



Research Report 2014–2016

Max Planck Institute for Human Cognitive and Brain Sciences Leipzig

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Research Report 2014–2016



Preface

In the past three years, from 2014 to 2016, the Max Planck Institute for Human Cognitive and Brain Sciences in Leipzig continued to pursue its internationally successful research and development. The Institute currently houses four full departments, six research groups, and three methods and development units. Up to 400 members of staff work at the the Institute and contribute to its lively atmosphere of cutting-edge science, buzzing work, and multicultural communication.

The Institute remains in a spirit of constant development: The youngest of our departments, the Department of Neurophysics headed by Nikolaus Weiskopf who joined the Institute as a new director from London in 2015, is currently being set up. Nikolaus Weiskopf brought with him two large-scale collaborative EU projects as well as a prestigious ERC Consolidator Grant. Two longitudinal studies—one on Eastern and Western methods of mental training, conducted by Tania Singer's department, and another on the neural basis of the development of syntax processing as a crucial capacity of the human species, conducted by Angela D. Friederici's departmenthave been successfully completed. The Department of Neurology continues to be involved in an unparallelled large-scale health study at the University of Leipzig, LIFE, on the cause and development of widespread common diseases.

Professor Robert Turner, former director of the Department of Neurophysics, retired in February 2014. He is still active as director emeritus and was awarded an honorary professorship at the University of Amsterdam. Four independent research group leaders have left the Institute for new positions: Jonas Obleser, who formerly headed the Max Planck Research Group "Auditory Cognition", has moved to Lubeck for a full professorship position, taking with him an impressive ERC Consolidator Grant. Tobias Grossmann, former leader of the Max Planck Research Group "Early Social Development", has moved to Virginia (US) for a professorship. The groups led by Florian Schlagenhauf and Petra Ritter came to an end in 2015. Both hold group leader positions at the Charité University Medicine in Berlin, where Petra Ritter also successfully secured a prestigious ERC Consolidator grant.

Two new Max Planck Research Groups started work in the reporting period: "Adaptive Memory" is headed by Roland Benoit, who joined the Institute from Harvard; "Early Social Cognition" is led by Stefanie Hoehl, who moved to Leipzig from Heidelberg.

The International Max Planck Research School on Neuroscience of Communication (NeuroCom) has continued its success in both recruiting promising new doctoral students and seeing students of the "old" cohort through to completing their PhDs.

We hope you will enjoy reading this report, which contains up-to-date scientific and administrative information about our Institute and its research.

> Angela D. Friederici Tania Singer Arno Villringer Nikolaus Weiskopf

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Emeriti

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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 decision to merge both centres of expertise into one followed the development of psychological, neuroscientific, and neurological research increasingly being conducted closely together. The creation of the centre in Leipzig also established exceptional conditions for interdisciplinary behavioural and neurobiological research into human cognition.

The Institute currently consists of four departments: Neurology, Neuropsychology, Social Neuroscience, and Neurophysics. The Institute also hosts several research groups, including four Max Planck Research Groups: "Adaptive Memory" (Roland Benoit), "Early Social Cognition" (Stefanie Hoehl), "Neural Mechanisms of Human Communication" (Katharina von Kriegstein), and "Neuroanatomy & Connectivity" (Daniel Margulies), as well as a Minerva Research Group "EGG (Emotion & neuroimaGinG) Lab" (Julia Sacher) and the Otto Hahn Group on the "Neural Bases of Intonation in Speech and Music" (Daniela Sammler). Three methods and development units facilitate scientists' access to the Institute's stateof-the-art technical equipment, while at the same time conducting their own research into the methodology of high-resolution imaging and digital data processing.

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 communication. 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 are increasingly being used in traditional psychological approaches. The Institute utilises and, most importantly, improves these techniques. Hosting the entire spectrum of techniques and approaches that are established within human cognitive and neurosciences, our Institute 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. A new cooperation agreement between all Leipzig Max Planck Institutes and the University of Leipzig, further extending and strengthening existing collaborations, is currently being finalised.

In 2010, a collaboration agreement with the Institute of Cognitive Neuroscience (ICN) at UCL, 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 organisation 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 UCL, UK.

All departments hold long-standing collaborations in the form of joint teaching and supervision projects with German and international universities and university hospitals, as well as with non-university research institutions like Helmholtz, Fraunhofer, or Wellcome Trust. Further collaborative links exist in the shape of joint supervision and assessment of doctoral students between the Max Planck Institute for Human Cognitive and Brain Sciences and several international graduate programmes like the Berlin School of Mind and Brain at Humboldt University.

Organisational structure





Professor Dr Arno Villringer Director

Plasticity

Department of Neurology

The Department of Neurology focuses on *mechanisms and therapeutic potential of brain plasticity in the pathogenesis of stroke & dementia.* With our clinical team at the Department of Cognitive Neurology at the University Hospital Leipzig, we strive to translate our findings into new strategies for improved *prevention, therapy, and recovery.*

We address three major research questions:

- How does behaviour and maladaptive brain plasticity influence medical risk factors for stroke and dementia?
- How do brain lesions affect brain structure, function, and connectivity?
- What are the neural mechanisms underlying sensorimotor processing and learning in health and pathology?

General research approach

While our studies in humans employ a combination of behavioural assessments in healthy subjects and patients, multimodal neuroimaging and stimulation as well as metabolic and genetic investigations, our overarching goal is to understand the neurophysiological processes. Linking continuously improved noninvasive methods to underlying physiology is thus a major theme of our work. For example, we aim at

- relating neuroimaging findings to cytoarchitectonics (in cooperation with Nikolaus Weiskopf's department) and new types of connectivity-based brain parcellations (in cooperation with Daniel Margulies' group)
- elucidating the role of oscillatory brain activity (EEG/MEG, TACS) in sensorimotor processing and its therapeutic modulation
- revealing brain mechanisms of information processing on the basis of complex temporal dynamics and cross-frequency interactions (group led by Vadim Nikulin, beginning of 2017)
- identifying molecular mechanisms (PET, pharmacological fMRI), especially in the dopaminergic and serotonergic systems and their role in pathogenesis of vascular risk factors and motor learning
- creating comprehensive neuro-computational models (for example in the computational modelling group led by Jane Neumann)

(1) Risk factors, behaviour, brain plasticity, and brain damage (Abstracts by Horstmann, Schaare, and Witte)

We investigate two medical conditions, obesity and hypertension, which are highly relevant risk factors for stroke and dementia (see abstract by Horstmann, abstract by Schaare). We specifically test the hypothesis that neurobehavioural changes—triggered by reward and exaggerated stress responses—are propagating to vicious cycles that lead to the development of risk factors for stroke and dementia (Fig. 1A, B). This line of work is supported by strong evidence for neural changes that appear very early in the development of this risk factor burden.

Obesity: The vicious cycle that we specifically hypothesise for the "addictive dimensionality" of obesity is illustrated in Figure 1A. When examining these processes in humans *in vivo*, however, we have to be aware that the relationship between obesity and "the brain" is highly complex since neural alterations in subjects with obesity have a multifactorial etiology (e.g. they could be due to individual genetic makeup/profile, neuropsychiatric comorbidities, overactivity of reward areas, but also due to obesity-related brain damage). Disentangling this multifactorial etiology is a major challenge and requires modelling based on large cohort studies and, ideally, additional evidence from intervention studies.

In our studies on obesity during the last few years we have achieved the following:

- We have identified several new genetic determinants of eating behaviour (Rohde et al. 2015a, Rohde et al, 2015b, Gast et al., 2013, Brain Behav, 3(5), 495–502, Horstmann et al., 2013, PLoS One 8(9):e74362).
- We have provided novel evidence for a quadratic (rather than linear) relationship of behaviour and

dopamine availability and BMI (see: abstract by Horstmann, Dietrich et al., 2016). This finding has important therapeutic implications since modulation of dopaminergic neurotransmission could be beneficial in some and harmful in other patients. Currently, we are developing a new dopaminergic transmission model and are integrating it into a modular neurocomputational model of behavioural control (group led by Jane Neumann). This will allow us (i) to theoretically test hypotheses of the direction and domainspecificity of cognitive effects induced by alterations in dopaminergic tone, and (ii) to inform pharmaceutical manipulation of dopaminergic neurotransmission relevant for modulating eating behaviour.

- Results of two pioneering studies using positron-emission tomography (PET) indicate a role for serotonin and norepinephrine in mediating a diminished sense of well-being in overweight subjects (Melasch et al., 2016).
- We have shown in an intervention study-design that leptin substitution is accompanied by long-term changes of hedonic and homeostatic central nervous networks regulating eating behaviour, decreased hunger feelings, and diminished incentive value of food (Schlögl et al., 2016).
- In a large population-based cohort study (Löffler et al., 2015), we find widespread brain atrophy associated with obesity in elderly subjects (Kharabian et al., 2016), show that grey and white matter changes are interrelated (Müller et al., 2014), and demonstrate reduced connectivity in the default mode network (Beyer et al., submitted, see abstract by Witte). Interestingly, these findings are similar to findings in early Alzheimer's disease.



Figure 1 (A) Addictive dimensionality of obesity, (B) Hypertension as neural maladaptation hypothesis

Hypertension. Regarding the pathogenesis of hypertension, we pursue the hypothesis that repetitive stressrelated overshooting of blood pressure responses plays an important role ("hypertension as maladaptation hypothesis" or "learned hypertension hypothesis", Figure 1B). Using an "emotion task" during fMRI and simultaneous continuous blood pressure monitoring, we have identified areas involved in blood pressure regulation in human subjects (Okon-Singer et al., 2014). Furthermore, we provide evidence that high blood pressure is associated with substantial neural alterations already in young subjects (18–39 years) and—even more alarmingly at blood pressure levels which are clearly below levels classified as "hypertensive" (see abstract by Schaare). In a joint study with the group led by Hadas Okon-Singer

(2) Cognition, white matter lesions, stroke, and dementia

(Abstracts by Khalil, Lampe, Steele, Obrig, and Schroeter)

Figure 2 illustrates how we view the "path towards stroke and dementia". It is well known that cognitive decline over the life course is strongly influenced by risk factors such as hypertension. Furthermore, we know that a (silent) accumulation of pathogenic proteins such as amyloid or tau starts many years before dementia is diagnosed. Adding in the slow accumulation of white matter lesions and other subclinical ischemic events, we regard the clinical diagnosis of stroke and dementia as the tip of the iceberg of a long-lasting development. (now University of Haifa), we further show attenuated amygdala reactivity (a mediator of stress-related blood pressure increases) to aversive information after training of a non-emotional executive control task (Cohen et al., 2016).

Current **interventional studies** for investigating the development of risk factors include a combined exercise and calorie-reduction programme and a placebocontrolled randomised trial of resveratrol (see abstract by Witte). In close collaboration with the group led by Hadas Okon-Singer (University of Haifa), we are currently developing strategies for improved emotion regulation in order to prevent further progression of elevated blood pressure in young prehypertensive subjects.

Stroke: Perfusion and oxygen metabolism

It is well established that a drop in cerebral blood flow (CBF) and the consecutive deterioration of cerebral metabolism constitute the crucial events in the pathogenesis of cerebral ischemic lesions. While there are several methods to assess CBF and oxygen metabolism in humans, they typically require administration of a contrast agent (in MRI or PET). This invasive procedure is associated with the risk of side effects which limit its use for therapy monitoring and/or for scientific purposes. We



Figure 2 From risk factors to stroke and dementia

therefore continue to develop and improve the application of noninvasive MR-based methods to assess CBF (see abstract Khalil) as well as oxygen metabolism (Fan et al., 2016). The BOLD-delay method, which we pioneered to assess cerebral ischemia (Lv et al., 2013, Ann Neurol, 73, 136-40), has also been successfully applied by other groups (Amemiya et al., 2014, Radiology, 270, 548–555). We have validated the BOLD delay findings in an animal model (Khalil et al., in preparation), and further established it in human stroke patients by comparing it to standard (contrast agent based) perfusion imaging (Khalil et al., under review). In addition, we demonstrate the usefulness of this approach for monitoring reperfusion after recanalisation in acute ischemic stroke (Khalil et al., submitted). Interestingly, in some patients we found a discrepancy between plasma perfusion and blood cell perfusion. This discrepancy may be a proxy for capillary narrowing due to postischemic pericyte constriction (Hall et al., 2014, Nature, 508, 55-60). The noninvasive method for the assessment of oxygen metabolism based on quantitative susceptibility mapping (QSM) which we implemented and validated in human subjects in vivo (Fan et al., 2016) has now also been successfully applied in human stroke patients (Fan et al., in preparation). We envision the joint application of the BOLD delay and the QSM approach for a better and noninvasive definition of the ischemic penumbra and treatment monitoring in stroke patients.

Functional and structural consequences of focal lesions (including white matter lesions)

We have established a conceptual framework by modelling local and distant effects of focal lesions on brain structure and connectivity (see abstract by Steele). In several lines of work, we have investigated the effects of ischemic stroke and white matter lesions on functional connectivity (Ovadia-Caro et al., 2013, J Cereb Blood Flow Metab, 33, 1279-1285; Ovadia-Caro et al., 2014; Schäfer et al., 2014) and—based on the large population-based LIFE-cohort—on cognition (Kynast et al., submitted) and on grey matter (Lampe et al., submitted, abstract Lampe). In close cooperation with the Center for Stroke Research in Berlin, we study the effect of thalamic lesions on the subsequent development of pain (Krause et al., 2016; Krause et al., 2016). Our prospective clinical study on pain development in a sample of 100 "somatosensory stroke" patients has recently completed successful recruitment.

Aphasia

Aphasia is a frequent burden after stroke, and it is thus both a clinical and research focus at the Department of Cognitive Neurology at the University Hospital Leipzig. The language and brain plasticity group (see abstract by Obrig) relates multimodal neuroimaging findings to clinical features of aphasia (Henseler et al., 2014, Obrig et al., 2016). Furthermore, Hellmuth Obrig's team investigates how imaging findings can contribute to predicting the outcome of aphasia following a stroke. The Department of Cognitive Neurology at the University Hospital Leipzig is committed to continuously improving patient care. Thus, our joint research explores how therapeutic intervention can be tailored based on an individual multidimensional assessment in order to provide an environment for the best individual recovery. The language and brain plasticity group routinely participates in multicentre intervention studies (Breitenstein et al. Lancet, in press).

Dementia

The work on dementia is based on two pillars:

In cooperation with the University Hospital Leipzig (Prof. Riedel-Heller), we perform epidemiological studies on cognitive development with a particular focus on occurrence and prognosis of mild cognitive impairment (MCI) and Alzheimer's disease (e.g. Luck et al., 2016; Luck et al., 2015a; Luck et al., 2015b; Roehr et al., 2016). The largest study to date is the LIFE study (Leipzig Research Center for Civilization Diseases, Prof. Löffler, Prof. Thiery). In this population-based cohort project, 10,000 residents of Leipzig have been recruited and more than 2,800 have received extensive cognitive testing, functional and structural MRI as well as medical, metabolic, and genetic (GWAS) screening (Löffler et al., 2015). The baseline examination phase of this cohort was completed by the end of 2015, and we have successfully identified obesity and hypertension as two essential determinants for brain structure (Raschpichler et al., 2013, BMJ Open, 3:e001915; Kharabian et al., 2016; see abstract by Schaare). Furthermore, we systematically characterise and detail the relationship between cognition and brain structure (see abstract by Lampe). Based on multimodal brain imaging data, we have developed a measure for brain age which is sensitive to differences in cognition (Liem et al., in press). Studies on the contribution of genetic profiles to resting-state connectivity and cognition, the role of heart-rate variability and stress, and a prospective evaluation of risk factor development and cognition during and after menopause are in progress. The first 5-year follow-up of the LIFE cohort will begin in early 2017.

The cognitive neuropsychiatry group (see abstract by Schroeter) uses multimodal neuroimaging (MRI, PET, PET-MRI, SPECT) to facilitate early diagnosis of dementia and to identify preclinical stages of Alzheimer's disease (AD).

Furthermore, Matthias Schroeter's group aims to differentiate subforms of dementia by relating clinical symptoms to network disturbances, as well as specific molecular and cellular events. To this end, several quantitative meta-analyses have been performed and identified, for example, for the behavioural variant of frontotemporal dementia (FTLD), the frontomedian cortex, basal ganglia,

(3) Neural mechanisms of sensorimotor processing and learning

(Abstracts by Gundlach, Martins, Bazin, Sehm, Sacher, and Fritz)

Somatosensory processing

The somatosensory system is our model system for understanding basic neurophysiological processes and functional neuroanatomy underlying sensory function. Specifically, we aim to understand the functional role of background oscillations and the effect of modulating these oscillations with transcranial stimulation. Furthermore, we investigate the long-term effect of cerebral infarcts involving the somatosensory system, particularly the development of maladaptive plasticity leading to post stroke pain (see above).

We have recently been able to establish sensorimotor somatotopy in individual subjects without any task or stimulation, solely based on resting-state fMRI (Long et al., 2014). In a clinical lesion study, we identified subregions within the secondary somatosensory cortex that are important for the sensation of touch, further clarifying the functional neuroanatomy of the ventral somatosensory pathway (Preusser et al., 2015). We have continued our studies on processing subliminal stimuli and have shown that they go along with an evoked potential after 60 ms (P60), but no further ERP component, a transient increase in alpha rhythm strength, and a drop in SI connectivity (Nierhaus et al., 2015). Recently, we have shown that the P60 is modulated by attention and alpha rhythm amplitude (Forschack et al., under review). Furthermore, we have used fMRI to identify the network that underlies modulation of tactile attention (Goltz et al., 2015). We can attribute a causal role of alpha rhythm for somatosensory processing by showing the modulation of somatosensory perception by transcranial alternating current stimulation at alpha rhythm frequency (Gundlach et al., 2016). Recently, employing simultaneous transcranial stimulation and fMRI, we have been able to show that TACS at individually adjusted alpha frequency very specifically decreases BOLD signal in the sensorimotor cortex (see abstract by Gundlach).

Sensorimotor learning

We aim to identify neurobehavioural mechanisms underlying sensorimotor learning. To this end, we invesanterior insulae, and thalamus as most relevant hubs (Schroeter et al., 2014; Bisenius et al., 2016). By combining amyloid PET with MRI (Schütz et al., 2016; Werner et al., 2016), a method for minimising partial volume effects in amyloid PET data has been successfully established and applied to develop better histopathological fingerprints of dementia syndromes (Rullmann et al., 2016).

tigate neural plasticity associated with short-term and long-term learning:

Mauricio Martins studies the role of hierarchical processing in motor learning. By systematically comparing motor learning via a "fractal" (hierarchical rule versus a "repetitive" procedure during fMRI), he identifies a functional network for hierarchical motor learning (abstract by Martins) which does not include the presumable domain-general areas in the inferior frontal gyrus (especially BA 44) as is assumed by current standard theory.

While these functional neural modulations typically occur in the early phase of motor learning, we have previously suggested that during continuous learning, neurobehavioural alterations follow a multiphase model sequentially involving different neural networks. Thus, in addition to the functional network modulation during the very first learning phase (minutes) of a balance learning task, we found transient (presumably structural T1) changes within the first hour in the primary motor cortex (Taubert et al., 2016), and subsequent changes in premotor (1–2 weeks) and frontal brain areas (months) (Taubert et al., 2010, J Neurosci, 30, 11670-11677, Taubert et al., 2011, NeuroImage, 57, 1492–1498). In order to disentangle neuroplastic changes during the first five days of motor learning in more spatial detail and with physiological specificity, we are currently assessing neural plasticity during a motor learning task with highresolution quantitative and physiologically-informed MRI at 7 Tesla (see abstract by Bazin). This work follows up on our recent proposal for the use of quantitative MRI as physiologically-specific markers of brain plasticity (Tardif et al., 2016). Furthermore, as functional and structural MRI findings cannot, in principle, provide causal evidence for the role of certain brain areas in mediating learning, we complement these studies with transcranial stimulation experiments: transcranial magnetic stimulation (TMS), transcranial direct current stimulation (TDCS), and transcranial alternating current stimulation (TACS). By applying TMS, TDCS, and TACS, we are able to differentially modulate the activity of specific brain areas during motor learning tasks (Kaminski et al., 2013, Neurosci Lett, 552, 76–80; Kaminski et al., 2016; Taubert et al., 2016).

On the other end of the temporal evolution of learning-related neural alterations, we investigate long-term changes associated with many years of training, for instance, in athletes and musicians. For example, we identified anatomical features which correlate with specific aspects of athletic performance (Wenzel et al., 2014; Taubert et al., 2015). We show that mirror activity associated with hand grip is associated with fractional anisotropy in the posterior midbody of the corpus callosum (Sehm et al., 2015). In a high-resolution connectivity study, we could establish a detailed map of motor versus non-motor topography in the human cerebellum (Steele et al., 2016).

In two current studies, we are assessing the effect of dopaminergic and serotonergic modulation on motor learning. The latter ties in with work of Julia Sacher's group on the role of serotonergic neurotransmission in mediating brain connectivity (Schäfer et al., 2014; abstract Sacher).

Sensorimotor learning studies in patients

Previous and current work on motor learning has been performed in several patient groups: In patients with Parkinson's disease (PD), we show different brain areas (particularly in the cerebellum) being modulated during learning as compared to age-matched healthy controls (Sehm et al., 2014).

Fritz et al. confirm the beneficial effect of music on gait in PD patients and provide compelling evidence for the dependence of this beneficial effect on perceived pleasantness of music (see abstract by Fritz). These findings suggest a fundamental role for dopaminergic modulation on the observed beneficial effect of music on gait in PD. A study on motor learning combined with TDCS in stroke patients is under way, as well as a follow-up study on the effect of "Jymmin" (Fritz et al., 2013, Proc Natl Acad Sci, 110, 17784–17789) in stroke patients.

Publications

During the 2014–2016 period, we published 290 papers in peer-reviewed international journals. It is probably fair to say that we have contributed significantly to the "neuroimaging literature" given that—during these three years—we have published 48 papers in the two top neuroimaging journals *Neuroimage* (37) and *Human Brain Mapping* (11). Among leading clinical and neurological journals there were, for example, 6 publications in Brain and further papers in *The Lancet, The Lancet Diabetes and Endocrinology, Trends in Endocrinology and*

Metabolism, Stroke, Biological Psychiatry, European Heart Journal, JAMA Psychiatry, Diabetes, and Journal of Nuclear Medicine. Among leading neuroscience journals there were publications, for example, in Journal of Neuroscience (6), Cerebral Cortex (9), Journal of Cerebral Blood Flow and Metabolism (2), and Cortex (6). The computational focus is illustrated by 5 papers in PLOS Computational Biology. Finally, there were 2 publications in Current Biology and 2 in Proceedings of National Academy of Sciences.

Careers

In the last three years, six members of the Department have received professorships: Patrick Ragert (University of Leipzig, Germany), Marco Taubert (University of Magdeburg, Germany), Jane Neumann (University of Applied Sciences, Jena, Germany), Claudine Gauthier (Concordia University, Montréal, Canada), Tom Fritz (visiting professorship at Ghent University, Belgium), Florian Schlagenhauf (Charité University Medicine Berlin, Germany). In addition, Claudia Döge, former PhD student and postdoc with Arno Villringer, received an assistant professorship at Columbia University, New York, USA, and Hadas Okon-Singer, former postdoc, at University of Haifa, Israel. Arno Villringer received an adjunct professorship at Vienna University, Austria. Two members of the Department have attained their habilitation at University of Leipzig, Germany (Bernhard Sehm, Julia Sacher).

Julia Sacher has become a Minerva group leader and won a NARSAD (Brain&Behavior Research Foundation) Young Investigator Award, and Annette Horstmann won the Young Investigator Award of the German Society of Obesity.

Annette Horstman and Julia Sacher have been chosen to participate in the Sign Up! Careerbuilding Programme for excellent female scientists of the MPG, a highly competitive programme, which aims to support women with leadership potential in their career planning and to prepare them for management positions in science in order to bring more women into leading positions in research.

Major project grants

Arno Villringer is PI in a project grant on Obesity at University of Leipzig funded by the German Ministry of Research (BMBF), PI in a Collaborative Research Center (SFB) 1052 on Obesity funded by the German Research Foundation (DFG), Speaker of Berlin School of Mind and Brain funded by the German Research Foundation (DFG), and PI in the Excellence Cluster NeuroCure funded by the German Research Foundation (DFG).

Director: Professor Dr Arno Villringer

Research Group Leaders

PD Dr Burkhard Pleger (48) (*) (in cooperation with the University of Leipzig) PD Dr Julia Sacher (49)

Group Leaders

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1.1 Obesity and dopamine – An intimate relationship?

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Over the past years, evidence has accumulated to show that obesity is intimately linked to the integrity of the fronto-striatal system of the human brain (García-García et al., 2014; García-García et al., 2015; Horstmann et al., 2011). However, the nature and causality of this relationship remains elusive. The fronto-striatal system is responsible for higher order cognitive functions such as learning, working memory, decision-making, and cognitive control. Further, it determines the individual propensity to actively seek out rewards in the environment or to avoid possibly punishing situations. One of the major neurotransmitters of this system is dopamine. Recently, we suggested that markers of obesity are linked to markers of the dopaminergic system in an inverted U-shaped manner (Horstmann et al., 2015), with profound differences between individuals with moderate and severe obesity (Fig. 1.1A). Cross-sectional observations of dopamine-associated functions such as general reward sensitivity and anticipation support this hypothesis (Fig. 1.1B) (Dietrich et al., 2014). But how does this observation relate to eating behaviour? Food craving is a driving force for overeating and obesity. In a recent study (Dietrich et al., 2016), we investigated brain mechanisms of foodcraving regulation using functional magnetic resonance imaging in individuals with a wide range of Body Mass



Index (BMI). Participants were presented with visual food stimuli individually matched by tastiness and healthiness and were instructed to either admit or regulate their upcoming food craving. BMI predicted regulatory brain activity in the putamen, amygdala, and insula in an inverted U-shaped manner (Fig. 1.1C). Additionally, functional connectivity of the amygdala with the pallidum and visual areas was non-linearly associated with BMI. Thus, this study reveals quadratic relationships of foodrelated brain processes and BMI, possibly linked to the dopaminergic system. Because of the fundamental role of the dopaminergic system in cognitive domains such as learning (Mathar et al., 2016), prediction formation, cognitive control, and working memory, obesity-associated changes in this system should also be reflected in non-food contexts. Indeed, we could demonstrate that obese individuals are impaired in utilising information from negative prediction errors, a dopaminergic "teaching" signal, to guide their behaviour in a non-food learning context (Mathar et al., under review). Taken together, these data suggest a dynamic relationship with the dopaminergic system during the development of obesity, possibly based on processes of neuroplasticity. In the future, we will employ a combination of pharmacological modulation and computational modelling using neuro-

> cognitive behavioural models to specifically and differentially investigate the nature of the relationship between dopaminergic signals in the brain and markers of obesity.

> Figure 1.1 (A) Quadratic relationship between Positron Emission Tomography (PET) markers of dopaminergic tone and Body Mass Index (BMI)(4). BP: Binding Potential of PET tracer. (B) Inverted U-shaped relationship between reward sensitivity and BMI (Dietrich et al., 2014). (C–E) Modulatory effect of BMI on brain activity associated with the volitional regulation of food craving (Dietrich et al., 2016). BMI is nonlinearly related to BOLD activation in a cluster of the left putamen, amygdala (C), and insula (D). (E) Inverted U-shaped relationship between BMI and BOLD effect size in the left putamen. (Colour-coding refers to t-values, p<.001 voxel level, p<.05 FWE cluster level whole brain).

Neuroanatomical correlates of resting blood pressure variations in young adults

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In elderly subjects, essential hypertension (EH) has been associated with reductions of grey matter volume (GMV) and other signs of brain damage such as white matter hyperintensities and cortical (micro-) infarcts. It has recently been suggested that the risk of developing EH may be related to brain alterations already present in young age (Gianaros et al., 2008, J Neurosci, 28(4), 990–999; Jennings & Zanstra, 2009, NeuroImage, 47(3), 914–921; Matthews et al., 2004, Circulation, 110(1), 74–78; Okon-Singer et al., 2014). This could be relevant to better understand the pathogenesis of EH, as well as for targeting and monitoring prophylactic measures. Thus, we aimed at describing the relationship between blood pressure (BP) and brain structure in young adults.

We used four datasets with a total of 423 participants (age = 27.7 ± 5.3 years, range 19–40 years, 177 women, systolic BP (SBP) = 123.2 ± 12.2 mmHg, diastolic BP (DBP)

= 73.4 ± 8.5 mmHg), without previously diagnosed EH, intake of antihypertensive drugs, or severe chronic diseases. For each participant one structural (T1-weighted) 3 Tesla MRI and at least one BP measurement was acquired. BP levels were classified into four categories (*optimal:* SBP < 120 mmHg and DBP < 80 mmHg, *normal:* SBP 120–129 mmHg or DBP 80–84 mmHg, *pre-hypertensive:* SBP 130–139 mmHg or DBP 85–89 mmHg and *hypertensive:* SBP ≥ 140 mmHg and DBP ≥ 90 mmHg) and related to GMV derived from voxel-based morphometry. Before combining the results in a voxel-based meta-analysis to obtain cumulative evidence across all datasets, we analysed the datasets separately first.

