement for vision is to identify interesting and relevant regions of the environment for further processing. In this project we mapped neural representations of graded saliency versus the subsequent winner-take-all (WTA) mechanism using images of natural scenes. FMRI signals in early visual cortex and posterior intraparietal sulcus (IPS) correlated with graded saliency as defined by a computational saliency model. Multivariate classification of fMRI signals revealed that the most salient position in the visual field was encoded in anterior IPS and FEF, thus reflecting a potential WTA stage. Our results confirm that graded saliency and WTA-thresholded saliency are encoded in distinct neural structures.

### 7.2.3 Cortical surface-based searchlight decoding

Chen, Y.¹², Soon, C. S.¹, & Haynes, J.-D.¹²

¹ Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany  
² Bernstein Center for Computational Neuroscience, Charité University Medicine Berlin, Germany

We developed a cortical surface-based searchlight approach to pattern localization. Voxels are grouped according to distance along the cortical surface—the intrinsic metric of cortical anatomy—rather than Euclidean distance, as in volumetric searchlights. Group analyses of accuracy maps produced by both methods show similar distributions of informative regions. The surface-based method achieves a finer spatial specificity with comparable peak values of significance, while the volumetric method appears to be more sensitive to small informative regions and might also capture information not located directly within the grey matter. Furthermore, our findings show that a surface centered in the middle of the grey matter contains more information than the white–grey boundary or the pial surface.
PhD Thesis

Bode, S. From stimuli to motor responses: Decoding rules and decision mechanisms in the human brain. University of Leipzig, Germany.

Published Papers


The International Max Planck Research School on Neuroscience of Communication: Function, Structure, and Plasticity (IMPRS NeuroCom) is an interdisciplinary PhD programme which was originally initiated by the Max Planck Institute for Human Cognitive and Brain Sciences. The school is based at the Max Planck Institute for Human Cognitive and Brain Sciences and the University of Leipzig, and also involves the Max Planck Institute for Evolutionary Anthropology, Leipzig, and the Institute of Cognitive Neuroscience at University College London, UK. The IMPRS NeuroCom is a project mainly funded by the Max Planck Society and the Max Planck Institute for Human Cognitive and Brain Sciences, but also by the University of Leipzig. The official inauguration of the IMPRS NeuroCom was on 15 October 2009. This graduate school has strengthened the working relationships between all participating institutions.
## PhD Students and Projects

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<th>Franziska Knolle (née Grimm)</th>
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<td>Attentional modulation of somatosensory processes</td>
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<th>Klaus-Martin Krönke</th>
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<td>[18F]NCFHEB-PET in Alzheimer’s disease: Relationship between nicotinic receptor availability and cognition</td>
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<td>Jana Hoyer (née Rambow)</td>
<td>Barbara Strotmann</td>
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<tr>
<td>Neuronal and cognitive correlates of eating behavior</td>
<td>Structural and functional connectivity of the hypothalamo-limbic system</td>
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### Methods: Modern Neuroimaging Techniques, Biophysics, and Signal Processing

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<th>Štefan Holiga</th>
<th>Stefan Philips</th>
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<td>Multivariate pattern analysis on electrophysiological data</td>
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<td>Peng Wang</td>
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<td>Parameter estimation in neural mass models</td>
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## Faculty

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<th>Name</th>
<th>Institution and Department</th>
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<tr>
<td>Professor Dr Balthasar Bickel</td>
<td>University of Leipzig, Dept of Language Typology</td>
</tr>
<tr>
<td>Professor Dr Bernhard Comrie</td>
<td>MPI for Evolutionary Anthropology</td>
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<tr>
<td>Professor Dr Angela D. Friederici</td>
<td>MPI for Human Cognitive and Brain Sciences</td>
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<tr>
<td>Professor Dr Thomas Jacobsen</td>
<td>University of Leipzig, Dept of Psychology I</td>
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<tr>
<td>Professor Dr Jörg Jescheniak</td>
<td>University of Leipzig, Dept of Psychology I</td>
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<tr>
<td>PD Dr Sonja A. Kotz</td>
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<tr>
<td>Dr Katharina von Kriegstein</td>
<td>MPI for Human Cognitive and Brain Sciences</td>
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<tr>
<td>Dr Jonas Obleser</td>
<td>MPI for Human Cognitive and Brain Sciences</td>
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<tr>
<td>Professor Dr Thomas Pechmann</td>
<td>University of Leipzig, Dept of Linguistics</td>
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<tr>
<td>Professor Dr Erich Schröger</td>
<td>University of Leipzig, Dept of Psychology I</td>
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### Cognition II: Non-Verbal Communication (Action and Interaction)