Fig. 1.2.1 shows undirected associations between BP categories and whole-brain grey matter volume for each of the four samples (*F*-contrast). All samples yielded significant clusters encompassing the whole brain at an uncor-



Figure 1.2.1 Sagittal views of the *F*-contrast results showing the overall effect of BP category on GM volume. Each sample is represented in one row (A–D). Slice order runs from left hemisphere (left-hand side of the plot) to right hemisphere (right-hand side of the plot). Voxel threshold was set to p < 0.001 (uncorrected). BP: Blood Pressure; GM: Grey Matter.

1.2



Figure 1.2.2 Voxel-based meta-analysis results for the parametric contrast of a negative linear relationship between BP category and GMV decreases across all samples. Blobs indicate lower grey matter volume in the respective brain region for higher BP. Higher BP was linearly associated with GMV decreases in regions such as the left precentral gyrus, right cerebellum, right middle temporal gyrus, left cuneus, left paracentral lobule, right postcentral gyrus and supplementary motor area, left middle occipital gyrus, left IFG, and bilateral amygdala. Colour bar represents meta-analytic SDM *Z*-values. Voxel threshold was set to p < 0.005 with a peak height threshold of SDM-*Z* > 1.0 and a cluster extent threshold of $k \ge 10$ (validated for high meta-analytic sensitivity and specificity by Radua et al., 2012). BP: Blood Pressure; GMV: Grey Matter Volume; IFG: Inferior Frontal Gyrus; SDM: Signed Differential Mapping (Radua et al., 2012).

rected threshold of p < 0.001, however, the significance remained only in sample 1 after correction for multiple comparisons (cluster *p*FWE < 0.05). Specifically, BP categories and GMV in the left posterior insula were significantly related in sample 1.

The voxel-based meta-analysis relating blood pressure and GMV linearly across all samples (parametric contrast for the blood pressure categories, controlled for type I and II errors) showed negative correlations between BP and GMV in the bilateral somatosensory cortices, right cerebellum, right middle temporal gyrus, left cuneus, left middle occipital gyrus, left IFG, and bilateral amygdala (Fig. 1.2.2).

The contrast between hypertensive and optimal BP levels showed lower GMV in the right precuneus, bilateral inferior frontal gyrus (IFG), left operculum, bilateral infe-

rior cerebellum, left postcentral gyrus, and left cuneus. Interestingly, already pre-hypertensive BP levels were associated with lower volume in the bilateral thalamus, sensorimotor cortices, right anterior insula, and anterior cingulate cortices; whereas normal compared to optimal BP correlated with lower GMV in the bilateral precuneus, left somatosensory cortex, left IFG, left fusiform gyrus, right occipital cortex, and left temporoparietal junction. In conclusion, for the first time, we show structural brain alterations with higher BP in a large sample of young adults without previously diagnosed EH. The brain regions resulting from our study overlap with those found in previous studies of older hypertensive individuals. Thus, blood pressure-related brain damage may occur much earlier and at blood pressure levels below manifest hypertension.

1.3 Obesity-related brain damage – A target for intervention?

Kharabian Masouleh, S.¹, Beyer, F.², Zhang, R.¹, Huhn, S.¹, Lampe, L.^{1,5}, García-García, I.¹, Dietrich, A.¹, Löffler, M.^{5,6}, Scholz, M.^{5,6}, Luck, T.^{4,5}, Schroeter, M. L.^{1,3}, Riedel-Heller, G. S.⁴, Villringer, A.^{1,2,3}, & Witte, A. V.^{1,2}

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Midlife obesity has been associated with accelerated cognitive decline during ageing and an increased risk of dementia. Yet, recent discussions question this detrimental relationship, especially for older populations (Emmerzaal et al., 2015, J. Alzheimers Dis. 43, 739e755). Considering the rapidly increasing prevalence of both obesity and Alzheimer's disease (AD) (WHO, 2016; Alzheimer's Association, 2016), this relationship is a debate of paramount importance. Our group aims to systematically assess the effects of obesity as well as obesity-associated genes and lifestyle factors on brain structure and function in ageing.

Using a large population-based cohort of older individuals (LIFE-study (Loeffler et al., 2015), we were able to show that a higher body mass index (BMI) is significantly associated with lower grey matter volume in widespread cortical and subcortical areas (Fig. 1.3.1, Kharabian et al., 2016) and with reduced functional connectivity in the default mode resting-state brain network (Beyer et al., submitted), even after conservative adjustment for confounders. In addition, path analyses indicated that these changes partially mediated negative effects of both BMI and age on cognitive performance.



Figure 1.3.1 Association between higher BMI and lower grey matter volume (GMV). Significant clusters, surviving a voxel-level threshold of p < 0.001 (uncorrected) and a cluster level threshold of p < 0.05 (FWE-corrected), are displayed in the cerebrum (A) and cerebellum (B), superimposed on a study-specific grey matter template. Colour bar shows the t-value at each voxel (n = 617).



Figure 1.3.2 Higher waist-to-hip ratio was associated with lower grey matter volume in a network of multimodal regions (IC3, A) that also correlated negatively with age (B) and memory performance (C). Scatter plots show the individual's loading on each network (white dots) and linear fit. Colours indicate positive (red/yellow) or negative (blue/light-blue) co-variations within the network (z > 4), maps are drawn on a standard brain (n = 617).

Moreover, we found that especially visceral obesity, measured using waist-to-hip ratio (WHR), correlated with subtle changes in white matter microstructure and in grey matter networks that were linked to ageing and memory decline (Kharabian et al., submitted, Zhang et al., in prep.). These novel MRI-based measures, possibly displaying changes in the myelin sheeths of inter- and intracortical axons (Douaud et al., 2014, Proc Natl Acad Sci. 2014;111(49):201410378), could be indicative of how detrimental effects of visceral fat, for example due to chronic inflammatory cytokine release that is affecting the myelination, would eventually boost or trigger cognitive impairments. Upcoming 5-year follow-up analyses of the LIFE study starting from 2017 will enable us to further test these hypotheses.

To eventually develop preventive strategies that might help to combat or delay age- and obesity-associated brain damage, we run interventional RCT studies that implement dietary modifications of glucose metabolism and low-grade inflammation (reviewed in Huhn et al., 2015). Here, we test effects of a daily intake of the polyphenol resveratrol over 6 months on memory performance and brain structure in 60 normal- and overweight older adults (end of follow-up in 02/2017). Sensitive cognitive testing together with high-resolution structural and diffusion-weighted imaging at 7T as well as detailed assessments of anthropometrics, lifestyle habits, bloodbased markers, and genetic pre-dispositions are conducted to examine potential underlying mechanisms.

1.4 Using the BOLD signal to assess cerebral perfusion in ischaemic stroke

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Identifying changes in brain perfusion following ischaemic stroke is relevant both for clinical decision-making and studying the pathophysiology of the disease, but is currently hindered by the need to administer intravenous contrast agents. We are developing and validating a non-invasive method for assessing cerebral perfusion, based on changes in the temporal dynamics of the blood-oxygen-level-dependent (BOLD) signal. In the very early stages of stroke, we found that localised delays in BOLD signal oscillations (relative to healthy tissue) reflect both bulk blood flow delays and microvascular perfusion assessed using conventional (contrastenhanced) perfusion MRI techniques (Fig. 1.4.1A). BOLD delay recovers following recanalisation of previously occluded arteries and can therefore also be used to monitor changes in the natural history of stroke (Fig. 1.4.1B and Fig. 1.4.1C).





The precise pathophysiological basis of BOLD delay is unknown, but depends on alterations in low frequency oscillations of the BOLD signal (< 0.1 Hz). We observed this in a mouse model of acute focal brain ischaemia using an MR imaging sequence with very high temporal resolution (10 Hz), where cyclical cardiac and respiratory activity can be excluded (Fig. 1.5.2A). Preliminary data from stroke patients scanned using multiband echo planar imaging sequences, acquired with a repetition time of 0.4 seconds, confirm this observation (Fig. 1.5.2B). BOLD delay is a promising non-invasive method for assessing perfusion after stroke and is most likely driven by slow modulations of cardiac and/or respiratory activity.



Figure 1.4.2 Resting-state functional MRI with high temporal resolution in mice (A) and humans (B) shows that BOLD delay is driven by low frequency oscillations (0.01–0.1 Hz) in the BOLD signal.

Lesion location matters: Effects of white matter hyperintensities on grey matter and cognition in the healthy elderly

1.5

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White matter hyperintensities (WMH) are a common phenomenon in the ageing brain. However, little is known about the importance of the WMH location for cognitive functions. In this work we assessed spatial specificity of WMH effects on cognition in healthy, nondemented elderly.

WMH were assessed with T1-weighted MPRAGE and FLAIR images (1 mm isovoxel respectively) in 700 healthy, elderly participants (60–82 years) from the LIFE study (Loeffler et al., 2015) via LesionTOADS, a revalidated segmentation algorithm originally designed for multi-

ple sclerosis lesions (Shiee et al., 2010, NeuroImage, 49, 1524–1535). Cognitive factors were extracted with an exploratory factor analysis from a neurocognitive testing battery. Binary WMH masks were registered into standardised space with ANTS (Avants et al., 2008, Med Image Anal, 12, 26–41), and subsequently multiplied with orthogonalised, *z*-scored cognitive factors to create WMH frequency masks for each respective cognitive factor. Decreased scores of Factor 1 (executive function), Factor 2 (memory/learning), and Factor 3 (motor speed performance) were significantly related to total WMH volume.

All three cognitive factors showed circumscribed clusters in different locations across the white matter. Factor 1 was primarily clustered in the frontal white matter adjacent to the frontal horns; Factor 2 showed the highest cluster size in the parietal white matter; Factor 3 was related to WMH clustering in the upper deep white matter, including the corticospinal tract. All clusters were symmetrical.

Our study shows that WMH have a distinctive impact on different cognitive functions depending on their location across the white matter in the non-demented healthy elderly. We conclude regionally specific, causal effects of WMH for age-related cognitive decline. Furthermore, this study underlines the significance of WMH for subclinical cognitive changes in the healthy elderly. In-depth cognitive testing batteries are a valuable tool to detect early stages of vascular dementia.

Figure 1.5 WMH frequency maps of negative impact: thresholded above 5 on (A) Factor 1 ("Executive Function/Language"), (B) Factor 2 ("Memory/Learning"), and (C) Factor 3 ("Motor Speed Performance"); (D) all three cognitive factors thresholded above 10 with logical colour-coding of intersecting clusters.



1.6 Quantifying the effects of lesions with the tractography-based lesion assessment standard (TractLAS)

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In the clinical setting, structural brain lesions are visually assessed to classify their type, extent, and general location (Wahlund, L.O. et al, 2001, Stroke, 32, 1318–1322), often reported with the clinically-relevant Fazekas score (Fazekas, F. et al., 1987, American Journal of Roentgenology, 149, 351–356). Lesion segmentation approaches can also be used to quantify location, volume, and extent (Bates, E. et al., 2003, Nat Neurosci, 6, 448–450), but there is no information about how lesions may impact the structural connections *between* regions



Figure 1.6.1 (A) Tract-density images from the TractLAS. A single-voxel mask at the GM/WM boundary served as the seed and target mask. Top: 0.5-mm (axial, coronal) and .1-mm (saggital CC) colour-coded TDI - descending cortical spinal tract fibres are notably absent because they are not included in the GM mask. (B) Depiction of streamlines disrupted by a simulated lesion spanning GM and WM in the posterior temporal lobe. Streamlines (red; 1 in 1000 shown) disrupted by the lesion (green) are overlaid on the T1w template and tractography seed mask.

(i.e. quantify the amount of structural disconnection). A network-based perspective could provide a more complete characterisation of the structural impact of lesions (Ovadia-Caro, S. et al., 2013, J Cereb Blood Flow Metab, 33, 1279–1285), however, tractography through lesions is problematic and may result in metrics that are difficult or impossible to compare across individuals. To address these issues, we created a diffusion tractography atlas standard (TractLAS) that can be used to quantify the impact of lesions on brain connectivity.

Thirteen whole-brain diffusion imaging datasets (3T MRI, 60 directions, b=1000) from healthy participants were preprocessed to calculate the diffusion tensor, and fractional anisotropy images were co-registered to MNI space. Individual fODFs were derived with MRtrix (Tournier, J-D. et al., 2007, NeuroImage 35, 1459–1472), and the TractLAS was created by seeding/terminating in the WM/GM boundary of each individual with 50 million streamlines. Individual T1w images were transformed into the standard space, and GM atlases were then back-projected into individual diffusion space to generate region-based streamline connectivity matrices. These matrices were used to calculate the normative connective connective

tivity mean/variability of the TractLAS. To assess disconnection and facilitate comparison with functional data and measures of clinical outcome, patient lesion masks were transformed into individuals' streamline space, affected streamlines were removed, and the matrices were re-computed to generate relative *disconnection matrices*. Super-resolution tract-density images were generated to confirm that the fine details of white-matter trajectories are readily identifiable in our standard (Fig. 1.6.1A). Individual relative disconnection matrices can be computed (without the need for diffusion tractography in patients; Fig. 1.6.1B) and related to measures of clinical behaviour, brain function, and disease progression/recovery (Fig. 1.6.2).

We created a standard model of structural connectivity that can be used to assess and monitor the individual effects of lesions during disease progression and rehabilitation. Our model allows clinicians and researchers to generate individual structural disconnection maps that can be used to quickly identify affected white-matter tracts and connected regions. This network-based approach will help researchers and clinicians understand the complex functional effects of focal brain lesions.



Figure 1.6.2 Preliminary results from patients with white-matter hyperintensities of differing severity. Left column: lesion segmentation. Middle column: 3D rendering of lesions and the streamlines that pass through them (streamline subsampling at 1/1000 for display). Right column: on the right (multicoloured) is the model region to region connectivity matrix after the removal of streamlines passing through the lesion masks (affected matrix); the inset matrix on the left (in red) is the ratio of the affected matrix to the standard model, thus representing a disconnection matrix that highlights the connections that are proportionally most affected.

1.7 Lesion-behaviour analyses in persons with aphasia (PWA)

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Investigating the correlation between lesion patterns and behaviour has been a pillar of neurolinguistic research ever since its inception by the groundbreaking work of Broca, Wernicke, and their followers (Heilman, K.M., 2006, J Clin Neurol, 2:149–162). Previously based on single case studies showing patholinguistic dissociations suggesting separate neuronal networks to afford the respective linguistic process, high resolution imaging and continuous behavioural data can be used to address patho- and neurolinguistic questions in a statistically meaningful way (Bates, E. et al., 2003, Nat Neurosci, 6, 448-450). Our group has (i) targeted clinical issues pertaining to the relevance of syndromatic and symptomatic classifications of the widely variable presentations of aphasia and (ii) addressed a basic question of neurolinguistic research, that is, the interplay between language universals and



Figure 1.7.1 Sketch of lesion symptom associations for syndromes and symptoms based on data of 103 patients.



Figure 1.7.2 Results of an EEG lesion analysis. This analysis suggests that violations of universals of phonotactics rely on dorsal stream processing, while language specifics are processed along the ventral stream. specifics in existing languages. Furthermore, a focus of our group's ongoing research is to use lesion pattern analysis to predict outcome and ideally devise evidencebased therapy depending on the patholinguistic profile.

- (i) In our work we could show that syndrome- and symptom-based classification of aphasias correlates with dissociable patterns of the lesion (Henseler, I. et al., 2014). This is remarkable since previous work has challenged such a tight coupling (Willmes, K., 1993, Brain, 116(Pt 6), 1527–1540). Moreover, the work demonstrates that syndrome- and symptom-based classifications result from an interplay between disease-related (vascular) patterns and neuronal "hubs", affording more or less specific linguistic processes.
- (ii) Regarding basic neurolinguistic research, we used EEG in patients with an acquired left hemispheric brain lesion to disentangle universal and language specific aspects on the linguistic level of phonology (Obrig, H. et al., 2016). Since specific rules govern the way in which phonemes are combined in a given language (phonotactics), we used pseudowords and tested in how far violations of the acquired (Obrig, H. et al., 2016) language specific (German) rules and regularities which have been suggested to form phonotactic universals map to different brain areas. The



general layout of imaging repository

Figure 1.7.3 Sketch of an imaging repository within an international grant (iPraise, within H2020)

results suggest a clear distinction between a more word-form oriented processing of universal rules and a lexico-semantic processing of acquired languagespecific rules.

(iii) Currently we aim at combining the results of (i) with its use for therapy. Using clinically acquired imag-

ing in a cohort of patients undergoing a highly controlled therapy intervention (Breitenstein, C. et al., accepted for publication, Lancet), we ask how imaging may contribute to the outcome prediction and beyond this in how far therapeutic intervention may be tailored according to a multidimensional assessment.

Multimodal imaging (MRI, PET, PET-MRI) in dementia

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Recently, neurodegenerative diseases have been conceptualised in the framework of "molecular nexopathies", where disease-specific changes in brain networks are related to histopathological alterations. Multimodal imaging approaches represent the optimal way to disentangle the relationship between regional networks and molecular changes. Here, in a first step, we identified prototypical disease-specific neural correlates for the most important dementia syndromes such as Alzheimer's disease and subtypes of frontotemporal lobar degeneration (Fig. 1.8) by conducting comprehensive systematic and quantitative meta-analyses and calculating anatomical likelihood estimates, separately for atrophy as measured with MRI and glucose consumption and perfusion as measured with FDG-PET/SPECT (Bisenius et al., 2016; Schroeter & Neumann, 2011, Front Aging Neurosci, 3, 10; Schroeter et al. 2014).

In a second step, we applied these disease-specific networks to enable and improve early individual prediction of dementia syndromes in uni- and multicentric cohorts (Dukart et al., 2011, PLoS One, 6(3):e18111; Dukart et al., 2013, Psychiatry Res, 212(3), 230–236). Based on cuttingedge pattern recognition algorithms—support vector machine classification—we could reliably classify single patients compared to healthy control subjects (diagnosis) and compare them to other disease groups (differential diagnosis) with high accuracy. Of note, accuracy was increased by multimodal imaging, including MRI and FDG-PET and by focusing analyses on meta-analytically generated ROI approaches compared to whole-brain approaches.



1.8



Figure 1.8 illustrates the potential of multimodal MRI/PET in the diagnosis and understanding of neurodegenerative diseases. (A) Neural correlates of behavioural variant frontotemporal dementia as revealed by anatomical likelihood estimates meta-analyses—separately for atrophy (MRI) and glucose metabolism (FDG-PET). (B) Partial volume effect correction (PVEC) for amyloid PET with structural MRI increases sensitivity in revealing amyloid deposits in hippocampal regions in Alzheimer's disease (AD) —in particular in cases with severe atrophy (bottom vs. top images, MTLA mesiotemporal lobe atrophy according to Scheltens Score). Grey matter (GM)-PET denotes analysis limited to GM regions (Schroeter et al., 2014; Tiepolt et al., 2016).

Finally, simultaneous MRI/PET was used to detect histopathological fingerprints in dementia syndromes (Barthel et al., 2015; Schütz et al., 2016; Werner et al., 2016). Here, early amyloid PET images were developed as surrogate biomarkers for neuronal injury in Alzheimer's disease (Tiepolt et al., 2016). As illustrated in Figure 1.8, we applied structural MRI to correct for partial volume effects in amyloid PET scans and, hence, decisively improved the analysis of amyloid PET (Rullmann et al., 2016).

1.9 Transcranial oscillatory stimulation at individual somatosensory alpha frequency specifically decreases network centrality of S1

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Amplitude and phase of ongoing alpha oscillations might reflect the functional state of certain brain networks as has been shown for several sensory systems (Becker, 2011, J Neurosci, 31(30), 11016–11027. For example, we have previously shown that ongoing alpha rhythm inversely relates to local BOLD signal and influences evoked activity in the visual system (Becker et al., 2011, J Neurosci, 31(30),11016-11027) and the somatosensory system (Reinacher et al., 2009, J Neurosci Methods, 183(1), 49-56). Recently, we found that transcranial alternating current stimulation applied at an individual somatosensory mu alpha frequency (mu-tACS) induces a phasic modulation of somatosensory perception, suggesting a causal interference with somatosensory processing (Gundlach et al., 2016). Here, we aimed at investigating underlying functional brain changes on a whole-brain level by concurrent mu-tACS and resting-state functional MRI. Based on the suggested inhibitory nature of alpha, we hypothesised that mu-tACS decreases functional connectivity of the primary somatosensory cortex.

In a randomised single-blind crossover design, 20 healthy subjects underwent 2 separate sessions of functional magnetic resonance imaging during either 6 minutes of mu-tACS applied over the somatosensory cortex or sham stimulation. Eigenvector centrality mapping (ECM) was used to investigate mu-tACS-induced changes (as compared to sham stimulation) in functional connectivity across the whole brain.

In line with our hypothesis, our results demonstrate that mu-tACS induces a specific decrease in whole-brain centrality of the left primary somatosensory cortex (whole-brain analysis, p<.05, cluster corrected, voxelwise threshold: z>2.576, cluster size: 59 voxels). These findings (i) add causal evidence to previous correlative findings and underline the inhibitory nature of functional relevant alpha rhythms, and (ii) demonstrate the potential of transcranial stimulation methods to specifically modulate brain function when adjusting the stimulation to intrinsic oscillatory frequencies.



Figure 1.9 Whole-brain analysis of ECM values during mu-tACS as compared to sham stimulation: mu-tACS induces a specific decrease in whole-brain network centrality of the primary somatosensory cortex.



Cognitive and neural mechanisms underlying the generation of motor hierarchies

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It is widely assumed that the generation of hierarchies in the human brain depends on activity in the inferior frontal gyrus (IFG), particularly in area BA 44 (for reviews see Friederici, A.D. et al., 2011, Biolinguistics, 5(1–2), 087–104; Fitch & Martins, 2014). We tested this assumption for the generation of motor hierarchies using fMRI. We devised an innovative procedure in which the execution of hierarchical sequences could be elicited using three different strategies ("fractal", "iterative", and "repetition", Fig. 1.10 left). We then compared the cognitive and neural mechanisms underlying these strategies. The task is based on the execution of finger movement sequences following a rhythmic structure using the thumb, index, and middle fingers (denoted in red, green, and blue in Fig. 1.10 left) on an MR compatible keyboard. We tested 20 participants and found that the generation of motor hierarchical structures via the application of recursive "fractal" rules was supported by a neural system used for motor learning, planning, and imaging in general (Elsinger et al., 2006, NeuroImage, 31(3), 1177–1187; Hardwick et al., 2013, NeuroImage, 67, 283–297; Hétu et al., 2013, Neurosci Biobehav Rev, 37(5), 930–949) (Fig. 1.10 right) and did not seem to require the recruitment of multi-domain systems hypothesised to play a crucial and specific role in the processing of hierarchies (e.g. BA 44). While these other neural systems might be important to parse hierarchical structures, they do not seem to be specific for the contrast tapping into the generation of new hierarchical levels, which is at the core of generative procedures.



1.10



Figure 1.10 Fractals in action. Left: experimental design and contrasting conditions (I, II, and III denote the iterative steps used to generate hierarchical structures. d_1 , d_2 , and d_3 denote the duration of each key press in the respective generating steps); Right: fMRI results (N = 20): the generation of new hierarchical levels (in the "planning phase", between steps II and II) specifically activated regions within the somatomotor and premotor cortices, cerebellum, lateral occipital cortex, and the left pallidum.

This finding is consistent with previous work in the visual-spatial domain (Martins et al., 2014). In these experiments, we showed that the generation of new hierarchical levels is represented by brain networks that bind information from the visual ventral and visual dorsal streams (Kravitz et al., 2011, Nat Rev Neurosci, 12(4), 217– 230). Again, we found no specific activations within IFG, suggesting that the generation of new hierarchical levels, at least in the motor and visual domains, might also be achieved using domain-specific mechanisms.

1.11 Quantification and physiological specification of training-related motor plasticity: The Multi-Modal Plasticity Initiative (mMPI)

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Noninvasive neuroimaging can identify brain plasticity associated with learning and training (Draganski et al., 2004, Nature, 427, 311–312). We and others have contributed evidence for some rapid, transient (Taubert et al., 2016), as well as slow and persistent (Taubert et al, 2011, NeuroImage, 57, 1492-1498; Penhune & Steele, 2012, Behav Brain Res, 226, 579-591; Steele & Penhune, 2010, J Neurosci, 30, 8332–8341) neural and vascular changes upon motor learning (multiphase model of brain plasticity). However, current evidence for training-related neuroplasticity is primarily based on studies investigating between one and three physiologically ambiguous imaging metrics over the course of longitudinal training (Draganski & Kherif, 2013, NeuroImage, 2013, 73, 255-259). With some exceptions, studies utilise T1-weighted (T1w) images as a proxy to assess grey matter structure, fractional anisotropy (FA) for white matter structure, and BOLD fMRI for brain function. Both T1w and BOLD fMRI are non-quantitative measures and, as with FA, the relationship to the underlying physiology is ambiguousmaking longitudinal assessment and physiological inference of plasticity-related changes problematic (Tardif et al., 2016).

Current evidence for training-related neuroplasticity is primarily based on studies investigating between one and three imaging metrics over the course of longitudinal training (Draganski & Kherif, 2013, NeuroImage, 2013, 73, 255–259). The Multi-Modal Plasticity Initiative (mMPI) was formed to address these issues. Based on quantitative high-field MR imaging and new computational pipelines for data integration and analysis, it will provide physiological and quantitative specificity for our understanding of human neuroplasticity. Our aim is to develop the first quantitative and physiologically-informed model of human neuroplasticity.

Participants were scanned with a 7T MRI scanner (32-channel head coil, Siemens) three times over the course of five days of training on a sequential pinch force task (Gryga et al., 2012, Front Syst Neurosci, 6, 37). Each participant was also scanned prior to training onset to establish baseline brain structure and function, and to collect a functional localiser, and in a follow-up scan one


Figure 1.11.1 Multi-modal MRI segmentation and analysis: (A) Quantitative contrasts extracted from multi-modal MRI mapped onto the cortex of one subject, (B) Dominant modes of variation across the cortex and their weighting among the contrast for 5 different subjects, (C) Brain and cortex segmentation obtained from DWI, compared to the segmentation of T1-weighted images.

week after the cessation of training. Our multi-modal MRI battery includes MP2RAGE T1 maps (qT1,PD,T1w), T2* (QSM), DWI (FA,MD), ASL (resting: rCBF), high resolution BOLD fMRI (resting state: rsfMRI, 1.2-mm isometric, 1.1-s TR), and vascular space occupancy during task performance (interleaved BOLD/VASO: relative blood volume). We are currently completing data collection for this project, with a planned total of 20 active participants (trained on a difficult learning sequence and baseline control sequence) and an additional 20 controls (trained only on the baseline control sequence).

We have developed new computational pipelines to coregister all these MR contrasts in space and time in order to study common and diverging patterns of change. Additionally, we performed brain and cortex segmentations and estimations of cortical and myelinated thickness (Rowley et al., 2015) and were able to extract distinct modes of spatial variation in structural parameters across the cortex (Fig. 1.11.1A, B), corresponding in decreasing order to indications of myelination, diffusivity, and iron content.

As co-registering different contrasts with distortions and artefacts is challenging, we have also explored methods to segment and analyse brain images from contrasts other than T1-weighted, starting with diffusion imaging. We have established a procedure to build atlases of intensity priors from contrasts co-registered to T1-weighted data in order to adapt our multi-contrast segmentation method (Bazin et al., 2014) to process FA and MD maps, and to automatically adjust the priors to match the segmentations (Fig. 1.11.1C).



Figure 1.11.2 Mean rsfMRI time course from a single subject. The high spatial resolution makes it possible to identify small details such as cortical folding and subcortical structures on the functional image (1.2-mm isometric).

These methods will be complemented with new tools for longitudinal segmentation, inter-subject registration (Tardif et al., 2015), vasculature segmentation (Bazin et al., 2016), hippocampal labelling, and longitudinal statistics to support our ongoing plasticity studies. The resulting pipelines will be integrated into open access and open source software (http://www.nitrc.org/projects/cbstools/ and http://www.github.com/piloubazin/cbstoolspublic/) to promote reproducibility and Open Science.

Towards quantitative assessment of brain plasticity

We first set out to characterise the resting-state fMRI changes over the course of learning. Most previous studies measured only relatively few time points and employed analysis methods that are difficult to interpret over the course of learning (e.g. independent component analyses), making the characterisation of the specific time course of functional plasticity during motor learning problematic. The mMPI more finely characterises functional plasticity with higher spatial resolution (1.2-



Figure 1.11.3 Comparison between BOLD and VASO. Left top: M1 region of interest time course for a single subject; Left bottom: map of temporal signal to noise ratio showing greater specificity for grey matter with VASO. Right: Z-statistics illustrate the significant correlation between force production and BOLD/VASO on the first day of training. (A=anterior; R=right; PMC=premotor cortex; SMA=supplementary motor area; PLs=superior parietal lobule)

mm isometric) and temporal sampling (5 time points over the course of learning, with a 1.1-s TR to more accurately assess functional networks) to address this issue (Fig. 1.11.2).

The image processing pipeline for calculating eigenvector centrality maps (ECM) and seed-based functional correlations in regions of interest has been under development and is currently being used to process the highresolution ECM maps. Once the data collection is finalised and processing is complete, rsfMRI metrics (ECM, seed-based correlations) will be compared across time, between groups, and modulated with behavioural performance to determine the time course of alterations in the networks supporting training-related functional plasticity. This work will be combined with the task-based functional and longitudinal structural data to specify the physiological relevance of BOLD rsfMRI changes and derive the first multimodal model of training-related neuroplasticity. This work will be further specified by reference to the interleaved BOLD and VASO functional images that were acquired during task performance. In an initial step, we assessed whether or not VASO results in increased spatial specificity within the first session of learning. We found that VASO was more spatially specific (primarily restricted to grey matter regions) and significantly less influenced by draining veins when compared to BOLD, but had decreased temporal SNR (Fig. 1.11.3). This work will be extended to assess training-related changes over the course of learning, with the hypothesis that VASO provides a more spatially- and physiologically-specific measure of functional plasticity that can be better linked with concomitant rsfMRI and structural changes.

Mirror motor activity during right-hand contractions and its relation to white matter in the posterior midbody of the corpus callosum

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Cortical activity during simple unimanual actions is typically lateralised to contralateral sensorimotor areas, while a more bilateral pattern is observed with an increase in task demands. In parallel, increasing task demands are associated with subtle mirror muscle activity in the resting hand, implying a relative loss in motor selectivity. The corpus callosum (CC) is crucially involved in unimanual tasks by mediating both facilitatory and inhibitory interactions between bilateral motor cortical systems, but its association with mirror motor activity is yet unknown. Here, we used diffusion-weighted imaging and bilateral electromyographic (EMG) measurements during a unimanual task to investigate potential relationships between white matter microstructure of the CC and mirror EMG activity. Participants performed a unimanual pinch force task with both hands alternatively. Four parametrically increasing force levels were exerted while EMG activity was recorded bilaterally from first dorsal interosseus muscles. Consistent with previous findings, mirror EMG activity increased as a function of force. Additionally, there was a significant relationship between the slope of increasing mirror EMG during right-hand contractions and fractional anisotropy in transcallosal fibres connecting both primary motor cortices. No significant relationships were found for fibres connecting dorsal premotor cortices or supplementary motor area, indicating the local specificity of the observed brain–physiology relationship.





Partial correlation controlled for age, sex, and Δ – FA SMA fibres and FA PMd fibres $\Delta\Delta$ – FA M1 fibres and FA PMd fibres $\Delta\Delta\Delta$ – FA M1 fibres and FA SMA fibres

Figure 1.12 Probabilistic tractography of transcallosal fibres using DWI. Seed regions for interhemispheric tractography in bilateral M1, S1, SMA, and PMd (upper panel, left side). Interhemispheric fibre tracts were found for all brain areas tested. Note the craniocaudal somatotopic and partially overlapping topography of the callosal fibres connecting bilateral M1, SMA, and PMd (lower panel and upper panel, right side).

1.12

1.13 Serotonin, sex hormones, and neuroplasticity

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Serotonin shapes brain networks and modulates a wide spectrum of neuronal function ranging from perception and cognitive appraisal to emotional responses and mood. Given the significant interplay between serotonin and sex hormones in brain organisation (Barth, Villringer & Sacher, 2015), the Emotion NeuroimaGingG (EGG) Lab aims to unravel neuroplastic processes on an acute time scale through two fundamental directions: (1) Harnessing hormonal transition periods as natural experimental conditions, we investigate how physiological fluctuations of sex hormones impact mood (Sacher et al., 2015), behaviour (Hoyer et al., 2013, PLoS One, 8(4)), and brain functional (Arelin et al., 2015) and structural connectivity (Barth et al, 2016). Exploring hippocampal dynamics across the menstrual cycle *in vivo*, we found significant modulations in hippocampal microstructure



Figure 1.13 Estrogen-modulated FA differences and time course across the menstrual cycle in the bilateral hippocampus. Threshold-Free Cluster Enhancement (TFCE) voxelwise FA correlation with respective oestrogen levels in hippocampal ROI-masks left (A) and right (B) hippocampus are displayed. Red voxels outlined in black, superimposed on respective t-values, correspond to significant FWE-corrected results (p < 0.05). In (C), FA (left) and RD (right) values from significant clusters, respectively peak voxel, are extracted and plotted versus oestrogen levels (in red) across the menstrual cycles assessed.

associated with physiological sex-hormonal changes. Based on 30 sequential diffusion-weighted imaging scans of a single healthy female subject, we observed a significant positive correlation between fractional anisotropy (FA) values and oestrogen in the hippocampus bilaterally, revealing a peak in FA closely parallelling ovulation (Fig. 1.13). In light of recent attempts to neurally phenotype single humans, our findings suggest the combination of menstrual cycle monitoring in parallel with highly sampled individual neuroimaging data to address fundamental questions about the dynamics of plasticity in the female brain. (2) We study the effects of short-term serotonergic challenges on brain function (Barth et al, 2015), connectivity (Schaefer et al., 2014), and—using positron emission tomography (PET) in cooperation with the Clinic for Nuclear Medicine at University Hospital Leipzig-the interaction between

the serotonin transporter and neurotrophins (Sacher et al., 2016, ACNP, W113). Our recent findings suggest that even in health, acute serotonergic modulation influences brain responses of emotional processing depending on cognitive demands (Barth et al., 2015, ECNP, P.1.026). Further studies are underway to test the hypothesis that serotonergic drugs can enhance neuroplasticity during learning and recovery after lesions, which offers a perspective for rehabilitation or psychotherapy, for example (Castren, 2005, Nat Rev Neurosci, 6(3), 241-246; Maya Vetencourt et al., 2008, Science, 320(5874), 385-388). Building on our previous work (Schaefer et al., 2016) and with regard to clinical studies in stroke patients (Chollet et al., 2011, Lancet Neurol, 10(2), 123–130), we combine pharmaco-rsfMRI with motor learning tasks in order to test for SSRI-enhanced plasticity in the motor network.

Modulation of dopamine-related movement parameters with music

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Neuro-scientifically informed music-associated therapy is a highly promising novel approach for medical/social intervention. Our group investigates neural and molecular mechanisms underlying the beneficial effect of music in healthy subjects and several patient groups (Fritz, 2016; Fritz et al., 2013; Front Neurosci, 10(448); Fritz et al., 2013; Proc Natl Acad Sci, 110(44), 17784–17789; Fritz et al., 2015). One key element of the effect of music is



Figure 1.14 Effect of valence of music on spatial and kinematic gait parameters (velocity, stride length, step length) in PD patients. Post hoc tests with Bonferroni correction revealed a significant (*) difference between consonant and dissonant music for velocity (p = .021; d = 0.3), step length (p = .016; d = 0.2), and stride length (p = .026; d = 0.2). Dissonant music was also shown to significantly deteriorate stride length compared to silence (p = .020). Error bars represent standard error.





1.14

certainly the dopaminergic system. In an fMRI study, we recently showed that one major network node, the ventral striatum/nucleus accumbens, is crucial in the temporal dynamics of a mediation of a reward response during music listening (Mueller et al., 2015). In a recent PET-MRI study in collaboration with the Clinic for Nuclear Medicine at the University of Leipzig, we furthermore showed for the first time that the brain response to music is not exclusively mediated by the D2-receptor system, but also involves the D1-receptor system.

In the current study, we investigated the effect of music in patients suffering from Parkinson's disease (PD). It was previously shown that PD patients experience a greater temporal de-freezing and otherwise relief of their symptoms during music listening than with visual or tactile stimulation (Lim et al., 2005, Clin Rehabil, 19(7), 695–713). The beneficial effects of music have been shown to positively influence gait kinematics (Brown et al., 2009, Arch Phys Med Rehabil, 90(9), 1578–1583; de Bruin et al., 2010,

Parkinsons Dis, 1578–1583; Thaut et al., 1996, Mov disord, 11(2), 193–200), but it has remained unclear whether this is due to only rhythm or also positive emotional response. Thus, in the current study, we systematically varied the perceived pleasantness of music with sensory consonance/dissonance in 18 PD patients while controlling for beat. As illustrated in Figure 1.14, we found that musical pleasantness modulated spatial and kinematic gait parameters that were previously reported to be dopamine sensitive, namely velocity, step length, and stride length (Blin et al., 1991, J Neurol Sci, 103(1), 51-54), whereas temporal kinetic parameters that have previously been shown to be dopamine resistant were not affected. This strongly suggests that the observed influence of musical pleasantness/unpleasantness on gait was mediated by dopamine and that perceived unpleasantness in audio-feedback paradigms can have detrimental effects on motor performance.

Congresses, Workshops, and Symposia

2014

- Villringer, A. & Babayan, A. (March). 2nd Mind, Brain, and Body Symposium. Mind-Brain Institute at Berlin School of Mind and Brain, Humboldt University, Berlin, Germany.
- Horstmann, A. (May). The body in the mind: Neural mechanisms of "embodiment" – Evidence from basic research and its relevance for psychopathology. Symposium. 2nd Meeting of the Society for Cognitive and Affective Neuroscience, Dortmund, Germany.
- Sacher, J. (May). Sex-Hormone Fluctuations as a Risk Model for Postpartum Mood Disorders. Joint Symposium. 69th Meeting of the Society of Biological Psychiatry (SOBP). New York City, USA.
- Villringer, A. (June). Brain Machine Interfaces: Foundations and Perspectives. LOC Symposium. 20th Annual Meeting of the Organization for Human Brain Mapping (OHBM). Hamburg, Germany.
- Villringer, A. & Babayan, A.(June). 1st Joined Turkish-German Symposium on Human Neuroscience. Humboldt University Berlin, Germany.
- Villringer, A. & Babayan, A. (August). *Leipzig Cohort for Mind-Body-Emotion Interactions (LEMON)*. Annual Meeting. Martin Luther University Halle-Wittenberg, Wittenberg, Germany.

2015 -

- Villringer, A. (January). Competence Network Stroke: Brain-Body-Interaction in Stroke. Symposium. Meeting of Neuro Intensive Medicine (ANIM). Deutsche Gesellschaft für NeuroIntensivMedizin and Notfallmedizin [German Society for Neuro Intensive Medicine and Emergency Medicine] (DGNI), Deutsche Schlaganfall-Gesellschaft [German Stroke Society] (DSG), Berlin, Germany.
- Villringer, A. (March). 6. Internationales Schlaganfallsymposium, Kompetenznetz Schlaganfall (KNS) & Centrum für Schlaganfallforschung Berlin (CSB) [6th International Stroke Symposium, Competence Network Stroke & Centre for Stroke Research Berlin]. Competence Network Stroke, Leipzig, Germany.
- Villringer, A. & Babayan, A. (March). 3th Mind, Brain, and Body Symposium. Symposium. Mind-Brain Institute at Berlin School of Mind and Brain, Humboldt University, Berlin, Germany.

2016.

- Babayan, A., Lachmann, U., Gaebler, M. & Villringer, A. (March). 4th Mind, Brain, and Body Symposium. Mind-Brain Institute at Berlin School of Mind and Brain, Humboldt University, Berlin, Germany.
- Deserno, L. (May). Dimensional approaches to psychiatric phenomena – implications from subclinical, clinical and transdiagnostic studies. Konferenz Psychologie und Gehirn [Conference Psychology and Brain], Berlin, Germany.
- Fritz, T. (July). Sport Innovation Network. Workshop. Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.

- Villringer, A. (November). *Mind the Brain! Mind the Brain!* Symposium on Neuroscience in Society. Humboldt University Berlin, Germany.
- Villringer, A. (November). 5. Prophylaxe-Seminar des Kompetenznetzes Schlagfanfall [5th Prophylaxis Seminar of the Competence Network Stroke]. Symposium. Leipzig, Germany.
- Schroeter, M. L. & Eickhoff, S. (November). Conceptualizing psychiatric disorders using meta-analyses and multimodal imaging. Annual Meeting DGPPN, Berlin, Germany.
- Schroeter, M. L. & Kloeppel, S. (November). Ethische Aspekte der Frühdiagnostik von Demenzen. [Ethical aspects of early diagnosis of dementia syndromes]. Annual Meeting DGPPN. Berlin, Germany.
- Schroeter, M. L. & Jessen, F. (November). Validierung bildgebender Verfahren für neurodegenerative Erkrankungen mit multizentrischen Studien. [Validating imaging approaches for neurodegenerative diseases with multi-centric studies]. Annual Meeting DGPPN. Berlin, Germany.
- Neumann, J. (June). Model-based Neuroscience Summer School. University of Amsterdam, The Netherlands.
- Villringer, A. (July). Summer School, IMPRS NeuroCom. Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.
- Deserno, L. & Mathys, C. (September). Computational approaches to schizophrenia. 5th European Congress of the Schizophrenia Research, Berlin, Germany.
- Horstmann, A. (September). 1st Leipzig International Meeting for Interdisciplinary Obesity Research (LIMIOR). Conference. Leipzig, Germany.
- Grund, M. (November). 14th Max Planck PhDnet General Meeting. Conference. Max Planck Institute for Solar System Research, Goettingen, Germany.
- Villringer, A. (November). 6. Prophylaxe-Seminar des Kompetenznetzes Schlagfanfall [6th Prophylaxis Seminar of the Competence Network Stroke]. Symposium. Leipzig, Germany.
- Villringer, A. (July). Summer School, IMPRS NeuroCom. Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.
- Deserno, L. & Cools, R. (September). Dopamine and flexible decision-making in humans. Conference Dopamine, Medical University of Vienna, Austria.
- Fritz, T. (September). Sportmarket USA. Workshop. Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.
- Grund, M. (September). 2nd Max Planck Career Fair. Conference. Harnack House Berlin, Germany.

- Grund, M. (September). 5th Visions in Science Break the Enigma. Conference. Harnack House, Berlin, Germany.
- Sacher, J. & Kreil, J. (September). Gender prospects in medicine (GPmed). Symposium. University of Leipzig, Germany.
- Grund, M. (November). 15th Max Planck PhDnet General Meeting. Conference. Max Planck Institute for Infection Biology, Berlin, Germany.

Degrees

Habilitation Theses

2016.

 Sacher, J. Modulators of individual responses to psychopharmacological intervention. University of Leipzig, Germany.

PhD Theses

2014

Bareither, I. Subliminal stimulation and inhibition of visual processing. Humboldt University Berlin, Germany.

2015.

- Goltz, D. Sustained spatial attention in touch: underlying brain areas and their interaction. University of Leipzig, Germany.
- Hellrung, L. Softwareframework zur universellen Methodenentwicklung f
 ür ein fMRT-BCI: Adaptive Paradigmen und Echtzeitanalyse. University of Leipzig, Germany.
- Kipping, J. Functional neuroanatomy of the cerebello-cerebral systems. Humboldt University Berlin, Germany.
- Long, X. Parcellation of the sensorimotor cortex of human brain and an acupuncture study on the somatosensory system. University of Leipzig, Germany.

2016.

 Hoyer, J. Peripheral physiological responses to distinct stressors: associations with behavioral and neural measures. University of Leipzig, Germany.

MD Theses

2014

- Benk, F. Transfereffekte zweier Arbeitsgedächtsnistrainings auf die kognitive Kontrolle im Vergleich. University of Leipzig, Germany.
- Jakuszeit, M. Top-down-Vorhersagen des linken inferiorfrontalen Kortex in der frühen Syntaxverarbeitung, untersucht anhand ereigniskorrelierter Potentiale bei Schlaganfall-Patienten. University of Leipzig, Germany.

2015.

 Burmann, I. Eine Einzeldosis des selektiven Serotonin-Wiederaufnahmehemmers Escitalopram verändert die funktionale Netzwerkorganisation des Gehirns. University of Leipzig, Germany.

- Horstmann, A. (November). Interaktion gesellschaftlicher und neurobiologischer Aspekte bei Adipositas [Interaction social and neurobiological aspects in obesity]. Symposium. 32nd Annual Meeting of the German Association for the Study of Obesity, Frankfurt, Germany.
- Villringer, A. (December). 7. Prophylaxe-Seminar des Kompetenz netzes Schlagfanfall [7th Prophylaxis Seminar of the Competence Network Stroke]. Symposium. Leipzig, Germany.
- Sehm, B. Neuroplastizität des menschlichen Gehirns: Mechanismen und Modulation mittels nicht-invasiver Hirnstimulation. [Neuroplasticity of the human brain: Mechanisms and modulation via non-invasive brain stimulation]. University of Leipzig, Germany.
- Macher, K. Influence of cerebellar tDCS on verbal working memory. University of Leipzig, Germany.
- Nierhaus, T. Investigation of neuronal inhibition during cortical processing of somatosensory stimulation by means of EEG and fMRI. Humboldt University Berlin, Germany.
- Quinque, E. M. Brain, mood and cognition in hypothyroidism. University of Leipzig, Germany.
- Rohr, C. Aspects of emotion processing in the brain's functional organization. Humboldt University Berlin, Germany.
- Schäfer, A. Identifying changes of functional brain networks using graph theory. University of Leipzig, Germany.
- Thiel, S. Mechanisms underlying somatosensory perception in humans. Humboldt University Berlin, Germany.
- Ovadia-Caro, S. Plasticity following stroke: the recovery of functional networks as measured by resting-state functional connectivity. Humboldt University Berlin, Germany.
- Kohlhoff, E. Circadianrhythmik von Aufmerksamkeitsfunktionen bei extremen Chronotypen [Circadian rhythms of attentive functions in extreme chronotypes]. University of Leipzig, Germany.
- Frauenheim, M. Motorische Reorganisation bei Hirntumoren – eine fMRT Verlaufsstudie. University of Leipzig, Germany.

 Kaminski, J. Stimulationsintensitäten in kognitiven Paradigmen [Stimulation intensities in cognitive paradigms]. University of Leipzig, Germany.

2016_

2014

- Klose, L. Zusammenhänge kognitiver Fähigkeiten und der Befindlichkeit bei Patientinnen mit Hepatitis C aus der Anti-D-Kohorte. University of Leipzig, Germany.
- Köhlert, K. Disruption oft the right temporoparietal junction using transcranial magnetic stimulation impairs the control of shared representations of action. University of Leipzig, Germany.
- Krabs, R. U. Der Einfluss von Musik auf das autonome Nervensystem von gesunden Probanden und Morbus Crohn-Patienten. University of Leipzig, Germany.
- Riedel, P. The visual cortex in auditory-only speech recognition-a neurostimulation approach. University of Leipzig, Germany.

Appointments

- Schnitzler, T. Der Einfluss von transkranieller Gleichstromstimulation auf das perzeptuelle Lernen degradierter Sprache. University of Leipzig, Germany.
- Schmidt, U. Anatomische Konnektivität von kortiko-subkortikalen Netzwerken mittels diffusionsgewichteter Bildgebung. University of Leipzig, Germany.
- Schreiber, J. Untersuchung des Einflusses von Persönlichkeitscharakteristika und Bewältigungsstrategien auf den Blutdruck bei Essentieller Hypertonie [The influence of personality traits and coping strategies on blood pressure in a sample with essential hypertension]. University of Leipzig, Germany.
- Woost, T. Neurale Korrelate des DemTect bei Patienten mit Alzheimer-Krankheit und frontotemporaler Lobärdegeneration [Neural correlates of DemTect in patients with Alzheimer's disease and frontotemporal lobar degeneration]. University of Leipzig, Germany.
- Gauthier, C. Assistant Professorship. Concordia University Pleger, B. W2 Professorship. University of Leipzig, Germany. Montreal, Canada. Ragert, P. W3 Professorship. University of Leipzig, Germany. 2015 -Fritz, T. Visiting Professorship. Ghent University, Belgium Sacher, J. W2 Minerva Research Group Leader position (in Department of Neurology). Max Planck Institute for Human Brain and Cognitive Sciences, Leipzig, Germany. 2016_ Neumann, J. W2 Professorship. University of Applied Taubert, M. W2 Professorship. Otto von Guericke University Sciences Jena, Germany. Magdeburg, Germany. Schlagenhauf, F. Heisenberg Professorship. Charité University Villringer, A. Adjunct Professorship, Medical University of Medicine Berlin, Germany. Vienna, Austria.
- Sehm, B. Private Lecturer (Privatdozent). University of Leipzig, Germany.

Awards

2014 Polyakova, M. et al. Poster Award. Research Festival, Deserno, L. Hans Heimann Award 2014. German Society for Psychiatry, Psychotherapy and Psychosomatics (DGPPN), Department of Psychiatry, University Hospital Leipzig, Germany. Germany. Mauricio, M. Best PhD presentation - Science Day 2014. Schroeter, M. L. Hirnliga Award. Hirnliga e.V., Wiehl, University of Vienna, Austria. Germany. Mauricio, M. Hurford Prize, 10th International Conference on Sjoerds, Z. Rubicon fellowship. Netherland's Organization the Evolution of Language, Vienna, Austria. for Scientific Research, Earth and Life Sciences cluster, the Netherlands. 2015 Deserno, L. Robert Koch Award. Charité University Medicine Deserno, L. Young Investigator Award. 15th International Congress on Schizophrenia Research, Colorado Springs, Berlin, Germany. USA.

- Kynast, J. et al. Poster Award. 3rd International Conference on Alzheimer's Disease & Dementia, Toronto, Canada.
- Neumann, J. Model-based Neuroscience Summer School.
 Summer School. Universiteit van Amsterdam, Amsterdam, The Netherlands

2016_

- Horstmann, A. DAG Research Award. Deutsche Adipositas Gesellschaft (DAG), Germany.
- Horstmann, A. "Sign Up! Careerbuilding". Max Planck Society, Germany.
- Kauffmann, L. PhD Award. French Society for Research in Magnetic Resonance Imaging, France.

Publications

Books & Book Chapters

Fritz, T. (2016). Musik - Eine grenzübergreifende Sprache? In G. Hofmann (Ed.), *Musik - Ein Spiel mit Grenzen und Entgrenzung* (pp. 9–21). Augsburg: Wißner.

Fritz, T. (in press). Jymmin - The medical potential of musical euphoria. In M. Lesaffre, P.-J. Maes, & M. Leman (Eds.), *The Routledge companion to embodied music interaction*. London: Routledge.

Goltz, D. (2015). Sustained spatial attention in touch: Underlying brain areas and their interaction. *MPI Series in Human Cognitive and Brain Sciences: Vol. 167*. Leipzig: Max Planck Institute for Human Cognitive and Brain Sciences.

Horstmann, A. (2015). The brain's got a taste for good food. In N. Avena (Ed.), *Hedonic eating: How the pleasurable aspects of food can affect our brains and behavior* (pp. 39–55). Oxford: Oxford University Press.

Macher, K. (2014). Die Beteiligung des Cerebellums am verbalen Arbeitsgedächtnis. *MPI Series in Human Cognitive and Brain Sciences: Vol. 158.* Leipzig: Max Planck Institute for Human Cognitive and Brain Sciences.

Mackey, S., Kan, K.-J., Chaarani, B., Alia-Klein, N., Batalla, A., Brooks, S., Cousijn, J., Dagher, A., de Ruiter, M., Desrivieres, S., Feldstein Ewing, S. W., Goldstein, R. Z., Goudriaan, A. E., Heitzeg, M. M., Hutchison, K., Li, C.-S.-R., London, E. D., Lorenzetti, V., Luijten, M., Martin-Santos, R., Morales, A. M., Paulus, M. P., Paus, T., Pearlson, G., Schluter, R., Momenan, R., Schmaal, L., Schumann, G., Sinha, R., Sjoerds, Z., Stein, D. J., Stein, E. A., Solowij, N., Tapert, S., Uhlmann, A., Veltmann, D., van Holst, R., Walter, H., Wright, M. J., Yucel, M., Yurgelun-Todd, D., Hibar, D. P., Jahanshad, N., Thompson, P. M., Glahn, D. C., Garavan, H., & Conrod, P. (2016). Genetic imaging consortium for addiction medicine: From neuroimaging to genes. In H. Ekhtiari, & M. P. Paulus (Eds.), *Neuroscience for addiction medicine: From prevention to rehabilitation; Methods and interventions* (pp. 203–223). Amsterdam: Elsevier. doi:10.1016/bs.pbr.2015.07.026.

- Schaare, L. Alberto Malliani Travel Grant. Alberto Malliani Association for Ethics and Research in Medicine, Italy.
- Sehm, B. *Research Award*. German Parkinson Association. Germany.
- Sjoerds, Z. Top Poster Award. Society of Biological Psychiatry. Jacksonville, USA.
- Mauricio, M. Best paper of 2015. Portuguese Association of Experimental Psychology, Portugal.
- Sacher, J. NARSAD Young Investigator Award. Brain & Behavior Research Foundation, USA.
- Sacher, J. "Sign Up! Careerbuilding". Max Planck Society, Germany.

Poessel, M. (2015). Sexueller Kindesmissbrauch -Unterscheidungsmerkmale in der soziosexuellen Entwicklung von Tätern mit und ohne Pädophilie. In W. Driemeyer, L. Rustige, B. Gedrose, & A. Hoyer (Eds.), *Grenzverschiebungen des Sexuellen: Perspektiven einer jungen Sexualwissenschaft* (pp. 43–60). Gießen: Psychosozial-Verlag.

Quinque, E. M. (2015). Brain, mood and cognition in hypothyroidism. *MPI Series in Human Cognitive and Brain Sciences: Vol. 171*. Leipzig: Max Planck Institute for Human Cognitive and Brain Sciences.

Sehm, B., & Obrig, H. (in press). Transkranielle Gleichstrom-Stimulation zur Unterstützung der Sprachtherapie: Wissenschaftliche Evidenz und klinische Perspektiven. In K. Bilda, J. Mühlhaus, & U. Ritterfeld (Eds.), *Neue Technologien in der Sprachtherapie*. Stuttgart: Thieme.

Watson, J., Welman, K. E., & Sehm, B. (in press). The effect of exercise on motor function and neuroplasticity in Parkinson's disease. In R. Watson (Ed.), *Physical activity and the aging brain: Effects of exercise on neurological function*. Amsterdam: Elsevier.

Journal Articles

Accolla, E. A., Aust, S., Merkl, A., Schneider, G.-H., Kühn, A. A., Bajbouj, M., & Draganski, B. (2016). Deep brain stimulation of the posterior gyrus rectus region for treatment resistant depression. *Journal of Affective Disorders, 194*, 33–37. doi:10.1016/j. jad.2016.01.022.

Accolla, E. A., Dukart, J., Helms, G., Weiskopf, N., Kherif, F., Lutti, A., Chowdhury, R., Hetzer, S., Haynes, J.-D., Kühn, A. A., & Draganski, B. (2014). Brain tissue properties differentiate between motor and limbic basal ganglia circuits. *Human Brain Mapping*, *35*(10), 5083–5092. doi:10.1002/hbm.22533.

Adamaszek, M., D'Agata, F., Kirkby, K. C., Trenner, M. U., Sehm, B., Steele, C., Berneiser, J., & Strecker, K. (2014). Impairment of emotional facial expression and prosody discrimination due to ischemic cerebellar lesions. *The Cerebellum*, *13*(3), 338–345. doi:10.1007/s12311-013-0537-0.

Adamaszek, M., Kirkby, K. C., D'Agata, F., Olbrich, S., Langner, S., Steele, C., Sehm, B., Busse, S., Kessler, C., & Hamm, A. (2015). Neural correlates of impaired emotional face recognition in cerebellar lesions. *Brain Research*, *1613*, 1–12. doi:10.1016/j. brainres.2015.01.027.

Albuquerque, L., Martins, M., Coelho, M., Guedes, L., Ferreira, J. J., Rosa, M., & Martins, I. P. (2016). Advanced Parkinson disease patients have impairment in prosody processing. *Journal of Clinical and Experimental Neuropsychology, 38*(2), 208–216. doi: 10.1080/13803395.2015.1100279.

Arélin, K., Mueller, K., Barth, C., Rekkas, P. V., Kratzsch, J., Burmann, I., Villringer, A., & Sacher, J. (2015). Progesterone mediates brain functional connectivity changes during the menstrual cycle: A pilot resting state MRI study. *Frontiers in Neuroscience*, *9*: 44. doi:10.3389/fnins.2015.00044.

Ashbrook, D. G., Delprato, A., Grellmann, C., Klein, M., Wetzel, R., Overall, R. W., & Badea, A. (2014). Transcript co-variance with Nestin in two mouse genetic reference populations identifies Lef1 as a novel candidate regulator of neural precursor cell proliferation in the adult hippocampus. *Frontiers in Neuroscience, 8*: 418. doi:10.3389/fnins.2014.00418.

Aybek, S., Nicholson, T. R. J., Draganski, B., Daly, E., Murphy, D. G., David, A. S., & Kanaan, R. A. (2014). Grey matter changes in motor conversion disorder. *Journal of Neurology, Neurosurgery & Psychiatry, 85*(2), 236–238. doi:10.1136/jnnp-2012-304158.