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<tr>
<td>Dr Peter Keller</td>
<td>MPI for Human Cognitive and Brain Sciences</td>
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<tr>
<td>Professor Dr Matthias Müller</td>
<td>University of Leipzig, Dept of Psychology I</td>
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<tr>
<td>Professor Dr Elena Lieven</td>
<td>MPI for Evolutionary Anthropology</td>
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<tr>
<td>Professor Dr Wolfgang Prinz</td>
<td>MPI for Human Cognitive and Brain Sciences</td>
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<tr>
<td>Dr Simone Schütz-Bosbach</td>
<td>MPI for Human Cognitive and Brain Sciences</td>
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<tr>
<td>Professor Dr Michael Tomasello</td>
<td>MPI for Evolutionary Anthropology</td>
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### Neuroscience: Basic and Clinical

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<th>Name</th>
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<tr>
<td>PD Dr Stefan Geyer</td>
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<tr>
<td>Professor Dr Ulrich Hegerl/PD Dr Peter Schönknecht</td>
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<tr>
<td>PD Dr Hellmuth Obrig</td>
<td>University of Leipzig, Clinic of Cognitive Neurology</td>
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<tr>
<td>Professor Dr Rudolf Rübsamen</td>
<td>University Hospital Leipzig, Dept of Neurobiology</td>
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<tr>
<td>PD Dr Matthias Schroeter</td>
<td>MPI for Human Cognitive and Brain Sciences</td>
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<tr>
<td>Professor Dr Tania Singer</td>
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<tr>
<td>Professor Dr Arno Villringer</td>
<td>MPI for Human Cognitive and Brain Sciences</td>
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<tr>
<td>Professor Dr Kai von Klitzing/Dr Annette Klein</td>
<td>University of Leipzig, Clinic for Children and Youth Psychiatry</td>
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Methods: Modern Neuroimaging Techniques, Biophysics, and Signal Processing

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Professor Dr Gerhard Heyer  
University of Leipzig, Dept of Natural Language Processing

Professor Dr Daniel Huster  
University of Leipzig, Dept of Medical Physics/ Biophysics

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Dr habil. André Pampel  
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Professor Dr Gerik Scheuermann  
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IMPRS NeuroCom

Since its inauguration in 2009, the overriding goal of the IMPRS NeuroCom has been to investigate the functional, structural, and plastic bases of human communication using an integrative and interdisciplinary approach. To this end, faculty members with diverse backgrounds—for example, neurobiologists, neuropsychologists, cognitive scientists, medical researchers, computer scientists, and physicists—have been involved in both the teaching and supervision of the doctoral students. Besides behavioural work, the programme draws on elaborate modern neuroimaging techniques such as functional and structural magnetic resonance imaging (MRI), electroencephalography (EEG), magnetoencephalography (MEG), near-infrared spectroscopy (NIRS), and transcranial magnetic stimulation (TMS).

In late 2009, the first cohort of 22 highly qualified and motivated young researchers from eight nations started their PhD projects. Coming from a wide variety of professional backgrounds, such as linguistics, psychology, biology, medicine, computer science, and engineering, enables the students to benefit from shared knowledge and resources. Depending on their professional background and the specific research topics within this broad area of academic endeavour, the PhD students have chosen an individual project within one of four modules. These four modules fall into two categories: two cognitive modules, and two more basic neuroscientific modules:

1. Cognition I: Verbal Communication (Language)
2. Cognition II: Non-Verbal Communication (Action and Interaction)
3. Neuroscience: Basic and Clinical

In 2010/2011 IMPRS students focussed on the research topics of their choice, and also received extensive expert information outside their chosen projects. This has broadened their horizons towards potential interdisciplinary approaches. Fundamental knowledge covering all four modules was imparted in the form of lectures, courses, and seminars run at both Max Planck Institutes and the University of Leipzig. As a result, the doctoral students have been trained in the multidisciplinary aspects of cognition, psychology, and neuroscience, which are involved in communicative action, as well as in modern neuroscientific methodologies. In addition, various series of colloquia, annual summer schools, and a final-year exchange programme have taken place.

The first IMPRS NeuroCom Summer School took place at the Max Planck Institute for Human Cognitive and Brain Sciences from 19–21 July 2010; the second ran from 6–8 July 2011 at the Institute of Cognitive Neuroscience, University College London. Both were a huge success among student attendees and lecturers alike. World-class lecturers and doctoral students from over 30 nations met and exchanged experience in research, discussed their current work and socialized with the aim of improving future collaborations.

The final lecture component for the current cohort of students concluded at the end of the summer semester 2011, which will allow students to concentrate on the completion of their PhD theses in the final year. A Speed Reading and also a Scientific Writing course were provided to assist students in developing and broadening skills essential to research. Furthermore, international candidates had the opportunity to participate in courses in German as a second language.

At the moment, the IMPRS is in the process of recruiting the next cohort of talented PhD students from all over the world.
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