Bareither, I., Chaumon, M., Bernasconi, F., Villringer, A., & Busch, N. A. (2014). Invisible visual stimuli elicit increases in alpha-band power. *Journal of Neurophysiology, 112*(5), 1082–1090. doi:10.1152/jn.00550.2013.

Bareither, I., Villringer, A., & Busch, N. A. (2014). Decreased visual detection during subliminal stimulation. *Journal of Vision*, *14*(12): 20. doi:10.1167/14.12.20.

Barth, C., Steele, C., Mueller, K., Rekkas, V. P., Arélin, K., Pampel, A., Burmann, I., Kratzsch, J., Villringer, A., & Sacher, J. (2016). Invivo dynamics of the human hippocampus across the menstrual cycle. *Scientific Reports, 6*: 32833. doi:10.1038/srep32833.

Barth, C., Villringer, A., & Sacher, J. (2015). Sex hormones affect neurotransmitters and shape the adult female brain during hormonal transition periods. *Frontiers in Neuroscience*, *9*: 37. doi:10.3389/fnins.2015.00037.

Barthel, H., Schroeter, M. L., Hoffmann, K.-T., & Sabri, O. (2015). PET/MR in dementia and other neurodegenerative diseases. *Seminars in Nuclear Medicine*, *45*(3), 224–233. doi:10.1053/j.semnuclmed.2014.12.003.

Bazin, P.-L., Weiss, M., Dinse, J., Schäfer, A., Trampel, R., & Turner, R. (2014). A computational framework for ultra-high resolution cortical segmentation at 7 Tesla. *NeuroImage*, *93*(2), 201–209. doi:10.1016/j.neuroimage.2013.03.077.

Benoit, C.-E., Dalla Bella, S., Farrugia, N., Obrig, H., Mainka, S., & Kotz, S. A. (2014). Musically cued gait-training improves both perceptual and motor timing in Parkinson's disease. *Frontiers in Human Neuroscience*, *8*: 494. doi:10.3389/fnhum.2014.00494.

Bianco, R., Novembre, G., Keller, P. E., Kim, S.-G., Scharf, F., Friederici, A. D., Villringer, A., & Sammler, D. (2016). Neural networks for harmonic structure in music perception and action. *NeuroImage.* doi:10.1016/j.neuroimage.2016.08.025.

Bianco, R., Novembre, G., Keller, P. E., Scharf, F., Friederici, A. D., Villringer, A., & Sammler, D. (2016). Syntax in action has priority over movement selection in piano playing: An ERP study. *Journal of Cognitive Neuroscience, 28*(1), 41–54. doi:10.1162/jocn_a_00873.

Bisenius, S., Neumann, J., & Schroeter, M. L. (2016). Validating new diagnostic imaging criteria for primary progressive aphasia via anatomical likelihood estimation meta-analyses. *European Journal of Neurology*, *23*(4), 704–712. doi:10.1111/ene.12902.

Bisenius, S., Neumann, J., & Schroeter, M. L. (2016). Response to the letter on 'Validating new diagnostic imaging criteria for primary progressive aphasia via anatomical likelihood estimation meta-analyses'. *European Journal of Neurology, 23*(8), e52e53. doi:10.1111/ene.13046.

Bisenius, S., Trapp, S., Neumann, J., & Schroeter, M. L. (2015). Identifying neural correlates of visual consciousness with ALE meta-analyses. *NeuroImage*, *122*, 177–187. doi:10.1016/j.neuroimage.2015.07.070.

Bitzer, S., Bruineberg, J., & Kiebel, S. J. (2015). A bayesian attractor model for perceptual decision making. *PLoS Computational Biology*, *11*(8): e1004442. doi:10.1371/journal.pcbi.100444.

Bitzer, S., Park, H., Blankenburg, F., & Kiebel, S. J. (2014). Perceptual decision making: Drift-diffusion model is equivalent to a Bayesian model. *Frontiers in Human Neuroscience*, *8*: 102. doi:10.3389/fnhum.2014.00102.

Blank, H., Kiebel, S. J., & von Kriegstein, K. (2015). How the human brain exchanges information across sensory modalities to recognize other people. *Human Brain Mapping*, *36*(1), 324–339. doi:10.1002/hbm.22631.

Boehme, R., Lorenz, R., Gleich, T., Romund, L., Pelz, P., Golde, S., Flemming, E., Wold, A., Deserno, L., Behr, J., Raufelder, D., Heinz, A., & Beck, A. (2016). Reversal learning strategy in adolescence is associated with prefrontal cortex activation. *European Journal* of *Neuroscience*. doi:10.1111/ejn.13401.

Bogler, C., Mehnert, J., Steinbrink, J., & Haynes, J.-D. (2014). Decoding vigilance with NIRS. *PLoS One*, *9*(7): e101729. doi:10.1371/journal.pone.0101729.

Boonstra, E., de Kleijn, R., Colzato, L., Alkemade, A., Forstmann, B. U., & Nieuwenhuis, S. (2015). Neurotransmitters as food supplements: The effects of GABA on brain and behavior. *Frontiers in Psychology*, *6*: 1520. doi:10.3389/fpsyg.2015.01520.

Böttger, J., Schäfer, A., Lohmann, G., Villringer, A., & Margulies, D. S. (2014). Three-dimensional mean-shift edge bundling for the visualization of functional connectivity in the brain. *IEEE Transactions on Visualization and Computer Graphics*, *20*(3), 471–480. doi:10.1109/TVCG.2013.114.

Böttger, J., Schurade, R., Jakobsen, E., Schäfer, A., & Margulies, D. S. (2014). Connexel visualization: A software implementation of glyphs and edge-bundling for dense connectivity data using brainGL. *Frontiers in Neuroscience*, *8*: 15. doi:10.3389/fnins.2014.00015.

Bresch, A., Rullmann, M., Luthardt, J., Arélin, K., Becker, G. A., Patt, M., Lobsien, D., Baldofski, S., Drabe, M., Zeisig, V., Regenthal, R., Blüher, M., Hilbert, A., Sabri, O., & Hesse, S. (2016). In-vivo serotonin transporter availability and somatization in healthy subjects. *Personality and Individual Differences, 94*, 354–359. doi:10.1016/j.paid.2016.01.042.

Bruineberg, J., & Rietveld, E. (2014). Self-organization, free energy minimization, and optimal grip on a field of affordances. *Frontiers in Human Neuroscience*, *8*: 599. doi:10.3389/ fnhum.2014.00599.

Brunetti, M., Morkisch, N., Fritzsch, C., Mehnert, J., Steinbrink, J., Niedeggen, M., & Dohle, C. (2015). Potential determinants of efficacy of mirror therapy in stroke patients: A pilot study. *Restorative Neurology and Neuroscience*, *33*(4), 421–434. doi:10.3233/RNN-140421.

Carius, D., Andrä, C., Clauß, M., Ragert, P., Bunk, M., & Mehnert, J. (2016). Hemodynamic response alteration as a function of task complexity and expertise: An fNIRS study in jugglers. *Frontiers in Human Neuroscience*, *10*: 126. doi:10.3389/fnhum.2016.00126.

Cohen, N., Margulies, D. S., Ashkenazi, S., Schäfer, A., Taubert, M., Henik, A., Villringer, A., & Okon-Singer, H. (2016). Using executive control training to suppress amygdala reactivity to aversive information. *NeuroImage*, *125*, 1022–1031. doi:10.1016/j. neuroimage.2015.10.069.

Cuevas Rivera, D., Bitzer, S., & Kiebel, S. J. (2015). Modelling odor decoding in the antennal lobe by combining sequential firing rate models with bayesian inference. *PLoS Computational Biology*, *11*(10): e1004528. doi:10.1371/journal.pcbi.1004528.

Daniels, J. K., Gaebler, M., Lamke, J.-P., & Walter, H. (2015). Grey matter alterations in patients with depersonalization disorder: A voxel-based morphometry study. *Journal of Psychiatry & Neuroscience*, *40*(1), 19–27. doi:10.1503/jpn.130284.

de Hollander, G., Keuken, M., Bazin, P.-L., Weiss, M., Neumann, J., Reimann, K., Wähnert, M., Turner, R., Forstmann, B. U., & Schäfer, A. (2014). A gradual increase of iron toward the medialinferior tip of the subthalamic nucleus. *Human Brain Mapping*, *35*(9), 4440–4449. doi:10.1002/hbm.22485.

de Hollander, G., Keuken, M., & Forstmann, B. U. (2015). The subcortical cocktail problem: Mixed signals from the subthalamic nucleus and substantia nigra. *PLoS One, 10*(3): e0120572. doi:10.1371/journal.pone.0120572.

Deserno, L., Heinz, A., & Schlagenhauf, F. (in press). Computational approaches to schizophrenia: A perspective on negavtive symptoms. *Schizophrenia Research*.

Deserno, L., Schlagenhauf, F., & Heinz, A. (2016). Striatal dopamine, reward, and decision making in schizophrenia. *Dialogues in Clinical Neuroscience*, *18*(1), 77–89. Deserno, L., Wilbertz, T., Reiter, A., Horstmann, A., Neumann, J., Villringer, A., Heinze, H. J., & Schlagenhauf, F. (2015). Lateral prefrontal model-based signatures are reduced in healthy individuals with high trait impulsivity. *Translational Psychiatry, 5*: e659. doi:10.1038/tp.2015.139.

Dietrich, A., de Wit, S., & Horstmann, A. (in press). General habit propensity relates to the sensation seeking subdomain of impulsivity but not obesity. *Frontiers in Behavioral Neuroscience*, *10*: 213.

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Neurocognition of Language: The Language Network

Department of Neuropsychology

Language makes us human. All animals can communicate, but only humans possess the language faculty which allows us to generate and understand an infinite number of sentences.

We now know that this ability is represented in the brain, not in single brain regions, but rather in a fronto-temporal network with different regions that are connected via white matter fibre tracts. Over the past years we have been able to specify this network in the adult brain with respect to the function of its different grey matter subparts, in particular BA 44 in the inferior frontal gyrus and the superior temporal cortex, with respect to the white matter connectivity and functional connectivity between these regions, and even with respect to the network's molecular specificity at the neurotransmitter receptor level (see section 2.1).

In parallel, we have been able to foster and expand our knowledge about the emergence of the language network during development. We found that BA 44 in the inferior frontal gyrus and the posterior temporal cortex develops towards a functional selectivity for processing complex syntax, that there is an increased functional and structural connectivity between these regions and, moreover, that these connectivities increase across development. Our work has not only provided us with new insights into the development of the language network during childhood, but has also allowed us to functionally specify particular fibre tracts by means of correlational analyses. The maturational status of the dorsal fibre tract connecting BA 44 and the posterior temporal cortex was found to predict comprehension performance on syntactically complex sentences across age groups. This finding, in turn, indicates that the dorsal white matter fibre tract targeting BA 44 is crucial for processing complex syntax (see section 2.2).

In earlier work we had shown that this dorsal fibre tract is not yet myelinated in newborns (Perani et al., 2011, Proc Natl Acad Sci USA, 108, 16056–16061), and the work of others had demonstrated that this fibre tract is weak in monkeys but strong in adult humans (Rilling et al., 2008, Nat Neurosci, 11, 426–428). This led to the hypothesis that if the dorsal tract targeting BA 44 is pimarily relevant for complex syntax, monkeys should be able to process the grammar types that prelinguistic infants can. In a collaboration with Newcastle University, we were able to demonstrate a striking similarity in the brain potentials of infants and monkeys when processing rule-based structures. We take these findings to suggest evolutionary conserved neurobiological processes (see section 2.2).

Based on these empirical findings, new theoretical advancements were achieved. Angela Friederici together with Wolf Singer, in *Trends of Cognitive Sciences*, proposed the view that language, as any other cognitive function, can be "grounded on basic neurophysiological principles" considering the interaction of local and distributed neural networks (Friederici & Singer, 2015). In *Nature Reviews Neuroscience*, Michael Skeide and Angela Friederici formulated a new model of the "Ontogeny of the cortical language network" proposing two major phases: one from birth to three years mainly recruiting temporal regions, and one beyond the age of three to late childhood with an increasing involvement of prefrontal regions in the maturing fronto-temporal language network (Skeide & Friederici, 2016). An ontogenetic and phylogenetic perspective on the "Evolution of the neural language network" is provided in a provoking paper by Angela Friederici, which argues that the white matter tract connecting BA 44 and the posterior temporal cortex is crucial for the human language faculty (Friederici, 2016).

Additionally, in the past year, Angela Friederici has written a book entitled *Language in our Brain*, which will appear with MIT Press. In her book she reviews the literature on the neurobiological basis of language, which, together with her own work, integrate to form a coherent view on language in the human brain.



Figure 2 Core language fibre tracts in the human brain. The two dorsal fibre tracts can be distinguished mainly by their target regions in the frontal cortex (PMC, premotor cortex) and BA 44. The two ventral pathways can be distinguished best by their target region in the temporal cortex. It is argued that all fibre tracts are language-relevant and that the arcuate fasciculus connecting BA 44 and the posterior temporal cortex is crucial for the processing of hierarchically complex sentences. FOP, frontal operculum; SLF, superior longitudinal fasciculus; IFOF, inferior-fronto-occipital fasciculus.

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The Adult Language Network

The adult language network consists of regions located in the inferior frontal, temporal, and parietal cortex. Temporal and frontal regions support the processing of sentence structure and content, whereas the parietal cortex is recruited when the demand on verbal working memory during processing is high. These regions are connected by white matter fibre tracts transmitting information between them. In our work, we focussed on the dorsally located fibre tracts and found that the tract connecting BA 44 in the inferior frontal gyrus and the posterior superior temporal cortex directly supports the processing of syntactically complex sentences. Here we report data that functionally specify grey and white matter subparts within the larger neural language network.

A fine-grained meta-analysis of syntactic studies revealed that BA 44 in the inferior frontal gyrus together with the posterior superior temporal cortex and the dorsal white matter fibre tract connecting these regions subserve the build-up of syntactic hierarchies in phrases and sentences (2.1.1), whereas the left angular gyrus supports semantic composition even at a two-word phrase level (2.1.2). Top-down modulation of the involvement of BA 44 was demonstrated during the processing of object-first sentences (2.1.3). Transcranial magnetic stimulation over the left angular gyrus leads to a suppression of the neural activity in the semantic network and induces an upregulation of the neighbouring phonological network (2.1.4).

In a further study, which focussed on the function of subparts of the dorsal pathway connecting the inferior frontal gyrus, the parietal cortex, and the posterior temporal cortex, we found that only the white matter fibre tract connecting the inferior frontal and parietal cortex is related to verbal working memory supporting language functions (2.1.5). In order to find out whether the neural language network is universal, we compared the structural language network across three languages. The data indicate that the classical white matter language network is present in all brains, but that it is modulated as a function of lifelong use of a particular language (2.1.6). Interestingly, the classical language network is present even in prelingual deaf signers for whom, however, major changes were observed in speaking and hearing pathways (2.1.7). The findings from the latter two studies on the one hand provide strong evidence for a certain robustness of the basic neural language network, but, on the other hand, reveal the network's plasticity as a function of language input. In addition to these functional aspects, the language network was analysed at the molecular level, revealing a strong similarity in the neurotransmitter receptorarchitectonics for those cortical regions that are part of the functional language network, as opposed to other cortical regions (2.1.8).

Crossing the border from language to mathematics, a new study compared the functional network for processing hierarchical structures in both domains, suggesting a certain separability of the two networks even when controlling for automaticity of processing (2.1.9).

A completely novel approach was taken to determine the impact of bottom-up acoustic processes and topdown syntax-based processes during sentence comprehension. Investigations of the interplay between syntax and prosodic acoustic oscillations, recorded during sentence comprehension, indicate a linguistic dominance over speech acoustics during language comprehension (2.1.10).

2.1.1 The neuroanatomical network of syntactic Merge for language

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Although human language is traditionally thought of as a complex cognitive function, its underlying mechanism reduces to a very basic computation, known as Merge in theoretical and evolutionary linguistics (Everaert et al., 2015, Trends Cogn Sci, 19, 729–743). Merge is the universal syntactic computation binding words together into bigger objects (phrases and sentences). At least three phases of structure formation can be distinguished within it: (1) String-Merge-words are strung freely in a set (the, man); (2) Label-Merge-strings are translated into hierarchies ([the man]); (3) Recursive-Merge-new words are added to previous hierarchies ([[the man] walks]) (Zaccarella & Friederici, 2016). Cortically, FOP/ adINS brings two elements together to form a set, regardless of hierarchical relations (Zaccarella & Friederici, 2015b). The anterior-ventral BA 44 determines asymmetric relationships between the two elements, by translating sets into labelled syntactic structures (Zaccarella & Friederici, 2015a). At this fundamental level, single Merge recapitulates complexity at higher levels. Depending on the type of categorical elements involved in the recursive phase, together with the pSTS/STG, structures with prominent syntax (phrases) activate BA 44 more, while those with prominent semantics (sentences) activate the anterior BA 45 more, still together with the pSTS/STG (Zaccarella et al., 2015). A recent meta-analytical investigation further confirms the fronto-temporal dorsal interaction between BA 44 (merge processor) and pSTS/STS (integrative processor) for syntactic processing (see Fig. 2.1.1 for a detailed description). The neurobiological validity of Merge strongly supports the view that linguistic structures consist of abstract mental representations and paves the way to new comparative trajectories defining the ontogeny and phylogeny of language development.



Content AND Function word list studies 📕 📕 Content OR Function word list studies

Figure 2.1.1 ALE Meta-analysis on Merge Processing. (A–C) Functional clusters obtained from an Activation Likelihood Estimation (ALE) meta-analysis of subsets of studies comparing Merge processing against word list processing. Only studies using either function or content word list control conditions (Content OR Function; green-yellow) appear to isolate areas relevant to syntactic processing (BA 44 and pSTS/STG), compared to studies using mixed word list control conditions (Content AND Function; red-yellow). (A) sagittal plane at x = -52; (B) transverse plane at z = 12. Red rectangle indicates Broca's region to show the activation split between the two subsets in BA 44 and BA 45. (C) sagittal plane at x = -58 showing activation overlap between the two subsets in pSTS/STG. (D) Probabilistic tractography between the two local maxima from the Content OR Function subset analysis (blue), used as spherical seeding points in BA 44 (-52, 12, 16) and in the posterior temporal cortex (-62, -48, 6). Brodmann Area (BA) 44/45; posterior superior temporal sulcus/gyrus (pSTS/STG; BA 22). Arcuate fascicle (AF)/superior longitudinal fascicle (SLF).

Syntactic and semantic contribution to basic phrasal composition

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Linguistic expressions consist of sequences of words combined together to form phrases and sentences. The neurocognitive process responsible for word combination is drawing increasing attention among the neuroscientific community, given that the underlying syntactic and semantic mechanisms of such basic computations-although essential to the generation of more complex structures—still need to be consistently determined (Bemis & Pylkkänen, 2011, J Neurosci, 31, 2801–2814; Zaccarella et al., 2015). The current experiment was conducted to disentangle the neural networks supporting syntactic computation and semantic integration at the two-word combination level. We manipulated linguistic processing by using words of different grammatical classes within a phrase to observe how the syntactic and semantic networks support phrasal building. Determiner-noun combinations were used to boost neural activity in syntax-related areas. Adjective-noun combinations were conversely used to measure higher semantic integration demands in corresponding anatomical areas. By means of fMRI, we found that syntaxrelated processing mainly activates the most ventral part of the inferior frontal gyrus, along the frontal operculum (FOP) and anterior insula. Fine-grained analysis in BA 44 confirmed that the most inferior-ventral portion is highly sensitive to syntactic manipulations driven by function words (Zaccarella & Friederici, 2016). Semantic integration, in contrast, engages the left angular gyrus (AG) (Bemis & Pylkkänen, 2013, Cereb Cortex, 23, 1859–1873). Our findings suggest that syntactic and semantic contribution to phrasal formation can already be differentiated at a very basic level. The two processes comprise non-overlapping areas on the cortex. Specifically, they confirm the role of the ventral IFG for the construction of syntactically legal linguistic constructions, and the importance of the AG in the establishment of conceptual relationships.



Figure 2.1.2 Syntactic and semantic contribution to phrasal composition. (A) Experimental conditions used in the fMRI study. Syntax-driven phrase (SYN, red). Semantics-driven phrase (SEM, blue). (B) Activation cluster from the univariate analysis. SYN > SEM (top) and SEM > SYN (bottom). Threshold at p < 0.001 voxel-level, corrected 0.05 FWE at cluster-level. Bar graphs show percentage signal change within the corresponding cluster, as measured with the MarsBaR Toolbox. Volume renderings done with MRIcron. FOP: frontal operculum; pMTG/STG: posterior middle temporal gyrus/superior temporal gyrus; AG: angular gyrus.

2.1.3 Investigating the neural mechanisms of syntactic expectations

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Processing of syntactic structure has been typically related to activation in the left inferior frontal gyrus (Friederici, 2011, Physiol Rev, 91, 1357-1392). In the current fMRI study, we asked whether this processing can be modulated by top-down factors such as expectations. Therefore, we implemented a paradigm in which a particular syntactic structure was either expected or unexpected depending on the speaker who produced the sentence. Twenty-eight participants were presented with sentences spoken by two different speakers. Sentences had either an easy Subject-Object-Verb (SOV) or a complex Object-Subject-Verb (OSV) structure. Crucially, the two speakers differed in the probabilities by which they produced a particular syntactic structure. One speaker had a high probability of producing a SOV structure and a low probability of producing an OSV structure (SOV Speaker), and vice versa for the other speaker (OSV Speaker). The association between speaker and structure was established in a prior training phase. This allowed participants to build up differential expectations about the syntactic structure of a sentence on the basis of speaker identity. The results show increased activation for OSV structures compared to SOV structures in a left fronto-temporal network including the IFG, precentral gyrus, pre-SMA, and posterior MTG (A). A ROI analysis was conducted to evaluate whether the activation of the left IFG was modulated by expectations for a particular syntactic structure (B). We observed increased activation for the OSV structure compared to the SOV structure when the SOV structure had been expected, however, this difference was abolished when the OSV structure had been expected. These results indicate that syntactic processing in the left IFG can be influenced by top-down factors such as expectations driven by speaker identity.



Figure 2.1.3 (A) Main effect of syntactic structure: Contrasting OSV structures > SOV structures on the whole-brain level (cluster-level p < .05, FWE-corrected, cluster-forming threshold of p < .0001). (B) ROI analysis of the interaction between the factors speaker and structure, F(1,27) = 9.436, p = .005. Post-hoc t-test showed a significant difference between SOV and OSV structure for the SOV Speaker [t(27) = -5.925, p < .001] but not for the OSV Speaker [t(27) = -0.764, p = .451]. The ROI was defined as BA 44 in the left hemisphere using the Juelich anatomy atlas (Eickhoff et al., 2005, NeuroImage, 25, 1325–1335). Error bars depict the standard error of the mean.

Reorganisation in the semantic language network after virtual lesion

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The plastic effects of stroke-induced lesions on the ipsilateral language network remain largely elusive. To investigate the potential for rapid short-term reorganisation and flexible redistribution of the functional weight in the semantic network, we combined focal virtual lesions in the healthy brain with effective connectivity analyses of neuroimaging data. To this end, effective or sham transcranial magnetic stimulation (TMS) was applied over the left angular gyrus (AG), a key node for semantic processing (see Hartwigsen et al., 2016b), or the neighbouring supramarginal gyrus (SMG). Subsequently, participants performed semantic word judgements during functional neuroimaging. Perturbation of the left AG induced suppression of neural activity in a large network of semantic language regions and compensatory upregulation of neighbouring areas for phonological processing (see Fig. 2.1.4A). Effective connectivity analyses unravelled the neural mechanism of the disruptive effect, demonstrating that after perturbation, AG increased its

inhibitory influence on another key node for semantic processing, the left anterior inferior frontal gyrus including BA 45 (alFG) (Fig. 2.1.4B). Critically, the inhibitory influence of AG on aIFG predicted the individual delay in semantic response speed (Fig. 2.1.4C), indicating for the first time that inhibition at remote network nodes is functionally relevant. Inhibitory functional changes were mediated via distinct anatomical connections. Moreover, the individual disruption of the AG predicted the compensatory upregulation of semantic activity in the neighbouring SMG (Fig. 2.1.4D). The beneficial contribution of a neighbouring network demonstrates the strong compensatory potential of ipsilateral networks, which is important for language recovery after stroke. These findings might reveal generic mechanisms of plasticity in cognitive networks and might inform models of strokeinduced reorganisation in the language network.







C Increased inhibitory influence of AG on aIFG predicts semantic response delay



D Inhibition of AG predicts upregulation of SMG



Figure 2.1.4 Adaptive plasticity in the semantic network. (A) Illustration of the strong TMS-induced suppression in the semantic network (in blue) and the compensatory upregulation of the phonological network that helped to maintain task processing (in red). All effects were significant at a threshold of p<0.05, FWE-corrected. pIFG = posterior inferior frontal gyrus, pMTG = posterior middle temporal gyrus. (B) Effective connectivity in the semantic network. The winning model identified with dynamic causal modelling assumed modulation of the connection from left AG to aIFG by TMS of left AG. Mean parameter estimates are given for the significant driving input to SMG, the facilitatory intrinsic connections from AG to aIFG and SMG (solid arrows), and the inhibitory modulation of the connection from AG to aIFG by TMS over AG (red line), p<0.05, (*) survived a Bonferoni-Holm correction. (C) Regression analysis. The individual increase in the inhibitory influence of AG on aIFG after TMS over AG predicted the individual mean semantic response delay after TMS over AG. p<0.05. (D) Regression analysis. The strength of the individual inhibition of left AG after TMS predicted the compensatory upregulation of left SMG. p<0.05.

2.1.5 Fractional anisotropy of the left superior longitudinal fasciculus predicts verbal working memory abilities

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Verbal working memory (VWM) is a key theoretical construct referring to the active maintenance and manipulation of a restricted amount of verbal information over a limited period of time through processes of subvocal rehearsal and storage of information. Previous neuroimaging studies have reported brain activation to rehearsal in the left frontal cortex (i.e. inferior frontal gyrus and motor-premotor cortex) and brain activation to storage in the left temporo-parietal cortex (i.e. posterior superior temporal gyrus and posterior inferior parietal gyrus). While these regions connect through the arcuate/superior longitudinal fasciculus (AF/SLF), the microstructural relevance of the AF/SLF in VWM is still unclear. In this study, we measured the VWM of German native speakers through a battery of three tasks and used automated tractography tools to segment the SLF and the AF in both hemispheres. We found that a VWM composite score derived by principal component analysis was predicted by the individual median fractional anisotropy (FA) of only the left SLF. While the negativity of the correlation might seem counterintuitive at first glance, previous research has shown that increased behavioural performance in phonological tasks was correlated with decreased FA along the AF/SLF. Decreased FA along a fibre tract has been proposed to stem from neurophysiological states of a mature brain, such as wide axon branching towards cortical termination areas. In addition, we showed that the left SLF terminated anteriorly in the premotor cortex and posteriorly in the inferior parietal cortex, whereas the left AF extended from the inferior frontal gyrus to the temporal gyrus. Our findings suggest distinct roles for the AF and the SLF, with the SLF supporting the rehearsal–storage interplay of VWM.



Figure 2.1.5 (A) Probability maps of the left and right superior longitudinal fasciculus (ISLF; rSLF) and arcuate fasciculus (IAF; rAF) in sagittal view, overlaid on a standard MNI brain template; colour map indicates the number of participants in which the fibre tract passes through each voxel; (B) Results of stepwise regression: the median fractional anisotropy (mFA) of the left SLF (black bar) is the only significant predictor of the verbal working memory (VWM) composite score; ICV: intracranial volume; (C) Significant correlation between the VWM composite score and the mFA of the left SLF overlaid by the regression line.
Modulation of the language network as a function of language type

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Every child is able to master his or her mother tongue regardless of fundamental differences among the languages of the world. Brain plasticity must therefore allow a predetermined neural language network to adapt to the specific needs of each language. In fact, human languages do not merely differ in the fact that they possess different words for the same concepts, but they also convey information in fundamentally different ways. We therefore expected the language network of individuals to reflect the specific processing demands of their respective mother tongue. In order to assess this hypothesis, we performed diffusion MRI tractography in speakers of different languages. Here, we show that three languages that represent different demands in language processing—Mandarin Chinese, English, and German lead to differences in the white matter fibre tracts connecting the language regions. English speakers showed stronger ventral connectivity, which captures the important role of meaning associations in this language.

German speakers, however, who can rely on numerous grammatical cues, correspondingly showed a greater dorsal temporo-frontal connectivity. Finally, Chinese speakers showed stronger temporo-parietal and transcallosal connectivity, linked to the phonological processing demands of this tonal language with frequent homophones. This study demonstrates for the first time that languages with different processing demands lead to structural differences in the neural language network. We show that acquisition and lifelong use of different processes pertaining to higher cognition affect how the brain is wired. These results challenge views that human behaviour is fully determined by neural hardwiring and rather suggest that the brain's predetermined structural network develops in response to cultural exposure. More specifically, we showed that the structural connectivity in the brain contains traces of the specific characteristics of one's mother tongue.



Figure 2.1.6 Cross-linguistic connectivity differences from Wernicke's area. Upper left: Seed regions of interest for probabilistic tractography in the posterior temporal cortex. Upper right: Significant clusters with stronger connectivity for each language in comparison with the other two in conjunction analysis (p<0.05 FWE) Centre: Probabilistic tractography between ROIs in Wernicke's area and areas with significantly higher connectivity in each of the three groups. The bar graphs show the relative connectivity strengths (CS, mean \pm 2 SEM) to target areas with significant connectivity differences for the different languages: Stronger dorsal connectivity to the frontal cortex in German speakers (in green), stronger ventral connectivity in English speakers (in blue), and stronger dorsal connectivity to the parietal cortex in Chinese speakers (in red). Abbreviations: p (posterior), STG (superior temporal gyrus), MTG (middle temporal gyrus), IFG (inferior frontal gyrus), IPL (inferior parietal lobe), ATL (anterior temporal lobe).

2.1.6

2.1.7 Differential modulation of the brain networks for speech and language in deaf signers

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The absence of oral speech in deaf signers offers the unique opportunity to disentangle speech from language circuits in the human brain. In newborns, the language network is not yet fully developed. We hypothesised that the connections within the language network are influenced by the modality of the language used during childhood. To test this, we measured diffusion weighted MRI to reconstruct neural fibre tracts and cortical networks. We performed quantitative probabilistic tractography from six major language regions of the dorsal language network in both hemispheres: BA 44, BA 6, the posterior superior and middle temporal gyri (pSTG and pMTG), Heschl's gyrus (HG), and the inferior parietal lobule (IPL). Quantitative comparison of the resulting connectivity maps of 10 adult prelingual deaf signers with those of a matched hearing control group confirmed that all major language tracts were present in both groups and did not differ qualitatively between signers and controls, confirming the concept of modality independence of language. However, pathways involved in the decoding and production of oral speech were weaker in the deaf group. These were tracts from the left BA 44 to the left SMA and thalamus in the production domain as well as interhemispheric connections between the auditory cortices via the corpus callosum related to early cortical auditory processing of spoken language. Furthermore, the left posterior temporal regions displayed a diminished connectivity with inferior parietal areas and precuneus. These results provide structural evidence for the modality independence of the language network and separate pathways necessary for speaking and auditory decoding from the tracts involved in general language processing. Based on these results, we argue that prelingual deafness does not affect the development of dorsal syntax pathways, but changes the connectivity of sensory and speech production areas used for the processing of spoken language.



Figure 2.1.7 Group differences in the speech and language network between deaf signers and controls. Top: Connectivity profile of the primary auditory cortex (turquoise) with significant reduced interhemispheric connectivity (orange) for left and right Heschl gyrus (HG) seed ROIs. Bottom left: Connectivity of left BA 44 shows the preserved syntax processing network (red) and reduced connectivity to the thalamus and the preSMA (orange, left). Bottom right: The posterior STG shows preserved temporal and inferior frontal connectivity (green) and reduced connectivity to the precuneus.

Molecular basis of the language network revealed by receptor architectonics

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The language network is a well-defined large-scale neural network of anatomically and functionally interacting cortical areas. Successful language processing requires the transmission of information between these areas. Since neurotransmitter receptors are key molecules of information processing, we hypothesised that cortical areas which are part of the same functional language network may show highly similar multireceptor expression patterns ("receptor fingerprint"), whereas those that are not part of this network should have different fingerprints. We found that the relation between the densities of 15 different excitatory, inhibitory, and modulatory receptors in eight language-related areas are highly similar and differ considerably from those of 18 other brain regions not directly involved in language processing. The tight clustering of the receptor fingerprints of all language-related areas in the left hemisphere is impressive despite their cytoarchitectonical diversity and the fact that they are topographically widely distributed throughout the brain from the IFG to the posterior part of the superior temporal gyrus. The multireceptor fingerprint analysis provides the first evidence for a common molecular basis of interaction in the functionally defined sentence comprehension network. Cortical areas, distinct by their multireceptor expression and defined by their function in encoding and decoding of words, and which are syntactically

complex, interact in this network when verbal working memory demands sentences. Thus, the fingerprints of all cortical areas underlying a large-scale cognitive domain such as language are a characteristic, functionally relevant feature of this network and an important prerequisite for the underlying neuronal processes of language functions.



Figure 2.1.8.1 Localisation of examined cortical regions projected on the lateral surfaces of the single subject MNI template brain. Areas with colour-coded labels in red are considered to be part of the larger language network; other colour-coded areas are outside this network. Red coloured regions are language regions identified in a functional experiment on sentence processing (Makuuchi et al., 2009, Proc Natl Acad Sci USA, 106, 8362–8367).



Figure 2.1.8.2 Hierarchical cluster tree and multidimensional scaling of receptor fingerprints in 26 cortical brain regions. (A) Hierarchical cluster tree of receptor distribution patterns in the left hemisphere. (B) Multidimensional scaling resulting in a 2D display of the 15-dimensional receptor feature vectors of the receptor fingerprints of 26 cortical regions measured in the left hemisphere.

2.1.9 What does "being an expert" mean to the brain? Functional specificity and connectivity in expertise

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The question of whether language and mathematics rely on the same neural network has recently been debated quite extensively. However, most of the studies did not take into consideration that the automaticity of processes in the two domains may be different, due to the lifelong use of language compared to less frequent practice of mathematics. Here we compared two groups, individuals with a high level and individuals with a low level of mathematical expertise, in order to answer two questions. First, are there differences in the processing of mathematical hierarchies between the two groups? And second, are there differences between the neural networks for language and mathematics once both domains are represented with a high level of expertise? We investigated processing of hierarchically structured sequences, which is a fundamental process for building complex structures in both domains. In the mathematical domain, results demonstrated a modulating expertise-dependent effect specifically for nonexperts in the left inferior frontal gyrus around pars triangularis and frontal sulcus, the left intraparietal sulcus, and the right inferior parietal lobule (see Figure 2.1.9.1). Interestingly, task-related functional networks were also modulated differently in the frontoparietal network for relatively good performance and in the frontostriatal network for poor performance. Thus, concerning the first question, the present data indicate that a high level of expertise in mathematics is evident in a small number of specific brain regions, whereas a low level of expertise is reflected by broadly distributed brain areas, along with divergent functional connectivity between experts and nonexperts.

Concerning the second question, a direct comparison of processing hierarchically structured sequences in the mathematical and language domain was conducted for the mathematical experts as these showed a high automaticity in both domains—as measured by an automaticity index. This analysis revealed critical differences in the neural activity pattern for the processing of these structures in the mathematical and language domain (Figure 2.1.9.2). These data suggest that the neural basis for processing hierarchies is partly separated for mathematics and language even when the level of expertise for the two domains is high.



Figure 2.1.9.1 Mathematical hierarchy in nonexperts compared to experts and correlations with mathematics scores. In the group comparison (nonexpert > expert), nonexperts showed more activation in the left inferior frontal gyrus (IFG) and bilateral inferior parietal lobules (IPL) compared with experts. Participants' mathematics scores (x-axis) were correlated with the percentage BOLD signal change (y-axis) in bar plots. The areas demonstrated stronger activation as the mathematical scores decreased. No significant activation was found in experts in comparison with nonexperts (expert > nonexpert) (*P < 0.05; error bars, SEM; n = 22 for each group; L, Left hemisphere; R, right hemisphere).



Language > Mathematics Language < Mathematics</p>

Figure 2.1.9.2 Direct comparison between language and mathematics for mathematical experts is displayed.

Linguistic bias modulates interpretation of speech via neural delta-band oscillations

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Language comprehension requires that single words be grouped into syntactic phrases, as words in sentences are too many to memorise individually. In speech, syntactic grouping patterns can mostly be inferred from acoustic markings in speech prosody. However, when ambiguous sentences allow for alternative syntactic grouping patterns, comprehenders may instead form phrases based on internal syntactic bias, even contradicting speech prosody. While neural delta-band oscillations have previously been known to phase-synchronise with speech prosody in a bottom-up manner, here we show that delta-band oscillations can also override the interpretational impact of speech prosody in a top-down manner. In our electroencephalography study, we found that biased syntactic grouping choices in ambiguous situations are accompanied by a characteristic delta-band oscillatory phase progression—decoupled from the speech envelope, predicting individual syntactic grouping bias. Delta-band oscillations thus serve to group a sentence's words into syntactic phrases of a preferred size, irrespective of speech acoustics.



Figure 2.1.10 (A) Stimulus materials: In no-boundary sentences (left; blue), the phrase "mit dem korrupten Anwalt (with the corrupt lawyer)" and the phrase "den Mörder (the murderer)" form the single joint phrase "den Mörder mit dem korrupten Anwalt" ("the murderer with the corrupt lawyer"); in boundary sentences (right; red), "mit dem korrupten Anwalt" forms a distinct, second phrase, interpreted as being linked to the phrase "Der Klient (the client)"; the two conditions are distinguished prosodically; participants indicated their grouping choice via button press (bottom); (B) behavioural results: While participants could clearly distinguish the two conditions, they also had a bias for assuming a boundary (i.e. more "boundary" interpretations of "boundary" sentences than "no-boundary" interpretations of "no-boundary" sentences); (C) delta-band oscillatory phase differs between "boundary" and "no-boundary" interpretations, irrespective of experimental condition (i.e. stimulus acoustics); (D) for assumed boundaries, entrainment to stimulus acoustics reduces, predicting the individual bias for assuming a boundary.



The development of the language network has been modelled to take place in two phases, in a first phase from birth to age three and a second phase covering the years from age three to late childhood. During these phases a child has to learn the phonology, word meanings, and syntax of a given language. But, moreover, children have to learn to read and write. Here we report on these aspects during development.

Very early during development, by the age of three months, infants are able to associatively learn new words. We demonstrated that at the end of the first year of life, infants are able to transform associatively learnt information into lexical-semantic memory after consolidation during sleep (2.2.1). Infants' early learning ability was also demonstrated for the extraction of non-adjacent rule-based dependencies from the auditory input-an ability that can be seen as a precursor for learning syntactic dependencies (2.2.2). Learning of dependencies from the auditory input is possible on a white matter network that connects auditory input to premotor cortex in the precentral gyrus. This pathway is present in human infants and in monkeys, whereas the second dorsal pathway targeting BA 44 responsible for syntax only matures slowly during ontogeny (Skeide, Brauer, & Friederici, 2016) and is weak in monkeys. This raised the hypothesis that monkeys should be able to process non-adjacent dependencies similarly to infants. Event-related brain responses measured in infants and monkeys provide initial evidence for this view (2.2.3).

Comparing syntax-related activation and functional connectivity within the language network in three-year-old and six-year-old children, we find that younger children demonstrate a functional connectivity of the posterior temporal cortex with BA 45, whereas older children show a stronger connectivity with BA 44 (2.2.4). These data indicate a specification of the connectivity between BA 44 and the temporal cortex towards the adult language network across development. Changes of the intrinsic functional connectivity in the language network point in the same direction: They suggest a long-range connectivity between the inferior frontal gyrus and the posterior superior temporal sulcus, which develops considerably between the ages of five and six years and becomes behaviourally relevant (2.2.5).

One of the intriguing guestions concerning the structural changes during development is to what extent these changes are causally driven by biological maturation or behavioural use. We approached this question in a training study with 4-year-old children. Semantic training caused changes in grey matter and white matter in the left anterior inferior frontal gyrus, in particular BA 45 as part of the semantic network (2.2.6). Syntactic training, in contrast, had no effect, neither behaviourally nor with respect to brain structure. These data may suggest that there are specific time windows of plasticity during which the developing brain is most responsive to particular input neither behaviorally nor brain-structurally. These data suggest that there are specific time windows of brain plasticity for different aspects of language. Brain structural changes also explain the development of another cognitive ability in humans, which is referred to as Theory of Mind (2.2.7).

The ability or disability of learning to read and write is mostly only detected in school. Two studies provide the basis for earlier classification. One study revealed that brain structure at the age of five years, in particular the strength of the white matter fibre tract connecting the parietal cortex to the inferior frontal cortex, can predict the emergence of dyslexia (2.2.8). The other study used a gene-brain-behaviour approach and found a gene associated grey matter volume of the visual word form area even before school can predict later emergence of dyslexia (Skeide et al., 2016) (2.2.9). Both studies have demonstrated the effective use of brain data to predict the impairment of reading and writing long before school, allowing the application of early intervention.

2.2.1 Infant word learning and sleep-dependent memory consolidation

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Early word learning is indicated by an N400 semantic priming effect that emerges in the ERP of 6-month-old infants when they are exposed to repeatedly presented, initially novel pairs of pictured objects and spoken words (Friedrich & Friederici, 2011, J Cogn Neurosci, 23, 3228-3240). In a follow-up study, we explored whether 3-month-olds are able to learn pairings of objects and words. We found that these young infants extract statistic regularities in the distribution of the co-occurrences of objects and words extremely quickly (Friedrich & Friederici, 2015). However, the type of brain response an increased late negativity instead of an N400 reduction-indicates that 3-month-olds do not build lexicalsemantic knowledge. Their ability to combine objects with words is caused by a primary learning mechanism that is based on the association of perceptual representations and is distinct from lexical-semantic learning in older infants.

In a very complex learning environment, even older infants recruit the primary learning mechanism: When 9- to 16-month-olds were exposed to object-word pairs and category-word pairs in parallel, the late negativity indicated the association of perceptual representations of objects and words. Infants who stayed awake during the retention period of about 1.5 hours lost these associations, but infants with a short post-encoding nap retained the pairings (Friedrich, Wilhelm, Born, & Friederici, 2015). Moreover, even though infants did not encode categoryword pairings during learning, an N400 effect to novel category exemplars in the memory test indicated new lexical-semantic memories in infants who napped between learning and testing. This result provides evidence for the offline generalisation of perceptual associative memories and their transformation into lexical-semantic knowledge. Thus, for the first time, we could show how the infant brain reorganises itself during sleep.



Figure 2.2.1 ERP data and the spatial distribution of learning and memory effects (the difference between consistent/correct and inconsistent/ incorrect pairings) of 9- to 16-month-old infants. Late negativity indicating perceptually-based associations between objects and words during learning (A). No evidence for the acquisition of category–word pairings during learning (B). N200–500 word form effect in the memory test indicating long-term memory for the object–word pairings in the nap group (C). N400 generalisation effect indicating the newly built lexical-semantic long-term memory of the nap group (D).

Ontogenetic perspective on grammar learning: Infants' ability to process 2.2.2 nested dependencies

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The ability to process nested dependencies is a prerequisite for complex grammar and potentially speciesspecific. Behavioural data suggest a late development of the ability to process nested dependencies in natural language (see Figure 2.2.2A for an example). Here, we probed the core computational mechanisms supporting this ability at a much younger age, using a novel experimental design with minimised perceptual and memory loads. In two experiments, we examined 5-month-olds' ability to process nested dependencies in 5- and 7-tone sequences. Both sequence types implemented a mirror grammar with corresponding tone pairs around a constant centre-marker, resulting in one or two levels of centre-embedding (Figure 2.2.2C & 2.2.2D). For both structures, we obtained event-related brain potentials from a passive listening oddball paradigm. Frequent rule-conforming sequences as standards were occasionally interspersed with rule-violating sequences as oddball deviants (Figure 2.2.2B), forming a mismatch condition. Deviants differed from standards only in the dimension of the validity of the underlying nested dependency. For both experiments, event-related potentials revealed negative infant mismatch responses to rule-violating sequences compared to rule-conforming sequences (Figure 2.2.2E & 2.2.2F). These results show for the first time that infants as young as 5 months of age can process nested dependencies, not only for one, but even for two levels of embedding. Thus, infants show the mastery of a complex grammar, which is considered to be human-specific, at very early stages of ontogenetic development. The applied minimised learning paradigm will enable comparative studies to further refine our understanding of the distribution of grammar learning abilities in the phylogenetic tree.



Figure 2.2.2 (A) Example of nested dependencies in natural language. (B) Passive listening oddball paradigm including sequences as individual oddball elements (C) Nested dependencies in 5-tone sequences. (D) Nested dependencies in 7-tone sequences. (E) Grand-averaged ERPs for differences between deviants and standards for 5-tone sequences, revealing negative infant mismatch responses as indicator of rule acquisition. (F) Grand-averaged ERP results for differences between deviants and standards for 7-tone sequences, revealing negative infant mismatch responses as indicator of rule acquisition.

2.2.3 Phylogenetic origins of syntax: Non-adjacent dependency processing in human and non-human primates

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The human language faculty crucially relies on syntactic abilities that involve the processing of adjacent and nonadjacent relations between input elements. Recently, we have found that infants as young as 3 months detect non-adjacent dependency (NAD) violations, as measured by mismatch responses (MMR) in the event-related brain potential (Mueller, Friederici, & Männel, 2012, Proc Natl Acad Sci USA, 39, 159–207). Interestingly, these responses displayed similarly for infants' detection of pitch and NAD rule deviants in the speech input (Figure 2.2.3A), indexing early occurring, automatic brain processes. Human adults, in contrast, showed no signs of NAD processing under passive listening, as they only revealed an MMR to pitch violations, but not NAD rule violations (Figure 2.2.3B). When adults received task instructions aimed at the underlying structure, however, they showed signs of NAD rule learning. Here, violation detection was apparent in a later occurring negativity (N2) and a Late positivity, indicative of more controlled processes (Figure 2.2.3D). Together these data deliver insights into the origin and developmental change of humans' sensitivity to complex sequencing relations. Yet, it is an open question as to when this ability evolved in the evolutionary lineage of primates. Thus, we extended the ontogenetic study by comparative data from non-human primates tested on the identical NAD speech structures under passive listening. Interestingly, for both pitch and NAD rule violations, macaque monkeys showed an MMR that was strikingly similar to the responses observed in human infants, both with respect to polarity and timing (Figure 2.2.3C). However, macaques also showed a Late

positivity, indicating that the underlying processes do not completely overlap across species. Our results impressively evidence that NAD sequencing relations can be processed by non-human primates, and illustrate evolutionarily conserved brain processes that remarkably resemble those seen during early ontogenesis.



Figure 2.2.3 Event-related brain responses to non-adjacent dependency (NAD) processing in human and non-human primates. The comparison of human infant brain responses (A) and human adult brain responses (B, D) indicates relevant ontogenetic differences, while the comparison of human infant brain responses and adult macaque brain responses (C) points to potential phylogenetic origins of human abilities.

2.2.4 The neural network underlying syntax by the age of three and six years

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The organisation of the language network undergoes continuous changes during development as children learn to understand sentences. To date, little is known about the functional interplay of language-related brain areas in young children. Our study was set up to explore these functional connections in the language network at two stages in language development, that is, the transition from the use of word order to case marking cues. In a passive listening paradigm, 21 3-year-old children (3yo), 29 6-year-old children (6yo), and 21 adults (age range: 21-35 years, M = 26.5, SD = 3.7) were exposed to spoken German transitive sentences while lying in a 3 T MRI scanner. We manipulated the case marking of the nouns, resulting in two variations of word order: subject-initial (SI) and object-initial (OI) sentences. Sentence comprehension was assessed via an offline picture matching task. To ensure that children were reliably involved in the task, we selected those who were capable of processing the SI sentences above chance-level accuracy for subsequent behavioural and functional data analyses. The children had better performance for the SI compared to OI sentences and showed a marginal interaction, driven by an age effect (6yo > 3yo) in the SI condition. As a control group, the adults showed expected activation along the left inferior frontal and posterior superior temporal regions (Fig. 2.2.4A) for the main effect of word order (i.e. OI > SI sentences). Activation peaks in three a priori defined regions—the left Brodmann Areas (BAs) 44, 45 and left posterior superior temporal gyrus (pSTG)—were subsequently used to generate ROIs for the analysis with children. While both 3yo and 6yo only showed a main effect of word order in the left pSTG (Fig. 2.2.4B), the behavioural interaction of word order and age corresponded to the functional connectivity (FC) patterns between the groups. The FC between the left pSTG and left BA 44 was stronger in 6yo compared to 3yo in the SI condition, whereas no difference was found in the OI condition (Fig. 2.2.4C). For the 3yo group, the FC between the left pSTG and left BA 45 was stronger than that between the left pSTG and left BA 44 in the SI sentences (Fig. 2.2.4C). Our study revealed the ongoing development of the neural language network by demonstrating that while task-related activation was comparable, behavioural differences between age groups were reflected in the underlying functional connectivity within the network.



Figure 2.2.4 (A) Whole-brain activation map for the main effect of word order (i.e. object-initial > subject-initial sentences) in adults (cluster-defining threshold of p < 0.005, cluster ≥ 139 voxels, equivalent to cluster-level FWE-corrected p < 0.005). (B) Percent signal change of both experimental conditions for 3-year-old and 6-year-old children in the left pSTG showed a main effect of word order. Error bars show ± 1 SEM. * p < 0.05. (C) Effect sizes for correlational analyses between left BA 44, BA 45, and the posterior STG. * p < 0.05.

Resting-state functional connectivity and its relation to language development in preschool children

2.2.5

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The development of language abilities in childhood is closely related to the maturation of the brain. Specifically, the left fronto-temporal connection within left perisylvian regions supporting syntactically complex sentence processing is still immature at preschool age. We used resting-state functional magnetic resonance imaging (rs-fMRI), a powerful technique to study the whole-brain neural connectivity, and found that the functional con-



Figure 2.2.5 Comparison of degree of connectivity (A) and comparison of functional connectivity based on posterior STG/STS (B) between children at age 5 and age 6. Red–yellow colours in Figure A and B indicate a stronger degree of connectivity or stronger connectivity at age 6 than age 5. Correlations between changes in functional connectivity seeded in the left posterior STG/STS cluster (green circle) and changes in language comprehension performance from age 5 to age 6 in children more advanced in language abilities (C) and children less advanced in language abilities (D). All results were corrected by using Gaussian random field theory (Z > 2.3, cluster-wise p < .05). L, left hemisphere; R, right hemisphere. STG/STS, superior temporal gyrus and sulcus; IFS, inferior frontal sulcus; IFG, inferior frontal gyrus, PCC, posterior cingulate cortex; VMPFC/ACC, ventromedial prefrontal cortex/anterior cingulate cortex.

nectivity within the left fronto-temporal connection covaries with complex syntax processing in 5-year-olds (Xiao, Friederici, Margulies, & Brauer, 2016a). Further, we performed a longitudinal study with a sample of children at age 5 and a one-year follow-up (Xiao, Friederici, Margulies, & Brauer, 2016b). Sentence comprehension performance and rs-fMRI data were acquired at both time points. We aimed to examine the longitudinal changes in intrinsic brain connectivity and their relation to the concurrent language development. Using degree centrality, increases in connectivity with age were found in a cluster within the left posterior superior temporal gyrus and sulcus (STG/STS) (Fig. 2.2.5A). Based on this cluster, seedbased functional connectivity was calculated at both time points, and developmental changes were found in the left inferior frontal sulcus and left angular gyrus (Fig. 2.2.5B). We also evaluated the behavioural relevance of these changes in functional networks. Children more advanced in language abilities showed correlations with functional connectivity increase between the left posterior STG/STS and other language-related regions; instead, children less advanced in language performance showed correlations in regions within the default mode network (Fig. 2.2.5C and D). These findings suggest that intrinsic functional connectivity develops considerably from age 5 to 6 and becomes behaviourally relevant. They provide primary evidence for language-related neuroplasticity in intrinsic functional connectivity in preschool children.

The effect of language training on the structural network in the developing brain

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In early childhood, both the brain and language proficiency still change at a rapid pace. We explored whether brain development and the language learning process are susceptible to intervention. We were interested in both grey and white matter changes, measured by cortical thickness (CT) and fractional anisotropy (FA). It has been shown that in typical development CT decreases across the brain from age 3-4 (Walhovd, Fjell, Giedd, Dale & Brown, 2016, Cereb Cortex, doi: 10.1093/cercor/ bhv301) and FA, an index of white matter integrity, increases in language pathways throughout childhood. We conducted a 3-week training study with 4-year-old children scanning them pre (T1) and post (T2) intervention. They were divided into three groups: semantic training (SEM), syntax training, and control (CON). Here we report results from SEM and CON. SEM underwent a lexical training of 60 novel creatures' labels. Since the anterior inferior frontal gyrus (aIFG), part of the ventral language pathway, is suggested to play a role in lexical semantic processing, we expected training-related effects for CT and FA in this area. The data revealed that children excelled at the training (accuracies shown in Fig. 2.2.6A). In a ROI analysis of CT, the left pars triangularis (BA 45) showed a significant difference in changes from T1 to T2 when comparing SEM and CON (Fig. 2.2.6B). In a wholebrain analysis correlating the FA change with the behavioural training data, we found a positive correlation in the left aIFG (Fig. 2.2.6C). Our results show that CT in SEM and CON developed differently. We interpret this group difference as semantic training counteracting developmental change in CON. As hypothesised, we found that children with higher accuracy at the beginning of training had a larger increase in FA between T1 and T2 in the left alFG. We suggest that this indexes the relationship between the speed of word learning and the underlying structural mechanisms. Taken together, these results indicate that the language network shows training-induced changes, both in grey and white matter.



Figure 2.2.6 (A) Semantic group performance in Training sessions between T1 and T2 and Post-test at T2. (B) Group difference in CT changes in left IFG pars triangularis between the semantic (SEM) and control (CON) group. The CON group showed a decrease in CT, whereas the SEM group showed no significant change. (C) Significant cluster illustrating a positive correlation in SEM between FA change and combined accuracy of Trainings 1 and 2; significant difference in the aIFG. On the group level the accuracy in SEM was above chance after Training 2, therefore we combined the accuracy of Trainings 1 and 2 to represent the difference in learning rates of lexical entries between children.

2.2.6

2.2.7 White matter maturation supports the emergence of Theory of Mind

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The ability to represent the mental states of other agents (i.e. their thoughts and beliefs) is considered to be a hallmark of human cognition. This ability is referred to as Theory of Mind (ToM), and understanding others' false beliefs is considered to be a crucial test of it. A developmental breakthrough in ToM is consistently observed between the age of 3 and 4 years, when children start passing such false belief tests. To date, however, we lack any understanding of the neural mechanisms which support this crucial step in the development of human social cognition. In the present study, we related this behavioural change-from failing the false belief tests to passing them-to the maturation of brain structure in 3- and 4-year-old children. A tract-based spatial statistics (TBSS) analysis with 43 children showed that development of false belief understanding correlated with age-related increases in white matter maturation in the right temporoparietal junction (TPJ), medial temporal gyrus, pre-

cuneus and medial prefrontal cortex, regions known to constitute the ToM network in adults. Probabilistic tractography from seeds in these regions yielded a dorsal and a ventral pathway connecting temporoparietal with prefrontal regions via the arcuate fascicle and the inferior fronto-occipital fascicle respectively. Children's false belief performance correlated in particular with connectivity between TPJ and the anterior tip of the arcuate fascicle in the inferior frontal gyrus (IFG). These associations were independent of any co-occurring development of language or executive functions and differed from earlier-developing anticipatory looking false belief tasks. Our findings indicate that the maturation of the core belief processing regions and their connection to the anterior IFG, which has been suggested to support hierarchical processing, pave the way for the emergence of a mature metarepresentation of mental states.



Seeds for tractography from TBSS analysis

Figure 2.2.7 Correlation of false belief score with streamline density: The streamline density correlated with the children's false belief scores (N = 43, correlating regions in red, cluster-size corrected at p < 0.05 (two-sided), Bonferroni corrected for the number of tracts): (a) in the left IFG at the anterior tip of the left arcuate fascicle, (b) in the right IFG at the anterior tip of the right arcuate fascicle, and (c) in the right MTG along the IFOF. The effects were independent of age and of co-developing abilities.

Predicting early signs of dyslexia at a preliterate age by combining behavioural assessment with structural MRI

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Recent studies suggest that neurobiological anomalies are already detectable in pre-school children with a family history of developmental dyslexia (DD) (Vandermosten et al., 2015, Dev Cogn Neurosci, 14, 8–15). However, there is a lack of longitudinal studies showing a direct link between those differences at a preliterate age and the subsequent literacy difficulties seen in school. It is also not clear whether the prediction of DD in pre-school children can be significantly improved when considering neurobiological predictors, compared to models based on behavioural literacy precursors only. We recruited 53 pre-reading children either with (N = 25) or without a family risk of DD (N = 28). Quantitative T1 MNI data and literacy precursor abilities were assessed at kindergarten age. A subsample of 35 children was tested for literacy skills either one or two years later, that is, either in first or second grade. The group comparison of quantitative T1 measures revealed significantly higher T1 intensities in the left anterior arcuate fascicle (AF), suggesting reduced myelin concentration in preliterate children at risk of DD (see Figure 2.2.8). A logistic regression showed that DD can be predicted significantly better (p = .024) when neuroanatomical differences between groups are used as predictors (80%) compared to a model based on behavioural predictors only (63%). The Wald statistic confirmed that the T1 intensity of the left AF is a statistically significant predictor of DD (p < .05). Our longitudinal results provide evidence for the hypothesis that neuroanatomical anomalies in children with a family risk of DD are related to subsequent problems in acquiring literacy. In particular, solid white matter organisation in the left anterior arcuate fascicle seems to play a pivotal role.



Figure 2.2.8 Comparison of the averaged T1 intensities in the anterior, posterior, and long segment of the arcuate fascicle (AF) as well as in the inferior fronto-occipital fascicle (IFOF) in preliterate children. Compared to children without a family risk of DD (N = 28), children with a family risk of DD (N = 25) showed significantly increased T1 intensities, indicating reduced myelin concentration in the left anterior AF (p < .05 FWE-corrected, Cohen's d = .501). In all other tracts, no statistically significant differences were found between the risk and the control group. Error bars indicate standard errors of mean (SEM). All tracts are shown for a single representative subject in native space.

2.2.9 Gene-associated grey matter volume of the visual word form area reveals dyslexia before school

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Literacy learning depends on the flexibility of the human brain to reconfigure itself in response to environmental influences (Dehaene et al., 2010, Science, 330, 1359–1364; Brem et al., 2010, Proc Natl Acad Sci USA, 107, 7939–7944). At the same time, literacy and disorders of literacy acquisition are heritable and thus to some degree genetically predetermined (Peterson & Pennington, 2012, Lancet, 379, 1997–2007). Here we employed a multivariate non-parametric genetic model to relate literacyassociated genetic variants to grey volumes derived by voxel-based morphometry in a cohort of 141 children. Subsequently, a sample of 34 children attending grades 4 to 8, and another sample of 20 children, followed from kindergarten to first grade, in a longitudinal study was classified as dyslexics and controls using linear binary support vector machines. The *NRSN1*-associated grey matter volume of the visual word form area achieved a classification accuracy of about 73% in literacy-experienced students and distinguished between later dyslexic individuals and controls with an accuracy of 75% at kindergarten age (Fig. 2.2.9). These findings suggest that the cortical plasticity of a region vital for literacy might be genetically modulated, thereby potentially preconstraining literacy outcome. Accordingly, these results could pave the way for identifying and treating the most common learning disorder before it manifests itself in school.



Figure 2.2.9 Case-control classification based on the grey matter volume of the visual word form area. Binary support vector machine classification weight maps are presented separately for two subsamples. (A, B) Advanced literacy: 17 dyslexic vs. 17 control individuals in grades 4 to 8 (C, D) Beginning literacy: 20 children MRI-scanned at a kindergarten age before literacy instruction and psychometrically diagnosed as dyslexic at the end of first grade (10 dyslexics vs. 10 control individuals). Five classification indices are displayed on the *x*-axes (Acc = total classification accuracy; Sens = sensitivity; Spec = specificity; PPV = positive predictive value; NPV = negative predictive value). The *y*-axes display the classification performance (0 to 100%). (E) Receiver operating characteristic curve illustrating the performance of the classifier in the combined sample. The overall performance of the classifier is quantified as the area under the receiver operating characteristic curve (AUC).

Congresses, Workshops, and Symposia

2014 _

- Brauer, J. (March). Fachtag Sprachentwicklungsforschung. Workshop. Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.
- Friederici, A. D. (June). 20th Annual Meeting of the Organization for Human Brain Mapping (OHBM).
 Conference. Hamburg, Germany. (Member of the local organizing team)
- Friederici, A. D. (June). Mapping the Human Language Network: Development, Disorder and Culture-specific Research. Symposium. 20th Annual Meeting of the Organization for Human Brain Mapping (OHBM), Hamburg, Germany. (Organiser together with Tianzi Jiang, Institute Of Automation, Chinese Academy of Sciences, Beijing, China)

2015.

- Friederici, A. D. (January). Leopoldina-INSA Conference "Human Evolution Towards Language". Pune, India. (Scientific lead on the side of the Leopoldina together with Shashidhara, L. S. on the Indian side)
- Winkler, M. (February). Open Access Ambassadors' and Librarians' Meeting Saxony/Thuringia. Workshop. Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.
- Winkler, M. (July). Open Access and Beyond. Symposium. Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.

2016.

- Hartwigsen, G., & Meyer, L. (May) The neural dynamics of language: From cortical oscillations to plasticity in language networks. Symposium. Psychologie und Gehirn 2016, Berlin, Germany.
- Anwander, A., & Goucha, T. B. (June). Shapes of the Language Network: From Primates to Second Language Acquisition. Symposium. 22nd Annual Meeting of the Organization for Human Brain Mapping, Geneva, Switzerland.
- Dell'Acqua, F., Beer, A. L., & Anwander, A. (June). MR Diffusion Imaging: From the Basics to Advanced Applications. Symposium. 22nd Annual Meeting of the Organization for Human Brain Mapping, Geneva, Switzerland.
- Anwander, A., & Goucha, T. B. (July). Shapes of the language network: From monkeys to humans. Workshop. 6th IMPRS NeuroCom Summer School, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.

Degrees

PhD Theses 2014

 Golombek, T. Die Rolle des Gyrus angularis der linken Hemisphäre beim auditiven Sprachverständnis: Eine rTMS-Studie. University of Leipzig, Germany. Friederici, A. D. (November). Brain development, socialization, education: Brain and Behavior. "Don't start too early"/"Don't start too late". Symposium of the VW-Foundation. Hannover, Germany. (Organiser together with Martin Korte)

- Friederici, A. D. (September). The "Error Signals from the Brain – 7th Mismatch Negativity Conference (MMN 2015)". Conference. University of Leipzig, Germany. (Member of the local organiser team)
- Winkler, M. (December). OpenCon 2015 Satellite Event Germany. Symposium. Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.
- Friederici, A. D. (July). Crossing Boundaries in Science. Workshop. Session 2 "Modeling Nature and Society – Can We Control the World?" Weimar, Germany. (Co-ordinator and chair of Session 2)
- Grigutsch, M., Knösche, T. R., & Maess, B. (July). How can we estimate functional brain connectivity from EEG or MEG data? Workshop. 6th IMPRS NeuroCom Summer School, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.
- Wang, L., Meyer, L., Pylkkänen, L., & Molinaro, N. (October) Neural mechanisms of language integration and prediction. Symposium. International Conference on Biomagnetism, Seoul, South Korea.

 Knierim, I. N. Rules don't come easy: Investigating feedback-based learning of phonotactic rules in language. University of Leipzig, Germany.

2015 -

- Bonhage, C. Memory and prediction in sentence processing. University of Leipzig, Germany.
- Fengler, A. How the brain attunes to sentence processing: Relating behavior, structure, and function. University of Potsdam, Germany.
- Poulain, T. Mother-child interaction and syntax acquisition: A longitudinal study. University of Leipzig, Germany.

2016 _

- Cunitz, K. Case-marking and animacy Sentence processing in five- and six-year-old children. University of Leipzig, Germany.
- Kraft, I. Predicting developmental dyslexia at a preliterate age by combining behavioral assessment with structural MRI. University of Leipzig, Germany.

Appointments

2015

 Hartwigsen, G. W2 Group Leader position (in Department of Neuropsychology), Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.

2016 _

 Farrugia, N. Associate Professor, Institut Mines Telecom, Brest, France.

- Schaadt, G. Visual, auditory, and visual-auditory speech processing in school children with writing difficulties. Humboldt University, Berlin, Germany.
- Verga, L. Learning together or learning alone: Investigating the role of social interaction in second language word learning. University of Leipzig, Germany.
- Zaccarella, E. Breaking down complexity: The neural basis of the syntactic merge mechanism in the human brain. University of Potsdam, Germany.
- Strotseva-Feinschmidt, A. The processing of complex syntax in early childhood. University of Leipzig, Germany.

 Jeon, H.-A. Assistant Professor. Department of Cognitive and Brain Sciences, Daegu Gyeongbuk Institute of Science & Technology (DGIST), South Korea.

Kotz, S. A. Professorship. University of Maastricht, the

Netherlands

Awards

2014

- Leuze, C., & Anwander, A. Art of Neuroscience 2014. Netherlands Institute for Neuroscience.
- Meyer, L. Otto Hahn Medal. Max Planck Society.
- Vavatzanidis, N.-K. Junior Researcher Award. German Audiological Society.

2015.

 Cheung, V. The Croucher Foundation Scholarship (2015). The Croucher Foundation/DAAD, Hong Kong.

2016.

- Anwander, A. Wellcome Image Award 2016. Wellcome Trust, London, UK.
- Heuer, K. Open Science Prize. Phase I. Her team is among the six finalists competing for first prize in a second phase of the competition.

Conference of German Society of Phoniatrics and Pediatric Audiology.Winkler, M. Poster Award (Jury) IMPRS Neurocom Summer

Vavatzanidis, N.-K. Rehder Poster Award, 2nd prize.

- School. Max Planck Institute for Human Cognitive and Brain Sciences and Institute of Cognitive Neuroscience UCL, UK.
- Grosse Wiesmann, C., Schreiber, J., Singer, T., Steinbeis, N., & Friederici, A. D. Best poster award IMPRS Neurocom Summer School 2015.
- Männel, C. "Sign Up! Careerbuilding". Max Planck Society, Germany.

Publications

Books & Book Chapters

Bonhage, C. (2015). Memory and prediction in sentence processing. *MPI Series in Human Cognitive and Brain Sciences: Vol. 165.* Leipzig: Max Planck Institute for Human Cognitive and Brain Sciences.

Fengler, A. (2016). How the brain attunes to sentence processing: Relating behavior, structure, and function. *MPI Series in Human Cognitive and Brain Sciences: Vol. 174.* Leipzig: Max Planck Institute for Human Cognitive and Brain Sciences.

Friederici, A. D. (to appear). *Language in our brain*. Cambridge, MA: MIT Press.

Friederici, A. D. (2016). The neuroanatomical pathway model of language: Syntactic and semantic networks. In S. Small, & G. Hickok (Eds.), *Neurobiology of Language* (pp. 349–356). Amsterdam: Elsevier.

Friederici, A. D. (2014). Is there a brain basis of recursion? In F. Lowenthal, & L. Lefebvre (Eds.), *Language and Recursion* (pp. 101–113). New York: Springer.

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Knierim, I. N. (2014). Rules don't come easy: Investigating feedback-based learning of phonotactic rules in language. *MPI Series in Human Cognitive and Brain Sciences: Vol. 156.* Leipzig: Max Planck Institute for Human Cognitive and Brain Sciences.

Kotz, S. A. (2015). Electrophysiological indices of speech processing. In D. Jaeger, & R. Jung (Eds.), *Encyclopedia of computational neuroscience* (pp. 1074–1078). New York: Springer.

Kotz, S. A., & Schwartze, M. (2016). Motor-timing and sequencing in speech production: A general-purpose framework. In G. Hickock, & S. Small (Eds.), *Neurobiology of Language* (pp. 717–724). Amsterdam: Elsevier. doi:10.1016/B978-0-12-407794-2.00057-2.

Meyer, L, & Friederici, A. D. (2015). Neural systems underlying the processing of complex sentences. In G. S. Hickok, & S. L. Small (Eds.), *Neurobiology of Language* (pp. 597–606). Amsterdam: Elsevier. doi: 10.1016/B978-0-12-407794-2.00048-1. Mueller, J. L., Männel, C., & Friederici, A. D. (2015). Biological preconditions for language development. In J. D. Wright (Ed.), *International Encyclopedia of the Social & Behavioral Sciences* (2nd Ed., pp. 650–655). Oxford: Elsevier.

Schaadt, G. (2015). Visual, auditory, and visual-auditory speech processing in school children with writing difficulties. *MPI Series in Human Cognitive and Brain Sciences: Vol. 169.* Leipzig: Max Planck Institute for Human Cognitive and Brain Sciences.

Schmidt-Kassow, M., Rothermich, K., & Kotz, S. A. (2015). The role of default stress patterns in German monolingual and L2 sentence processing. In R. Vogel, & R. Vijver (Eds.), *Rhythm in cognition and grammar: A germanic perspective* (pp. 83–110). Berlin: de Gruyter.

Skeide, M. A., & Friederici, A. D. (in press). Neurolinguistic studies of sentence comprehension. In E. Fernandez, & H. Cairns (Eds.), *Handbook of Psycholinguistics*. Hoboken: Wiley-Blackwell.

Teixidó, M., François, C., Bosch., L., & Männel, C. (to appear). The role of prosody in early speech segmentation and wordreferent mapping: Electrophysiological evidence. In P. Prieto, & N. Esteve-Gibert (Eds.), Prosodic Development in First Language Acquisition, Bd. Trends in Language Acquisition Research (TiLAR). Amsterdam/Philadelphia: John Benjamins.

Verga, L. (2015). Learning together or learning alone: Investigating the role of social interaction in second language word learning. *MPI Series in Human Cognitive and Brain Sciences: Vol. 170.* Leipzig: Max Planck Institute for Human Cognitive and Brain Sciences.

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Zaccarella, E. (2016). Breaking down complexity: The neural basis of the syntactic merge mechanism in the human brain. *MPI Series in Human Cognitive and Brain Sciences: Vol. 175*. Leipzig: Max Planck Institute for Human Cognitive and Brain Sciences.

Zaccarella, E., & Friederici, A. D. (2015). Syntax in the brain. In A. Toga (Ed.), *Brain Mapping: An Encyclopedic Reference: Vol. 3* (pp. 461–468). Amsterdam: Elsevier.

Journal Articles

Adank, P., McGettigan, C., & Kotz, S. A. (2015). Editorial: Current research and emerging directions on the cognitive and neural organization of speech processing. *Frontiers in Human Neuroscience*, *9*: 305. doi:10.3389/fnhum.2015.00305.

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Drummer, J., van der Meer, E., & Schaadt, G. (2016). Eventrelated potentials in response to violations of content and temporal event knowledge. *Neuropsychologia*, *80*, 47–55. doi:10.1016/j.neuropsychologia.2015.11.007.

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Engel, A., Hijmans, B. S., Cerliani, L., Bangert, M., Nanetti, L., Keller, P. E., & Keysers, C. (2014). Inter-individual differences in audio-motor learning of piano melodies and white matter fiber tract architecture. *Human Brain Mapping*, *35*(5), 2483–2497. doi:10.1002/hbm.22343.

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Figure 2A

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Professor Dr Tania Singer Director

Foundations of Human Sociality

Department of Social Neuroscience

The scientific focus of the Department of Social Neuroscience is on understanding the foundations of human social cognition and social behaviour. Through an interdisciplinary and multi-method approach, we study the neural, behavioural, hormonal, and developmental 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 clinical populations. Furthermore, we are interested in how social motivation and cognition influence social and economic decision-making and how they can be regulated and trained to achieve better cooperation, well-being, and health. One major focus is on investigating the plasticity of the social brain. This focus is reflected in a large-scale longitudinal mental training study, the ReSource Project, in which we investigate the effects of socio-affective and socio-cognitive mental training on structural and functional brain plasticity as well as on changes in subjective well-being, prosociality and economic decision-making, emotion regulation capacities, attentional and executive cognitive functions, and stress- and other health-related parameters in more than 200 subjects over a period of three to nine months.

The four major interconnected research foci of the department are:

- 1. Foundations of Human Sociality and Neuroeconomics
- 2. Developmental Social Neuroscience
- 3. Plasticity of the Social Brain
- 4. Psychopathology of the Social Brain

In this report we will not present any research related to Developmental Social Neuroscience as this was a major topic in the last report, and the senior researcher and the PhD candidate working in this field left the department in 2015. We are currently restructuring this focus with the goal to test plasticity of the developing social brain. This report will thus focus on the other three main research topics of the department.

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The first focus of the research agenda in the Department of Social Neuroscience is the identification and separation of the different routes that underlie and support successful social interaction and social understanding. While we seem to accomplish this task on a daily basis without much effort, this fascinating ability entails complex computations and mental processes. Over the last decades, social neuroscience has provided significant insights into distinct mechanisms that underlie this capacity and revealed affective and cognitive routes to understanding others (e.g. Frith & Frith, 2005, Curr Biol, 15, 17, R644-R646; Singer, 2012, NeuroImage, 61, 2, 437-449). The socio-affective route comprises social emotions such as empathy and compassion. Empathy can be defined as the capacity to share others' bodily and emotional states while being aware that the other is the source of the sensation (de Vignemont & Singer, 2006, TICS, 10, 10, 435-441). Meta-analytical evidence from neuroimaging studies suggests that the anterior insula (AI) and the middle anterior cingulate cortex (mACC) are core regions underlying empathic responses when witnessing others' suffering, regions that are also recruited when suffering oneself (e.g. Lamm et al., 2011, NeuroImage, 54, 3, 2492-2502; see Fig. 3.1). Recent studies suggest that what is shared in these brain regions involved in firsthand pain and vicarious responses to others' suffering is information related to the experience of negative affective states (Corradi-Dell'Acqua et al., 2016, Nat Commun, 7, 10904; Zaki et al., 2016, TICS, 20, 4, 249–259). Thus, while empathic responding has been linked to prosocial decision-making (Leiberg et al., 2011, PLoS ONE, 6, 3, e17798), excessive empathy with others' suffering might also be maladaptive for prosocial behaviour when it causes empathic distress and potentially increases the motivation to withdraw from distressing settings.

Complementarily to empathy, witnessing other people's suffering may also induce compassion referring to a feeling of concern for another and a strong motivation to help and support the other (Singer & Klimecki, 2014, Curr Biol, 24, 18, R875–R878). Thus, while empathy, when confronted with the suffering of others, leads to sharing the negative affect of the other, compassion rather comes with feelings of warmth and love and a strong prosocial motivation. And indeed, compassion has been found to rely on a neural network that is distinct from empathy, including areas linked to positive affect such as the ventral striatum (see Fig. 3.1), and targeted meditation-based compassion training has been shown to enhance prosocial helping behaviour (Leiberg et al., 2011, PloS One, 6, 3, e17798). By consequence and contrary to empathy, compassion when confronted with others' suffering does not bear the risk of empathic distress but may re-

Dissecting the Social Brain



Figure 3.1 Schematic representations of different routes of social cognition influencing prosocial behaviour and the respective brain networks that are involved in empathy (orange), compassion (red), and perspective taking (green).

present a strategy to build up resilience against the negative consequences associated with emphatic distress. An alternative strategy for dealing with negative emotional responses to others' suffering is reappraisal, which entails the cognitive generation of alternate interpretations of emotional events (McRae et al., 2012, Emotion, 12, 2, 250–255). Reappraisal can be distinguished from compassion based on the underlying neural network, including, for instance, the dorsal anterior cingulate (dACC), the ventrolateral prefrontal cortex (vIPFC), and the dorsolateral PFC (dIPFC). While this strategy seems efficient in modulating the negative impact of observed emotional events, research suggests that reappraisal can lead to decreased willingness to help others (Cameron & Payne, 2011, J Pers Soc Psychol, 100, 1, 1–5).

In addition to socio-affective and motivational routes to understanding others allowing one to share and understand affective states of others, a growing body of evidence points to a cognitive route related to inferring and reasoning about other people's beliefs, thoughts, or emotions, processes that are referred to as Theory of Mind (ToM), mentalising, or cognitive perspective taking (Frith & Frith, 2005, Curr Biol, 15, 17, R644–R646; Premack & Woodruff, 1978, Behav Brain Sci, 1, 4, 515–526). ToM is reliably linked to a neural network that includes the temporoparietal junction (TPJ), temporal poles (TP), the medial prefrontal cortex (mPFC), and the precuneus/posterior cingulate cortex (PCC) (Bzdok et al., 2012, Brain Struct Funct, 217, 4, 783–796; Schurz et al., 2014, Neurosci Biobehav Rev, 42, 9–34; see Fig. 3.1).

While the different facets and neural underpinnings of social emotion and cognition received increasing attention, it is yet unknown how they relate to each other, whether and how they differentially stimulate prosocial decisions, and whether and how they can differentially be trained by targeted interventions focusing on socio-affective and socio-cognitive skill learning.

Building on previous work in our department that suggests reliable differentiation of empathy and compassion-related neural activation, one of our goals during the last years was to extend this finding by distinguishing different facets of social understanding—empathy, compassion, and ToM—on the levels of brain and behaviour within the *same* individuals. To this end, we developed and thoroughly validated a new paradigm to study the interaction between different routes of social understanding (the EmpaToM) (see paragraph 3.1.1). Employing another novel paradigm, the donation task, we assessed the distinct contribution of affective versus cognitive understanding (i.e. sharing the feelings versus taking the mental perspective of others in need) to prosocial behaviour, and distinguished them from other processes that might account for recruitment of the respective neural networks (see paragraph 3.1.2). To advance our theoretical and neural understanding of affective empathy, we also subjected shared network accounts of empathy in the anterior insula and mACC to close scrutiny and explored what exactly is shared in these core areas between first-hand and vicarious experiences across various domains such as experienced pain, disgust, and unfairness (see paragraph 3.1.3). With respect to compassion, we investigated further the unique properties of compassion as a coping strategy by probing the behavioural and neural response to negative affective stimuli by expert practitioners of Compassion Meditation that used either reappraisal or compassion when confronted with others' suffering (see paragraph 3.1.4). Finally, a core topic of the department has always been the investigation of human prosociality and cooperation. Examining the differential effects of the distinct components of social understanding (e.g. empathy, compassion, and ToM) on prosocial behaviour requires the reliable assessment of human prosociality. To improve assessment and gain insight into the underlying structure of this heterogeneous construct, we integrated paradigms from various research disciplines into motivation-based subcomponents of human prosociality (see paragraph 3.1.5).

3.1.1 The EmpaToM: A novel task distinguishing neural networks and brain– behaviour relations for empathy and Theory of Mind—and showing their interrelation

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Successful social interactions require both affect sharing (empathy) and understanding others' mental states (Theory of Mind, ToM). We present a novel fMRI paradigm (the EmpaToM) that independently manipulates both empathy and ToM and allows measurement of both faculties on the level of brain activity and behaviour (Fig. 3.1.1.1).

We validated the task with established paradigms on a behavioural and neural level. Employing the EmpaToM

in an independent sample (N = 178) revealed clearly separable neural networks including the anterior insula for empathy and the ventral temporoparietal junction for ToM (Fig. 3.1.1.2, first line of panels A and B). These distinct networks were replicated in task-free resting-state functional connectivity. Importantly, brain activity in these two networks specifically predicted the respective behavioural indices (Fig. 3.1.1.2, scatterplots in panels A and B). Having established a paradigm that allows the si-



- her sister has given up the search and does not want another treatment
- that her sister wants to look for another treatment herself
- that her sister would probably be healed by the new treatment.



Figure 3.1.1.1 Overview of the EmpaToM task with an example video narration and corresponding question of the negative emotion/Theory of Mind condition.




Figure 3.1.1.2 (A) Brain activation for empathy (emotionally negative > neutral videos) (red) and parametric modulation with the valence ratings (yellow) in the EmpaToM. Meta-analytic masks are depicted as white outlines. Valence ratings of the EmpaToM and their correlation with the valence ratings in the Socio-affective Video Task (SoVT) are illustrated. Correlation of brain activation with a composite score of affect related behaviour. (B) Brain activation for ToM > factual reasoning during questions (green) and during videos (yellow). Performance in the EmpaToM and the correlation of the composite score of ToM performance in the EmpaToM with the composite score of the egocentricity bias in the Samson Visual Perspective Taking Task are shown. The correlation of brain activation with a composite score of ToM related.

multaneous assessment of affective and cognitive routes to understanding others, we addressed the question how empathy and ToM relate to each other. For instance, are people who strongly empathise with others also more proficient in mentalising? And how do the neural networks supporting empathy and mentalising interact in a given situation?

We show that people's capacities to empathise and mentalise are independent, both on a behavioural and neural level (Fig. 3.1.1.3). Thus, strong empathisers are not necessarily proficient mentalisers, arguing against a general capacity of social understanding. Secondly, we applied dynamic causal modelling to investigate how the neural networks underlying empathy and mentalising are orchestrated in naturalistic social settings. Results reveal that in highly emotional situations, empathic sharing can inhibit mentalising related activity and thereby harm mentalising performance (Fig. 3.1.1.3). Our findings argue against a unitary construct of social understanding and suggest flexible interplay of distinct social functions.





Figure 3.1.1.3 (A) Neural activity for empathy > ToM and ToM > empathy (Kanske et al., 2015, NeuroImage, 122, 6-19), and resting state networks seeded from the AI and the ventral TPJ. (B) Correlations of empathising (valence ratings) and ToM performance in the EmpaToM; correlations of neural activity related to empathy (emotional>neutral videos) and ToM (ToM > nonToM questions). DCM results depicting the winning model (significant coefficients depicted in bold).

As described above, the EmpaToM task simultaneously assesses and independently manipulates affective and cognitive processes that underlie our understanding of others' mental states. Results obtained with this novel paradigm demonstrate that socio-affective and socio-cognitive processes recruit distinct neural substrates during task and rest periods, brain regions that are also implicated in altruistic decision making. However, the roles of empathy and ToM in altruistic behaviour are almost always studied in isolation, rendering it impossible to tease apart their behavioural and neural contributions to human prosociality. This poses a challenge to our understanding of the mechanisms that drive individual differences in altruistic behaviour.

3.1.2 Decoding the charitable brain: Empathy, perspective taking, and attention shifts differentially predict altruistic giving

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We used multivariate decoding techniques together with an fMRI donation task to disentangle distinct social (empathy, perspective taking) and non-social mechanisms (attentional reorienting) underlying altruistic decision-making. Neural activation patterns in the AI (but not the TPJ) predicted trial-wise empathic responses for beneficiaries of real-world charities (Fig. 3.1.2A, left). Brain responses in the TPJ (but not the AI), on the other hand, encoded the level of cognitive perspective taking during donations (Fig. 3.1.2A, right). Relative contributions of both social processes differed across individuals: subjects that heavily weighted affective empathy in donation decisions showed improved decoding of generous giving in the AI, while stronger influences of cognitive perspective taking on giving decisions correlated with higher predictions of generosity in the TPJ. Notably, empathic

brain responses obtained in an independent EmpaToM task reliably predicted the subject-specific influence of empathy in subsequent donation decisions (but not of perspective taking) (Fig. 3.1.2B, left). Brain responses for perspective taking obtained in the EmpaToM task predicted the subject-specific inputs of perspective taking in charitable giving (but not of empathy) (Fig. 3.1.2B, right). These findings indicate that individual differences in the influence of empathy and ToM on altruistic behaviour might reflect the individual's more general propensity to either empathise or mentalise when faced with others' suffering. Finally, using cross-task decoding, we provide evidence for shared neural codes in the posterior superior temporal sulcus (pSTS) for stimulus-driven attention shifts and altruistic decisions (but not in the TPJ or AI). This result points to a role of domain-general at-



A AI (but not TPJ) encoded trial-wise empathic responses (left), TPJ (but not AI) encoded level of perspective taking during donation decisions (right)

B Process-specific neural responses in separate EmpaToM task predict relative contributions of empathy and perspective taking during donations

Figure 3.1.2 Neural decoding of empathy and perspective taking in charitable giving decisions. (A) Activation patterns in the right AI (red)—but not the TPJ—encoded trial-wise empathy for beneficiaries of real life charities during donation decisions (left panel), while responses in the right TPJ (green)—but not the AI—encoded trial-wise levels of perspective taking for beneficiaries (right panel) (p < .05, FWE-corrected). (B) Empathyrelated neural responses in a separate task (EmpaToM) predicted the level of contribution of empathy (but not of perspective taking) in donation decisions (left panel), while ToM-related EmpaToM responses predicted the degree to which perspective taking (but not empathy) affected altruistic choices (right panel).

tentional re-orienting in prosociality, but also supports the highly specific role of the AI for affective empathy and the TPJ for cognitive perspective taking as determinants of altruistic behaviour. Overall, our findings tease apart the behavioural and neural mechanisms via which these affective and cognitive routes of social cognition drive differences in altruistic behaviour across contexts and people.

A growing body of evidence on the neural bases of affective empathy suggests that witnessing others' suffering recruits the AI and dorsal anterior cingulate cortex (dACC), which are also involved in the processing of first-hand experience of these aversive events. However, both the AI and the dACC respond to a wide range of affective events (e.g. pain, disgust, and unfair treatment), which raises the question whether these "shared networks" in the AI and the dACC code for modality specific information (e.g. pain or disgust) or rather superordinate dimensions such as generalised affective unpleasantness.

Cross-modal representations of first-hand and vicarious pain, disgust, and fairness in the insular and cingulate cortex

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The fMRI study aimed to clarify the nature of information encoded in the AI and the dACC during empathic responses. More precisely, we tested whether neural responses in the AI/dACC (Fig. 3.1.3A) encode aversive states in terms of general affective features that generalise across various modalities (pain, disgust, unfairness)



Figure 3.1.3 (A) Network of the Al/dACC based on independent resting-state fMRI data used for ROI-based decoding analyses. (B) Illustration of d' values of within-task (outer diagonal line of each matrix), cross-target, and cross-modal decoding results, separately for each ROI. Labels refer to classification of an aversive event relative to condition-specific neutral control: (Ps) self-related pain, (Ds) self-related disgust, (Po) other-related pain, (Do) other-related disgust, (U) unfairness. Coloured cells illustrate significant results with the luminance reflective of magnitude of d' values, black cells illustrate d' values that did not yield significant results.

and the target of the experience (self, other), or rather via modality-specific or target-specific neural codes. To this end, we used multivariate pattern classification techniques and systematically compared neural response patterns triggered by painful, disgusting, and unfair events, directed at either the participant or a befriended confederate. Firstly, we found shared neural representations in the left AI and the dACC for first-hand and vicarious experiences, but also across various modalities of aversive events, including pain, disgust, and unfairness (Fig. 3.1.3B). These results speak in favour of embodied accounts of social cognition in the (left) AI and the dACC, but also circumscribe their reach. While we found neural activation patterns that encoded first-hand events and that were re-instated during empathic responses, they did not contain specific information on the modality (e.g. nociception, disgust) anymore. This finding indicates that others' states trigger a neural representation of non-specific properties such as an unpleasant bodily experience, which was an inherent dimension of all employed experimental conditions. Secondly, in addition to common neural codes, we also identified neural representations that were highly specific to the experienced modality (e.g. pain or disgust) and the target (self or other) of the affective experience, particularly in the right Al (Fig. 3.1.3B). Overall, these results suggest that the neural network of the Al and the dACC might subserve a comprehensive, multi-layer, representation of aversive experiences, which takes into account both modality- and target-specific information and more general affective properties of the event.

In sum, empathy is thus characterised by sharing an affective state with another, a state that in the case of sharing the suffering with others is mediated by functions in AI and mACC. In contrast, previous research has identified another brain network, including the striatum, the VTA, and the mOFC, which subserves a compassionate response to the suffering of others, a response that is marked by feelings of concern and positive affect rather than negative affect. Therefore, compassion seems to represent a coping strategy which may buffer the negative consequences of empathic distress. In the following, we investigated the differences between classical emotional regulation strategies such as cognitive reappraisal and compassion.

3.1.4 Compassion-based emotion regulation up-regulates experienced positive affect and associated neural networks

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The capacity to regulate emotions plays an important part in fostering mental health and resilience. Hitherto, emotion regulation research has primarily focused on techniques that attenuate or modulate the impact of emotional stimuli, with most studies being focused on the effects of actively generating alternate interpretations to emotional stimuli; that is, what has been called Reappraisal. Despite the attested efficacy of Reappraisal (McRae et al., 2012, Emotion, 12, 2, 250–255), recent evidence suggests it can be functionally detrimental in the context of interpersonal relationships, where it has been shown that reappraisal can induce callousness in the



Compassion <> Reappraisal

Figure 3.1.4 Bold activation (p_{FWEc} <.05) associated with Compassion Meditation (red-yellow) compared with Reappraisal (blue) during regulation of responses to negative stimuli. Cortically, Compassion is associated with activation of midline prefrontal and limbic structures, while Reappraisal preferentially activates cognitive control circuits anchored in bilateral prefrontal cortices, the pre-supplementary motor area, and the right temporoparietal junction. These results show the dissociable neural networks supporting Compassion and Reappraisal.

face of others' suffering (Cameron & Payne, 2011, J Pers Soc Psychol, 100, 1, 1–5). Presumably this is due to the down-regulation of negative affect resulting in reduced emotional connectedness. This suggests that alternate regulation techniques are called for to deal with emotional reactions stemming from social sources.

Here, we investigated one promising alternative to Reappraisal, namely the up-regulation of positive affect via Compassion Meditation. Using fMRI, we scanned 15 expert practitioners using Compassion Meditation or Reappraisal to modulate their emotional reactions to film clips depicting people in distress. Both strategies effectively, but differentially, regulated experienced affect, with Compassion primarily increasing positive and Reappraisal primarily decreasing negative affect relative to passive viewing. Relative to both passive viewing and Reappraisal, Compassion increased activation in regions involved in affiliation, positive affect, and reward processing including the ventral striatum and the medial orbitofrontal cortex (Fig. 3.1.4). This network was active prior to stimulus presentation, suggesting that the regulatory mechanism of Compassion is the stimulus-independent endogenous generation of positive affect.

In sum, we have described different routes of social affect and cognition that support better understanding of other people and how we relate to them, and that seem to be also involved in prosocial behaviour. However, human altruism is a heterogeneous concept and we know very little about its structure and motivations that drive various expressions of prosocial and cooperative behaviour. In order to bridge the gap between socio-affective and socio-cognitive processes on the one hand and prosocial behaviour on the other, a more comprehensive framework of human prosociality and cooperation is necessary.

3.1.5 The structure of human prosociality: Differentiating altruisticallymotivated, norm-motivated, strategically-motivated, and self-reported prosocial behaviour

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Societies depend on prosocial behaviour of their members, ranging from offering seats to the elderly to taking in refugees. Recently, the study of human cooperation and altruism has moved into scientific focus. However, human prosociality is a multi-faceted construct that has been studied using various specific assessments, typically implemented in isolation. In order to enhance its reliable scientific assessment and the understanding of its underlying structure, we integrated 14 paradigms from diverse disciplines to identify reliable subcomponents of human prosociality. A total of 329 participants performed game theoretical paradigms (e.g. the Dictator Game) and hypothetical distribution tasks (measures of social value orientation and social discounting) commonly used in behavioural economics and completed interactive computer tasks (a donation task and the Zurich Prosocial Game) and trait questionnaires typically employed in psychology and the neurosciences (e.g. the Prosocialness Scale).

Four subcomponents of prosociality were identified by exploratory factor analysis and verified by confirmatory factor analysis in an independent participant sample: altruistically-motivated prosocial behaviour, norm-motivated prosocial behaviour, strategically-motivated prosocial behaviour, and self-reported prosocial behaviour (Fig. 3.1.5). Further supporting the independence of these sub-components, altruistically-motivated behaviour was related to gender, enhanced cognitive skills, and reduced negative affect, while not showing a strong relation to self-reported prosocial behaviour. This study challenges existing conceptualisations of one domain general cooperative phenotype and provides a crucial step toward an overarching framework on prosocial behaviour that will benefit future research on predictors, underpinnings, and plasticity of human cooperation and prosociality.



Figure 3.1.5 Structure of human prosociality. The figure illustrates the identified relationship of various prosocial measures and four latent variables of prosociality. ZPG: Zurich Prosocial Game, SVO: Social Value Orientation, TG: Trust Game, DG: Dictator Game, IRI: Interpersonal Reactivity Index, Reci Effect: Reciprocity Effect, 2nd /3rd PP: 2nd and 3rd Person Punishment. +/- indicate positive/negative standardised regression weights.

Psychopathology of the Social Mind and Behaviour The overarching goal of the Department's fourth research focus on psychopathology of the social brain is to further our understanding of deficient social behaviour and the underlying mechanisms observed across most mental disorders. Thus, many conditions such as autism, alexithymia, psychopathy, depression, or narcissistic and borderline personality disorders are characterised by deficiencies in socio-affective or socio-cognitive processing including a lack of empathy (Silani et al., 2008, Soc Neurosci, 3, 2 97–112; Bird et al., 2010, Brain, 133, 5, 1515-1525; Singer, 2012, NeuroImage, 61, 2, 437-449), Theory of Mind (Frith & Happe, 2005, Curr Biol, 15, 19, R789-R790; Singer, 2006, Neurosci Biobehav Rev, 30, 6, 855–863) and emotion regulation (Kanske et al., 2015, Transl Psychiatry, 5, e497). While being trans-diagnostically important, studying the (1) disorder specific profiles of social behaviour deficits and (2) the affective and cognitive mechanisms underlying them will enable the development of more fine-grained diagnostic tools and targeted therapeutic interventions. The clinical research focus thus builds on the previous delineation of socio-affective and -cognitive processes in healthy individuals as described in Chapter 3.1.

Self-other distinction in empathic responding

As described in paragraph 3.1.1, we represent others' states by empathically sharing their emotions and by mentalising on their goals, intentions, and thoughts. A

central problem when trying to understand another's feelings and thoughts is overcoming the impact of one's own, possibly incongruent emotional and mental states. Thus, distinguishing between self- and other-representations is a key element of adaptive behaviour in social environments. Regarding cognitive self-other distinction, social neuroscience has provided ample evidence for the involvement of a specific neural network that critically includes the temporoparietal junction (TPJ), which is functionally and structurally coupled with further temporal regions (temporal poles, the superior temporal gyrus), the anterior medial prefrontal cortex, and the posterior cingulate cortex (Fig. 3.1.1.2). Overcoming emotional egocentricity to accurately represent another's affective state, in contrast, relies on a different network centred around more anterior temporoparietal regions (in particular the supramarginal gyrus, SMG), which is connected with insular cortices and the anterior cingulate cortex (ACC) (Fig. 3.1.1.2).

In line with our prior differentiation of impaired Theory of Mind capacities, but intact empathy in autism spectrum disorder (ASD) (Silani et al., 2008, Soc Neurosci, 3, 2, 97–112; Bird et al., 2010, Brain, 133, 5, 1515–25; Bernhardt et al., 2014, Cer Cor, 24, 12, 3258–3267), we could demonstrate that ASD patients are not impaired in a task requiring emotional self–other distinction, but show the well-known socio-cognitive impairment (Fig. 3.2.1). Interestingly, ASD patients also show decreased neural network connectivity when seeding from TPJ,

but not when seeding from SMG, in resting state data. Finding such a deficit in a task-free state, when the functions are not explicitly demanded, could suggest alterations in self-generated mental contents that somewhat mirror the deficits observed in socially interactive situations. In contrast to ASD, depression has been repeatedly associated with deficient empathic responding. Our research shows, however, that this description falls short of the actual complexities involved in representing others' emotions. Depression only causes deficient empathic responding when one's own emotional state is incongruent with that of the observed other, while general empathy impairments are completely explained by co-morbidly increased alexithymia, that is, the inability to accurately access and describe one's own affective states (Fig. 3.2.2). This conforms well with our previous work on empathy in ASD, which shows that any deficits in empathic responding are due to increased alexithymia in ASD (Bird et al., 2010, Brain, 133, 5, 1515–25). Non-alexithymic ASD patients do not show empathy impairments, while healthy individuals with alexithymia do show such deficits. It is thus specifically emotional selfother distinction that is impaired in depression, not empathic responding per se.

Classifying thought patterns in psychopathology

In addition to the interaction with the immediate social environment, enabled by socio-affective and socio-cognitive capacities such as empathy or Theory of Mind, much of our mental life is actually self-generated. We spend up to 50% of our waking time mind-wandering, (Killingsworth & Gilbert, 2010, Science, 330, 6006, 932) and excessive engagement in such stimulus independent thought has been demonstrated for several different mental disorders (e.g. Ottaviani et al., 2014, Front Neurosci, 8, 1–9). A crucial question here is whether it matters "where the mind wanders", that is, what the specific content of self-generated thoughts is. We could show that these thoughts can be described along different dimensions including a social factor (self- or other-related thoughts), a temporal factor (future- or past-oriented thoughts), and a valence factor (positive or negative) (Ruby et al., 2013, PLoS One, 8, 10, e77554; Ruby et al., 2013, Front Psychol, 4, 962), and that what we occupy our minds with is highly consequential for mood and for coping with psycho-social stress (Engert et al., 2014, Biol Psychol, 103, 283–291). Nevertheless, the specific types of thought patterns associated with different psychopathological conditions are largely underexplored.

Aiming to probe this guestion, we have started to employ similar methodology across different disorders and conditions, which indeed yielded highly specific fingerprints of self-generated thought content (for an overview see Fig. 3.2). Borderline personality disorder showed particular instability in self- and other-related thoughts, which was predicted by thought valence; greater instability meant more negative thoughts (Fig. 3.2.4). Higher narcissism was associated with increased mind-wandering, including more negative thoughts (Fig. 3.2.5). However, thoughts about themselves were particularly positive, reflecting their tendency to engage in fantasies of future grandiosity. Pilot data from highly aggressive people, in contrast, show particularly negative thoughts about others. Interestingly, the overall pattern thus shows a trans-diagnostic negative bias indicating increased negative and decreased positive thoughts, but specific fingerprints with borderline, narcissism, and aggression showing alterations in the social factor of self-generated



Figure 3.2 Fingerprints of self-generated thought content across borderline personality disorder (BPD), trait narcissism (Narcissism), depression (MDD), and aggressive individuals. Off-task thoughts indicate the amount of self-generated thought during a task, the other categories indicate how other- and self-related, negative and positive, past- and future-oriented thoughts were.

thought and depression showing changes in the temporal dimension (Fig. 3.2.3).

Beyond the studies outlined above, we have been continuously expanding the psychopathology research programme to more comprehensive assessments of differential social affective and cognitive deficits (e.g. showing distinct empathy deficits, but intact Theory of Mind in non-psychopathic, aggressive individuals) and interactive behaviour in micro-economic game paradigms (e.g. showing decreased generosity in narcissism). Testing many psychopathologies on these different markers of social affect and cognition, thought patterns and social behaviours will allow the identification of specific fingerprints unique to a given psychopathology, moving the field to a more fine-grained level of understanding of the exact nature of their social deficits.

3.2.1 Preserved self–other distinction during empathy in autism linked to network integrity of the right supramarginal gyrus

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Autism spectrum disorder (ASD) shows deficits in selfother distinction during Theory of Mind (ToM). In this study we investigated whether ASD patients also show difficulties in self-other distinction during empathy and if potential deficits are linked to dysfunctional resting-state connectivity patterns within the brain. In a first study, ASD patients and controls performed an emotional egocentricity paradigm (Silani et al., 2013, J Neurosci, 33, 39, 15466–15476) and a ToM task, the Movie for the Assessment of Social Cognition (MASC; Dziobek et al., 2006, J Autism Dev Disord, 36, 5, 623-636). During the emotional egocentricity paradigm, participants' hands were touched simultaneously with either pleasant or unpleasant stimuli and they had to judge either their own or the other participant's emotion. The emotional experiences of both participants could be either congruent

or incongruent. In the second study, resting-state connectivity of the right temporo-parietal junction (rTPJ) and right supramarginal gyrus (rSMG) were analysed using a large-scale fMRI dataset (see http://fcon_1000. projects.ni trc.org/indi/abide/). ASD patients exhibited deficient ToM but normal emotional egocentricity (Fig. 3.2.1), which was parallelled by reduced connectivity of regions of the ToM network and unimpaired rSMG network connectivity. These results suggest that unlike ToM and its associated underlying rTPJ network, self-other distinction during empathy and its underlying rSMG network remain spared in individuals with ASD. These findings provide further detail for a more fine-grained characterisation of social deficits in ASD, providing evidence for spared social-affective functioning, but deficiencies in socio-cognitive functioning.



Figure 3.2.1 (A) Display of the emotional egocentricity bias (EEB). Both groups displayed a significant EEB, but the size of the EEB was similar for individuals with ASD and healthy controls, suggesting intact self-other distinction during empathic judgements in ASD. (B) MASC total score. As expected, healthy controls showed a significantly greater MASC score than individuals with ASD, suggesting deficient ToM in ASD. (C) Display of significant group difference in resting-state connectivity in the rTPJ network. Findings revealed significant differences in the rTPJ but not rSMG functional connectivity between the two groups, with individuals with ASD showing reduced functional connectivity from the rTPJ to ITPJ, precuneus, PCC, and MPFC (FWE \.0.5, cluster corrected). (D) No significant group difference in resting-state connectivity in the rTPJ with decreasing symptom severity (ADOS social interaction) within the ASD sample (FWE \.0.5, cluster corrected). Stronger connectivity between regions of the PCC with rTPJ in individuals with ASD predicts smaller ADOS social interaction scores.

Having investigated the role of self-other distinction in autism spectrum disorder, the next section turns to empathic responding in major depression.

Empathy in depression: Egocentric and altercentric biases and the role of alexithymia

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Major depressive disorder (MDD) has been associated with empathy deficits (Schreiter et al., 2013, J Affect Disord, 150, 1, 1–16). The exact nature of these deficits and their relation to concurrent alexithymia remain unknown. In this study we tested under which conditions MDD patients with high and low alexithymia show deficient empathy, particularly investigating empathic abilities when inhibition of self-related emotional states is needed and when it is not. For this purpose, a group of healthy controls (low: n = 28, high: n = 14) and currently depressed MDD patients (low: n = 11, high: n = 18) with low or high alexithymia performed an established emotional egocentricity paradigm based on tactile stimulation (Silani et al., 2013, J Neurosci, 33, 39, 15466–15476). This task measures empathic judgements when emotional states of self and other differ and inhibition of self-related emotional states is needed, and when they do not, and thus empathic judgements can be based on simple projection mechanisms. Results showed that only alexithymia but not depression decreased empathy in situations when simple projection sufficed (Fig. 3.2.2). However, when inhibition of self-related emotional states was needed, MDD patients showed an egocentric bias during empathic judgements and an altercentric bias during self emotion judgements, the latter suggesting heightened emotional contagion, both independent of alexithymia. Across the entire sample, alexithymia decreased the size of the egocentric bias. These results suggest that MDD patients show intact empathic judgements when simple projection is required and no concurrent alexithymia is present. In situations when incongruent emotional states of self and other have to be resolved, MDD patients are prone to egocentric and altercentric biases.



Figure 3.2.2 (A) Empathic judgements during individual other condition. MDD patients showed intact empathic judgements when no inhibition of self-related emotional states was required. Alexithymia decreased empathic judgements, independently of depression. (B) MDD patients showed an increased egocentric bias during empathic judgements (Other incongruent – Other congruent) when inhibition of self-related emotional states was required, independently of alexithymia. Alexithymia decreased the egocentric bias independently of depression. (C) Altercentric bias during self emotion judgements (Self incongruent – Self congruent), namely emotional contagion. MDD patients showed increased altercentric bias during self emotion judgements, unaffected by alexithymia. (D) Significant positive correlation over the entire sample between altercentric bias and personal distress as measured by the Interpersonal Reactivity Index (IRI).

After exploring the role of self-other distinctions in autism spectrum disorder and depression, the following studies turn to self-generated thought in different mental disorders, starting with depression.

3.2.3 Where the depressed mind wanders: Self-generated thought patterns as assessed through experience sampling as a state marker of depression

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Self-generated thoughts (SGTs), such as during mind-wandering, occupy much of our waking life. Individuals with major depressive disorder (MDD) are less in the "here and now" and prone to rumination (Nolen-Hoeksema et al., 2008, Perspect Psychol, 3, 5, 400-424). Few studies have looked at SGTs in depression using experience sampling methods, in particular with respect to the specific contents of depressive SGTs and how they vary from one time point to another. In this study MDD patients (n = 25) and matched healthy controls (n = 26) performed an established mind-wandering task involving non-demanding number discriminations (Ruby et al., 2013, PLoS One, 8, 10, e77554). Intermittent probe guestions ask for participants' current SGTs, that is, how offtask the thoughts are, how positive or negative, self- or other- related, and past- or future-oriented. Multi-level

sive SGT was the decreased positive valence of thoughts (Fig. 3.2.3). MDD patients' future and past-oriented thoughts were particularly more negative compared to healthy controls. These findings suggest that MDD patients show a very specific SGT pattern, possibly reflecting ruminative and anxious thoughts. This SGT pattern in depression might represent a useful state marker and even constitute an etiological factor of this debilitating disease, considering the importance of current SGT on an individual's cognitive processes and affective states.

modelling revealed that MDD patients engaged in more

mind-wandering than healthy controls. Their SGTs were predominantly negative and less positive, more self-re-

lated and past- oriented. Strongest predictor of depres-



Figure 3.2.3 (A) Amount of SGT and SGT contents for healthy controls and MDD patients. Depressed patients showed increased negative and decreased positive as well as increased self- and past-related thoughts, relative to healthy controls (error bars represent standard errors). (B) In contrast to healthy controls, MDD patients show a significant positive relation between the negative valence and past-relatedness of SGTs. (C) In contrast to healthy controls, MDD patients show a significant positive relation between the negative valence and future-relatedness of SGTs.



MDD 📕 HC



The following study explores self-generated thought in a different condition, that is, in patients with borderline personality disorder.

The wandering mind in borderline personality disorder: Instability in self- <u>3.2.4</u> and other-related thoughts

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Diagnostic criteria for borderline personality disorder (BPD) include instability in identity and interpersonal relationships. Here, we probed whether instability is already present in BPD patients' thoughts about themselves and others. We tested BPD patients (n = 27) and



C Negativity and extremity of self-related thoughts



healthy controls (n = 25) with a mind-wandering task that assesses content and variability of stimulus-independent self-generated thoughts. Multi-level modelling revealed that while BPD patients and healthy controls mind-wander to a similar extent, BPD patients' thoughts



D Negativity and extremity of other-related thoughts



Figure 3.2.4 (A) Level of reported off-task thoughts, other- and self-related, positive and negative, and future- and past-oriented thoughts (rating scale numbers without unit varying between 0 and 100). (B) Extremity of ratings (squared deviations from mean ratings). * p < 0.05; # p < 0.10. Scatterplot depicting the relation of the level of negative thoughts to the extremity (squared deviations from mean ratings) of (C) self-related and (D) other-related thoughts, separately for BPD patients and HCs. Intra-individual standard errors are displayed in grey and model predictions from the multi-level model as lines in the respective colour.

are coloured predominantly negatively (Fig. 3.2.4). Most importantly, although their thoughts concerned the self and others as much as in controls, they fluctuated more strongly in the degree to which their thoughts concerned themselves and others and also gave more extreme ratings. Self- and other related thoughts that were more extreme were also more negative in valence. The increased variability supports current conceptualisations of BPD and may account for the instability in identity and interpersonal relationships.

Complementing the previous two studies, the last study presented in this chapter turns to narcissism and the question of "where the narcissistic mind wanders".

3.2.5 Where the narcissistic mind wanders: Increased self-related thoughts are more positive and future-oriented

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Narcissism is characterised by a preoccupation with fantasies of unlimited success, power, beauty and so on, which has been discussed as intra-individual regulation of a grandiose, but vulnerable self-concept. To explore where the narcissistic mind wanders, we used an experience-sampling approach in a sample with large variability in pathological narcissism inventory scores. Multi-level modelling revealed more mind-wandering in participants with higher levels of narcissism and a difference in the content of these thoughts (more self-, oth-





Low narcissism

High narcissism

100



C Self-relatedness and future thoughts

0



er-related, past-, future-oriented, negative thoughts; Fig. 3.2.5). Critically, in high levels of narcissism, the self-related thoughts were associated with more positive valence and were also more future-oriented. The results demonstrate the validity of the assumed grandiose, self-absorbed view of oneself in narcissism, which includes

self-indulgent fantasies of future success. Furthermore, we found additional evidence for negative, past-oriented thoughts in narcissism, a dysfunctional pattern reminiscent of rumination, possibly linked to the increased psychopathological vulnerability in narcissism.

Belasticity of the Social Brain

The third focus of this department is on the plasticity and malleability of the social brain. Is it possible to train socio-cognitive and socio-affective capacities, and does training lead to structural and functional brain changes, to changes in subjective feeling and behaviour, to changes in physiological parameters, such as autonomic nervous system and hormonal activity? So far, little is known about the neural correlates underlying socio-cognitive or socio-affective plasticity or about the long-term training of positive social affect, prosocial motivation, or compassion (Klimecki et al., 2013, Cer Cor, 23, 7, 1552-61; Kemeny et al., 2012, Emotion, 12, 2, 338-350). In order to study neural, physiological, and behavioural changes induced by mental training programmes, we developed the ReSource Project, so far the longest and largest study on contemplative mental training. The project was funded by the European Research Council (ERC) and the Max Planck Society and involved more than 300 training and control participants (see Fig. 3.3II for details), 17 teachers, and almost all researchers from the department. The testing period started in 2013 (while a pilot period and several related studies were already performed the years before) and finished with the last follow-up data assessment in 2016 (see Fig. 3.3II for a timeline). The training comprised three to nine months of intensive daily practice depending on the training cohorts tested. We used a multi-method approach, combining data from computer tasks, measurements of the autonomic nervous

system, game-theoretical paradigms, questionnaires, observer reports, subjective measures, virtual reality scenarios, immune and stress-physiological analyses, structural and functional fMRI, and analyses of gene variants and epigenetic markers.

Recently, we published a book on the design and structure of the *ReSource Project*, its theoretical backbone, the intervention protocol, participant recruitment, and participant compliance throughout the training (Singer et al., 2016).

Training was divided into three 3-month modules, each with two core exercises to be practised for a minimum of 30 minutes 5 times a week. The Presence Module trains attention and interoception via the core exercises of Body Scan and Breathing Meditation. The Affect Module trains socio-affective skills such as care, gratitude, compassion, dealing with difficult emotions, and prosocial motivation via the two core daily exercises of Loving-kindness Meditation and a dyadic contemplative dialogue exercise called the Affect Dyad. The Perspective Module cultivates socio-cognitive capacities such as meta-cognition and perspective taking on oneself and others via two daily core exercises: Observing-thoughts Meditation and the so-called Perspective Dyad (Fig. 3.3I). Additional practices were taught in weekly 2-hour courses together with teachers to deepen and widen the targeted skills and dispositions and foster their application in everyday life.

The order of the Perspective and Affect Module was interchanged for cohorts TC1 and TC2. Two retest control cohorts (RCC1 and RCC2) did not undergo training but were repeatedly tested. A later training cohort (TC3) was trained in the Affect Module only. The follow-up testing phases took place either 4.5 months or 10 months after the last training session (Singer et al., 2016).

Overall, the retention rate of training and control participants was very high, with an overall dropout rate during the baseline and training phases of only 7.83%. While enrolled in the study, participants engaged in each core practice for an average of 3 to 4 times per week, with some variance by type of practice as shown in Figure 3.3III.

While the study was still ongoing, we began to analyse baseline data to introduce and validate novel measures by relating them to known measures within and across domains (see for instance also paragraphs in 3.1.1 and 3.1.5). Project goals during this phase aimed at advancing the theoretical and conceptual understanding of the respective fields of research (e.g. social neuroscience, stress research, and motivation psychology) via the rich dataset of the *ReSource Project*. So far we have published 13 manuscripts on the basis of *ReSource* baseline data while many more are still under review or in preparation (see paragraph 3.1.1 as an example of such a baseline article).

The second phase is aimed at testing training-related and module-specific changes within pre-defined different domains (e.g. brain structure, stress-physiology, prosocial behaviour, etc.). So far, we have published 4 manuscripts (see paragraphs 3.3.2, 3.3.3, and 3.3.4 as an example). Most manuscripts (> 15 at the moment) in this domain are currently under review or in preparation. A future third phase will aim at integrating observed changes within larger conceptual contexts across the different domains as well as exploring individual differences in responsiveness to the training. This phase also involves assessing the stability of observed changes by analysing data from T4, the follow-up time points.

The following paragraphs (paragraphs 3.3.1-3.3.4) describe four studies that investigated training-related changes from the ReSource Project in the domain of subjective experience and body awareness and regulation. The first study (paragraph 3.3.1) looks at the phenomenological fingerprints of the experiences with the daily core meditations of the three different *ReSource* training modules to show their immediate (short-term) effect on affective and cognitive mental states and on body awareness. The next study (paragraph 3.3.2) introduces a new contemplative practice format, the Contemplative Dyads. In these partner exercises, participants practise with another person via a platform or a cell-phone app for 10 minutes daily, working on different intersubjective capacities. We report effects on perceived social connectedness and affective state, and compare their evaluation by participants to that of classic content-matched



Figure 3.31 The training model of the *ReSource Project*. This figure shows the topics of the respective training modules (Presence, Affect, and Perspective) together with the two main core exercises (Singer et al., 2016).

meditations done alone. The third and the fourth papers focus on interoceptive body awareness. Interoception has been found to be critical for both physiological and psychological health (Farb et al., 2015, Front Psychol, 6, 763). The first of these studies (paragraph 3.3.3) looks at changes in several aspects of interoception from mere noticing of body sensations to their integration with attentional, cognitive, and emotional processes. The second of these studies (paragraph 3.3.4) utilises an objective measure of interoception, accurate heartbeat counting, to investigate the malleability of body awareness. It also traces the interrelationships between changes in interoception and changes in emotional awareness, thus providing data that inform the value of contemplative interventions for the improvement of psychological and physiological health.



Figure 3.3II The timeline and design of the *ReSource Project*. The training cohorts were tested before the start of the training (T0) and towards the end of each module (T1–T3).



Figure 3.3III Weekly mean-per-participant compliance rates for all four practices as a function of cohort and module. The shaded area represents the Christmas vacation period, when practice was not required.

3.3.1 Phenomenological fingerprints of four meditations: Differential state changes in affect, mind-wandering, meta-cognition, and interoception before and after daily practice across nine months of training

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Here we tested whether and to what extent four types of mental practice differ in their psychological effects on momentary subjective experience. Specifically, we targeted change in affect, mind-wandering, meta-cognition, and body awareness assessed before and after each daily meditation practice session in the everyday lives of participants. Multi-level models were used in order to incorporate the intensively measured nature of the data; estimates from the models are shown in Figure 3.3.1. Across both TC1 and TC2 we found that the Body Scan led to the greatest state increase in interoceptive body awareness and the greatest decrease in thought content, Loving-kindness Meditation led to the greatest increase in positive thoughts about others, and Observing-thoughts Meditation led to the greatest increase in meta-cognitive awareness. All practices, including Breathing Meditation, increased positivity of affect, energy, and present focus and decreased thought distraction. Complementary network analysis of intervariate relationships revealed distinct phenomenological clusters of psychological change congruent with the content of each practice (Borsboom & Cramer, 2013, Ann Rev Clinic Psychol, 9, 9, 91–121).

Although the different meditation practices studied here have common beneficial effects, each practice is also characterised by a distinct short-term psychological fingerprint, the latter having important implications for the use of meditative practices in different intervention contexts and with different populations.



Figure 3.3.1 Model-derived means and 95% confidence intervals assessing change from before to after an individual meditation session, by module. Data is shown for training cohorts 1 and 2. Confidence intervals that do not intersect the 0 axis (grey line) represent statistically significant change at $\alpha = 0.05$.

Complementing the study of classical meditation practices just described, we next examine the state and trait effects of dyadic contemplative practices.

Effects of contemplative dyads on engagement and perceived social connectedness over 9 months of mental training. A randomised clinical trial

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Contemplative dyadic exercises are a type of loud meditation that have been used in therapeutic as well as contemplative contexts for a long time. However, hitherto only anecdotal evidence had pointed to their powerful transformative nature. Here, we systematically investigated the effects of two newly developed contemplative dyads, the so-called Affect and Perspective Dyad, introduced as 10 minutes of core daily practice in the Affect and Perspective Module of the ReSource programme on perceived social connectedness and affective state, and compared their evaluation by participants to that of classic single meditations. We focus on perceived social connectedness as a critical outcome because loneliness, a perceived lack of social connectedness, is a prospective risk factor for a wide range of mental and physical illnesses, culminating in premature mortality (Holt-Lunstad et al., 2015, Perspect Psychol Sci, 10, 2, 227-237). Interventions to bolster perceived social connectedness would thus have substantial benefits.

Compliance, motivation, and liking were similar between the dyads and the classical content-matched daily meditations of a given module. As shown in Figure 3.3.2, during each individual near-daily practice session, social closeness to the dyadic partner increased for both dyads (Affect Dyad $\Delta M = 1.49 \pm .12$, p < .001; Perspective Dyad $\Delta M = 1.06 \pm .12, p < .001$). In addition, pre-session feelings of social closeness increased over time for both dyads (Affect Dyad slope = $.016 \pm .003$; Perspective Dyad slope = $.012 \pm .003$). Self-disclosure increased over time for both dyads (Affect Dyad slope = $.023 \pm .004$; Perspective Dyad slope = $.006 \pm .005$), but increased more steeply for the Affect Dyad (ps < .005). We conclude that contemplative dyads represent a new type of contemplative practice including other practice partners on a daily basis targeting the increase in perceived social connectedness and intersubjective capacities deficient in many psychopathologies and people suffering from loneliness.



Figure 3.3.2 Effects of contemplative dyads on social closeness and self-disclosure. (A) Raw person-mean change in social closeness before and after practice, and self-disclosure during practice. (B) Model-estimated (lines) and weekly-mean raw (points) change over time in pre-practice social closeness and during-practice self-disclosure over the 3-month training modules. Shaded areas represent 95% confidence bands.

After examining the subjective impact of the various training practices, we turn to the effects of the training on mind-body interactions.

3.3.3 Differential changes in self-reported aspects of interoceptive awareness through three months of contemplative training

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Interoception is the sense of our internal physiological processes via afferent nerve fibres from the viscera, muscles, joints, teeth, and skin (Craig, 2003, Curr Opin Neurobiol, 13, 4, 500–505). This internal sensing is closely connected to emotional awareness and has implications for both physiological and psychological health. Here, we investigated how interoception changes through the 3-month Presence Module of the ReSource Project, which intensely targets interoceptive abilities through the daily practice of two core meditations, the Body Scan and the Breathing Meditation (Fig. 3.3A). We used a recently developed self-report instrument, the Multidimensional Assessment of Interoceptive Awareness (MAIA), which distinguishes between 8 different aspects of interoception. We first translated the MAIA into German and validated it using a large and diverse sample (N = 1076). We then analysed changes through the training. We found significant changes in 5 out of 8 aspects of self-reported interoception (Fig. 3.3.3). Interestingly, the changes

for the "Noticing" scale, that is, the ability to feel internal changes, showed small, insignificant effects. Large and medium sized changes were, however, found for aspects of mind-body connection. In particular, participants use awareness of body sensations much more frequently to regulate distress (Self-Regulation), listen to their body to gain insight into their own emotional state (Body Listening), and feel more at home in their bodies (Trusting). Participants also become more aware of the connection between emotions and physiological states (Emotional Awareness) and experience greater voluntary control about attention to body sensations (Attention Regulation). This pattern indicates that body sensations do no necessarily appear amplified after the Presence training, but that participants get a deeper understanding of their mind-body system and can use this understanding to foster emotional well-being.



Figure 3.3.3 Changes in different facets of interoceptive awareness. The *y*-axis represents effect size as Cohen's *d*. Significant time x training interactions were observed for Self-Regulation, F(1, 226) = 53.61, p < .001, Attention Regulation, F(1, 226) = 42.65, p < .001, Body Listening, F(1, 226) = 35.56, p < .001, Body Trusting, F(1, 226) = 14.90, p < .001, and Emotional Awareness, F(1, 226) = 4.34, p = .04, but not for Not-Distracting, Not-Worrying, or Noticing, ps > .10.

The next study complements the analysis of self-report data by objective data on interoception. It also takes a closer look at concomitant changes in emotional awareness and how they relate to changes in interoception.

Taking time to feel our body: Steady increases in heartbeat perception accuracy and decreases in alexithymia over 9 months of contemplative mental training

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Here, we investigated whether the ReSource training also influences interoceptive accuracy, that is, the ability to accurately perceive internal physiological signals via afferent nerves. To this end, we used a heartbeat perception task (Schandry, 1981, Psychophys, 18, 4, 483-88). Participants were asked to silently count their heartbeats in intervals of varying duration. An ECG was acquired at the same time, allowing us to quantify the accuracy with which participants interocept on their heartbeat. We found steady increases in heartbeat perception accuracy over the course of the training (Fig. 3.3.4). All training modules proved to be effective in this regard, probably because they all involve focus on body sensations to remain grounded in present moment awareness. Initial changes after only 3 months of training were not significant, corroborating our findings on subjective data described above (see paragraph 3.3.3). however, changes became significant after 6 months of training and continued to increase until the end of the study (9 months). Interoception has been linked to awareness of emotions (Bechara & Nagvi, 2004, Nat Neurosci, 7, 2, 102-103). It had, however, never been shown that changes in interoception lead to changes in emotional awareness. To close this gap, we also investigated alexithymia throughout the study. Alexithymia is characterised by deficits in identifying emotions, describing emotions, and an externally oriented thinking style. We found alexithymia to decrease over the study, particularly for participants with high initial scores (note that our participants had been screened to exhibit only subclinical levels of alexithymia). Importantly, changes in interoceptive accuracy both coincided with and predicted changes in alexithymia. Our findings thus provide strong evidence for the importance of interoception for emotional health and the malleability of both by contemplative mental training.



Figure 3.3.4 Changes in interoceptive accuracy, measured by a heartbeat perception task and emotional awareness, measured by the Toronto Alexithymia Scale (TAS-20). (A) The y-axis represents effect size as Cohen's d. Heartbeat perception accuracy increased more strongly in the training cohorts than in the retest control cohorts, F(1, 775.439) =5.685, p = .017. The pooled effect size of increase in heartbeat perception accuracy across the two 9-month training cohorts was d = .273. (B) Alexithymia scores decreased more strongly in the training cohorts than in the control cohort, F(1, 781.597) = 11.515, p < .001, indicating that training induced increases in emotional awareness. Pooled effect size was d = -.331.



Congresses, Workshops, and Symposia

2014

Singer, T. (March). Workshop "Cutting Edge Research on Human Development: Learning, Social Cognition, Action, and Emotion", Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.

2016.

- Singer, T. (February). Symposium "Frontiers in Computational Neuroscience", Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.
- Singer, T. (February). Symposium "Frontiers in Cognitive Neuroscience", Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.
- Kanske, P. (June). Wo/Man, Mind, Machine, Berlin, Germany.

Degrees

PhD Theses

2015.

 Hoffmann, F. Emotional egocentricity in development and psychopathology. PhD Thesis, Faculty of Life Sciences, Humboldt University, Berlin.

Habilitation Theses

2014

Kanske, P. Neural bases of emotional processing in affective disorders. Habilitation Thesis, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig.

Appointments

2015

 Böckler-Raettig, A. Junior Professor. Department of Psychology, University of Würzburg, Germany.

2016

 Bernhardt, B. C. Assistant Professor. Multimodal Imaging and Connectome Analysis Lab, Montreal Neurological Institute and Hospital, McGill University, Montreal, Canada.

Awards

2014.

Kanske, P. Fellowship in the mentoring programme for outstanding young scientists. Biological and Neuropsychology Section of the German Society for Psychology, Germany.

2015

- Böckler, A. (June). Fast Track Programme of the Robert Bosch Foundation, Stuttgart, Germany.
- Kanske, P. Member of Die Junge Akademie at the German National Academy of Sciences Leopoldina and the Berlin-Brandenburg Academy of Sciences and Humanities.

2015

- Valk , S. (June) Student and Post-doc event as part of OHBM. Network event. Honolulu, Hawaii, U.S.A.
- Singer, T. (June). The European Neurophenomenology, Contemplative, and Embodied Cognition Network (ENCECON), Château de la Bourlie, France.
- Valk, S. (June) Student and Post-doc event as part of OHBM. Network event. Geneva, Switzerland
- Kanske, P. (October). Fascination with the Unknown: The Other, Leipzig, Germany.

2016 -

Engen, H. G. On the endogenous generation of emotion. PhD Thesis, University of Leipzig.

2015 -

- Steinbeis, N. Neurocognitive mechanisms of development in socio-affective judgment and decision-making during childhood. Habilitation Thesis, University of Leipzig.
- Steinbeis, N. Assistant Professor. Institute of Psychology, University of Leiden, the Netherlands.
- Engert, V. W2 Group Leader Position (within Department of Social Neuroscience), Max Planck Society, Germany.

 Singer, T. The German "ManagerMagazin" voted Tania Singer to be among the top 50 most influential women for the German economy.

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 demonstrate the unique qualifications of the team members.

Books and Book chapters

Bernhardt, B. C., Di Martino, A., Valk, S. L., & Wallace, G. L. (2016). Neuroimaging-based phenotyping of the autism spectrum. In *Current Topics in Behavioral Neurosciences*. Berlin: Springer. doi:10.1007/7854_2016_438.

Chierchia, G., & Singer, T. (2016). The neuroscience of compassion and empathy and their link to prosocial motivation and behavior. In J.-C. Dreher, & L. Tremblay (Eds.), *Decision neuroscience* - An integrative perspective (pp. 247–257) San Diego, CA: Elsevier.

Engen, H. G., & Singer, T. (in press). Deconstructing social emotions: Empathy and compassion and their relation to prosocial behavior. In R. Davidson, A. Shackman, A. Fox, & R. Lapate (Eds.), *The nature of Emotion* (2nd ed.). New York: Oxford University Press.

Engen, H. G., & Singer, T. (in press). Fighting fire with fire: Endogenous emotion generation as a means of emotion regulation. In R. Davidson, A. Shackman, A. Fox, & R. Lapate (Eds.), *The nature of Emotion* (2nd ed.). New York: Oxford University Press.

Kanske, P., Böckler, A., & Singer, T. (2015). Models, mechanisms and moderators dissociating empathy and Theory of Mind. In M. Wöhr, & S. Krach (Eds.), *Current Topics in Behavioral Neurosciences* – Social Behavior from Rodents to Humans: Neural Foundations and Clinical Implications. (pp. 1–14). Berlin: Springer.

Klimecki, O. M., & Singer, T. (in press). The compassionate brain. In *Handbook of compassion science*. New York, NY: Oxford University Press.

Klimecki, O. M., & Singer, T. (2015). Compassion. In A. W. Toga (Ed.), *Brain mapping: An encyclopedic reference* (pp. 195–199). Oxford: Elsevier.

Kok, B. E., & Fredrickson, B. L. (2014). Well-being begins with "we": The physical and mental health benefits of interventions that increase social closeness. In F. Huppert, & C. Cooper (Eds.), Wellbeing: A complete reference guide [six volumes]: Interventions and policies to enhance well-being. (pp. 277–306). Chichester, UK: Wiley-Blackwell.

McCall, C. (2016). Mapping social interactions: The science of proxemics. In M. Wöhr, & S. Krach (Eds.), Current Topics in Behavioral Neurosciences - Social Behavior from Rodents to Humans: Neural Foundations and Clinical Implications. Berlin: Springer. doi:10.1007/7854_2015_431.

Polosan, M., & Favre, P. (2015). Imagerie des troubles bipolaires. In P. Fossati (Ed.), *Imagerie Cérébrale en Psychiatrie. Contributions Physiopathologiques de la Neuro-Imagerie.* Paris: Lavoisier/Médecine Sciences. Przyrembel, M. (2014). Empathische Egoisten: Eine interdisziplinäre Analyse zur Perspektive der zweiten Person. Freiburg: Alber.

Singer, T. (2015). Perspektiven der Empathie- und Compassion-Forschung. In J. Nida-Rümelin, I. Spiegel, & M. Tiedemann (Eds.), *Handbuch der Philosophie und Ethik* (pp. 256-264). Paderborn: Ferdinand Schöningh.

Singer, T. (in press). I feel your pain: The social neuroscience of empathy and compassion. In W. Hasenkamp, & J. R. White (Eds.), *Mind, matter, monastics: The making of a new contemplative science.* New Haven, CT: Yale University Press.

Singer, T., & Ricard, M. (Eds.). (2015). *Caring Economics: Conversations on Altruism and Compassion, Between Scientists, Economists, and the Dalai Lama.* New York: St Martin's Press.

Singer, T., Kok, B. E., Bornemann, B., Bolz, M., & Bochow, C. (2015). *The ReSource Project. Background, design, samples, and measurements.* (1st ed.). Leipzig: Max Planck Institute for Human Cognitive and Brain Sciences.

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Steinbeis, N. (2014). Neurowissenschaften. In W. Melzer, D. Hermann, U. Sandfuchs, M. Schäfer, W. Schubarth, & P. Daschner (Eds.), *Handbuch Aggression, Gewalt und Kriminalität bei Kindern und Jugendlichen* (pp. 152–155). Bad Heilbrunn: Klinkhardt.

Trautwein, M., Naranjo, J. R., & Schmidt, S. (2014). Meditation effects in the social domain: Self-other connectedness as a general mechanism? In S. Schmidt, & H. Wallach (Eds.), *Meditation – Neuroscientific approaches and philosophical implications*. (pp. 175–198). Wiesbaden: Springer.

Vrticka, P., Favre, P., & Singer, T. (in press). Compassion and the brain. In P. Gilbert (Ed.), *Compassion: Concepts, research and applications*. London, UK: Routledge.

Journal Articles

Baez, S., Kanske, P., Matallana, D., Montanes, P., Reyes, P., Slachevsky, A., Matus, C., Vigliecca, N. S., Torralva, T., Manes, F., & Ibanez, A. (2016). Integration of intention and outcome for moral judgment in frontotemporal dementia: Brain structural signatures. *Neurodegenerative Diseases*, *16*(3–4), 206–217. doi:10.1159/000441918.

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Bernhardt, B. C., Bonilha, L., & Gross, D. W. (2015). Network analysis for a network disorder: The emerging role of graph theory in the study of epilepsy. *Epilepsy and Behavior, 50*, 162–170. doi:10.1016/j.yebeh.2015.06.005.

Bernhardt, B. C., Hong, S.-J., Bernasconi, A., & Bernasconi, N. (2015). Magnetic resonance imaging pattern learning in temporal lobe epilepsy: Patient classification and prognostics. *Annals of Neurology*, *77*(3), 436–446. doi:10.1002/ana.24341.

Bernhardt, B. C., Klimecki, O. M., Leiberg, S., & Singer, T. (2014). Structural covariance networks of the dorsal anterior insula predict females' individual differences in empathic responding. *Cerebral Cortex, 24*(8), 2189–2198. doi:10.1093/cercor/bht072.

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Figure 3.2.5

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Figure 3.3I

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Figure 3.3II

Singer, T., Kok, B. E., Bornemann, B., Zurborg, S., Bolz, M., & Bochow, C. (2016). *The ReSource Project. Background, design, samples, and measurements.* (2nd ed.). Leipzig: Max Planck Institute for Human Cognitive and Brain Sciences.

Figure 3.3III

Kok, B. E., & Singer, T. (2016). Effects of contemplative dyads on engagement and perceived social connectedness over 9 months of mental training. A randomized clinical trial. *JAMA Psychiatry.*

Figure 3.3.1

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Figure 3.3.2

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Figure 3.3.3

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Figure 3.3.4

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Professor Dr Nikolaus Weiskopf Director

Non-invasive Imaging of the Anatomical and Functional Micro-Organisation of the Human Brain Department of Neurophysics

Our long-term research agenda is to develop and apply non-invasive magnetic resonance imaging (MRI) methods to reliably characterise the detailed anatomical and functional micro-organisation of the human brain.

Understanding the normal and diseased human brain crucially depends on reliable knowledge of its anatomical microstructure and functional micro-organisation (e.g. layers, columns, and stripes). To date, the micro-organisation can only be determined using invasive methods, such as post-mortem histology or invasive electrophysiology. This limits neuroscience, clinical research, and diagnosis.

This report describes some of the recent steps taken in the direction of micro-organisation imaging since the appointment of Nikolaus Weiskopf as Director of the re-established Department of Neurophysics in 2015, and some previous work leading to the new developments. The report also lays out the general research aim and approach.

To resolve the subtle micro-organisation and its changes in health and disease, unprecedented spatial resolution, minimal artefact levels, and high tissue specificity of the imaging are essential. To address these extraordinary methodological challenges, we pursue an integrated interdisciplinary approach consisting of:

- 1. MR physics developments
- 2. developments in biophysical modelling and image processing methods
- 3. neuroscientific proof-of-concept and validation studies

The successful development of *in vivo* histology using MRI (*hMRI*; Figure 4) of the anatomical and fMRI of the functional micro-organisation will have significant impact on research and clinical applications. Investigations of the structure–function relationship and plasticity at the microstructural level would become feasible longitudinally and across large human populations. *In vivo* studies of microstructural brain plasticity will also be enabled in humans. This will allow for an improved understanding of how brain structure determines function and functional demands affect structure.

Microstructure imaging is expected to provide sensitive biomarkers of nervous system changes due to trauma or neurodegeneration, and to facilitate novel insights into underlying mechanisms. These reliable and standardised biomarkers are expected to facilitate personalised medicine and clinical trials (e.g. for patient stratification and standardisation in multi-centre trials such as the NISCI trial on spinal cord injury).



Figure 4 From standard MRI to *in vivo* histology using MRI (hMRI). (A) MRI offers a multitude of contrasts that can be weighted towards particular MRI parameters, for example, proton density (PD), magnetisation transfer (MT) rate, longitudinal and transverse relation time (T_1 and T_2) and susceptibility effects as visible in the phase MR signal. (B) Quantitative MRI (qMRI) uses physical models to calculate quantitative parameter maps that depend nontrivially on the underlying tissue microstructure. (C) hMRI uses biophysical models to convert MRI or qMRI data to specific biological metrics such as myelin density, iron density, fibre orientation or g-ratio. This allows for the study of microstructural features that are smaller than the nominal voxel size by providing aggregate measures of them. (D) Ultimatively, hMRI may provide a detailed microstructural description of the brain, here, for example, the myeloarchitectural description of the cortical sheet (reprinted from Weiskopf et al, 2015).
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MR Physics Developments

Developments of MR hardware, data acquisition, and image reconstruction methods have been focusing on improving the contrast/signal-to-noise ratio (CNR/SNR), spatial resolution, quantification, and acquisition speed while minimising image artefacts.

The existing ultra-high field 7T MRI scanner and newly installed Connectom MRI scanner with a 300mT/m high performance gradient system (one of three worldwide) together with novel radio-frequency (RF) coils (e.g. flexible multi-channel surface coils) will provide a basis for high SNR imaging, ultrafast imaging, and improved resolution in real space and diffusion q-space. Ancillary hardware such as the high-speed optical prospective motion correction system (Kineticor, USA, HI) can maximise the image quality by correcting for motion and physiological artefacts (e.g. see abstract 4.1.1). Magnetic field cameras (Skope, Zuerich, CH) will be used to control for Eddy current artefacts and other instrumental artefacts related to the ultra high gradient amplitudes used in the Connectom scanner. A general MR acquisition and reconstruction theme supporting specificity and standardisation of MRI is the development of quantitative MRI methods, which are used both for ultra high resolution experiments (see 4.1.1 and 4.1.2) and clinical research (see 4.1.3).

Novel MRI pulse sequences complement the advances in MR hardware, enabling ultrafast (see 4.1.5) and very high spatial resolution imaging (see 4.1.4, see 4.1.1). Application of the latest image reconstruction techniques is enabled by establishing an open image reconstruction infrastructure based on the Gadgetron image reconstruction environment (see 4.1.5; collaboration: M. Hansen, NIH).

To address the issue of high specific absorption rate (SAR) and RF power deposition at 7T, electromagnetic simulations are being refined by using anatomically accurate human body models (see 4.1.6) in order to improve the assessment of new RF coil designs and finetune SAR estimates.

4.1.1 *In vivo* high-resolution quantitative multi-parameter mapping (MPM) at 7T using prospective motion correction (PMC)

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Recent years have seen a resurgence of interest in quantitative multi-parameter mapping (MPM) of the human brain, not least due to the strong link between key MR parameters and the absolute concentrations of myelin and iron in neural tissue (Stüber et al., 2014, NeuroImage, 93, 1, 95–106). There is a demand for methods which not only map several parameters, but do so accurately, robustly, and at sufficient resolution. To characterise subcortical structures such as columns and lamina, the resolution must be 400 μ m, or even higher. Quantitative MPM at such unprecedented resolution mandates the use of ultra-high field strength with its technical challenges, and the use of prospective motion correction (PMC), because physiologically-driven motion is unavoidable and is of order 300 μ m or more.

We have implemented the MPM method at 7 Tesla that simultaneously produces high-resolution maps of the longitudinal relaxation time constant T_1 , effective transverse relaxation time constant T_2^* , and magnetisation transfer saturation (Weiskopf et al., 2013, Front Neurosci, 7, 95), based on the acquisition of three 3D multi-echo FLASH MRI volumes. To correct the maps for the more inhomogeneous transmit RF field B_1 + at 7T, optimisations to B_1 mapping were made. Another challenge arises from the sheer size of the acquired datasets: a single mapping session generates over 25 times the scanner's standard data size limit, which necessitates alternative approaches to pulse sequence programming as well as the use of external image reconstruction systems. Nevertheless, we have succeeded in acquiring whole-brain MPM at an isotropic resolution of 400 µm, with sufficient image quality to visualise the striation in the primary visual cortex.

The amplitude of unavoidable physiologically-driven motion becomes comparable to the voxel dimensions at such high resolution. To address this source of image degradation, we have installed a camera-based optical tracking system (Kineticor, HI) and implemented PMC in our bespoke FLASH sequences. The position of the imaging volume is updated prior to each excitation at a rate of ca. 20 ms (Figure 4.1.1.1). With the PMC system enabled, we have demonstrated a 15% increase in white-matter regional signal-to-noise ratio (SNR), and a commensurate improvement in image quality, even in the absence of overt motion artefacts (Figure 4.1.1.2).



Figure 4.1.1.1 Motion traces as recorded by the tracking system (duration: ten seconds) of a healthy, highly compliant volunteer avoiding any head movement. Cardiac pulsation (small peaks at ca. 1-s intervals) and respiration related movement of the order of 200 μ m (higher amplitude harmonics with ca. 4-s periodicity) are comparable to the targeted image resolution of 400 μ m.



Figure 4.1.1.2 Sagittal view (T_1 -weighted 3D FLASH; 650 μ m isotropic resolution; echo time TE = 2.4 ms). Despite high image quality in both cases, the prospective motion correction system demonstrates improvement in grey/white matter tissue delineation (circled).

Fast *ex vivo* quantitative multi-parameter mapping (MPM) of R_1 , R_2^* , and MT with 100 µm resolution

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Quantitative multi-parameter mapping (MPM) provides measures of key determinants of MR contrast, for example longitudinal and effective transverse relaxation rates (R_1 , R_2^*), proton density (PD), and magnetisation transfer saturation (MT). In combination, these maps allow estimation of the macromolecular, myelin, iron, and water content (Callaghan et al., 2015, MRM, 73, 3, 1309–1314; Stüber et al., 2014, NeuroImage, 93, 1, 95–106).

We adapted an MPM protocol previously established at 3T (Weiskopf et al., 2013, Front Neurosci, 7, 95) to produce maps of R_1 , R_2^* , and MT on a 9.4T small bore scanner. The new protocol, optimised for formalin fixed post-mortem human brain tissue, consisted of spoiled multi-echo 3D FLASH acquisitions with T_1 -, PD-, and MT-weightings. For 100 µm isotropic resolution, the acquisition required one hour per weighted volume.

A 5 mm slab of human visual striate cortex was immersed in Fomblin and scanned using the MPM protocol. In the same session, the specimen also underwent gold-standard inversion-recovery R_1 -mapping with R_1 determined by a three-parameter non-linear fitting procedure.

The resultant R_1 and R_2^* maps depict high grey/white matter contrast and a highly myelinated line of Gennari (Figure 4.1.2.1). In a white matter region of interest, parameters were: $T_1 = 967$ ms, $T_2^* = 19.0$ ms, and mean MT = 2.51 p.u.. The mean T_1 derived from the IR data over the matching region of interest differed by less than 2%. In summary, a protocol for fast and very high resolution multi-parameter mapping was implemented at 9.4T. The increased signal-to-noise ratio due to the higher field and smaller sample/RF coil allowed reliable 100 µm resolution quantitative maps to be acquired in ca. 3 hr. A high comparability with gold-standard T_1 relaxometry was demonstrated. Work is ongoing to optimise the MT mapping and to correlate the maps with quantitative immunohistochemistry (Figure 4.1.2.2).



Figure 4.1.2.1 R_1 , R_2^* , and MT saturation maps for a single representative slice taken halfway through the tissue specimen. Blue outline (R_1) indicates the volume selected for region of interest analysis.



Figure 4.1.2.2 Photomicrograph of anti-myelin basic protein- (SMI 94-) stained section of the same human visual cortex specimen.

4.1.3 Developing quantitative magnetic resonance imaging (MRI) for a multicentre treatment trial of spinal cord injury

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Quantitative MRI (gMRI) provides valuable measures to assess neuronal degeneration-also for remote degenerative effects in the brain caused by spinal cord injury (SCI, Freund et al., 2013, The Lancet Neurology, 12, 9, 873-881). The recent development of an anti-NOGO-A antibody holds promise as a treatment for SCI that will be tested in an upcoming multi-centre clinical trial (NISCI, funded by EU Horizon 2020). We have been developing qMRI as a biomarker for tracking longitudinally neural de- and regeneration. Its cornerstones are quantitative multi-parametric maps (MPMs) of longitudinal relaxation rate (R_1), effective proton density (PD*), magnetisation transfer (MT), and effective transverse relaxation rate (R_2^*) based on multi-echo 3D-FLASH acquisitions (Weiskopf et al., 2013, Frontiers in Neuroscience, 7, 1-11). A high inter-site and long-term comparability was shown for this approach, which is central for the NISCI longitudinal multi-centre trial (Weiskopf et al., 2013).

The clinical trial requires that different MRI vendors with varying software and hardware versions (mostly 3T Siemens, but also GE and Philips scanners) are considered, MRI product sequences are used, and scans are short (~22 min). We have been assessing different acceleration methods (e.g. parallel imaging; Figure 4.1.3) for their impact on the quality of resulting MPMs on the different MRI systems in order to achieve the best trade-off of speed, specificity, sensitivity, long-term stability, and comparability.

The optimisation of the acquisition protocols is complemented by advancing the data post-processing. For the clinical trial setting, we are adapting methods for interscan motion artefacts (accounting for relative coil sensitivity changes; Papp et al., 2016), and robust estimation of R_2^* maps (Weiskopf et al., 2014, Front Neurosc, 8, 1–10).



Figure 4.1.3 SNR decrease due to increased acceleration (left to right). Axial slices of maps of R_1 (A-C; z = 58 in MNI space; grey scale window from black = 0/s to white = 2/s) and R_2^* (D-F; z = 65; window from 0/s to 50/s). Calculated from the proton-density (PD-) and T_1 -weighted data for the R_1 maps, and from all weightings combined for the R_2^* maps (ESTATICS, Weiskopf et al., 2014, Front Neurosc, 8, 1-10), respectively. 3D-FLASH MRI data (1-mm isotropic resolution) acquired with different parameters: T_1 - & PD-weighted images with 8 echoes each, a repetition time of TR = 25 ms, acquisition time TA = 5:16 min (A/D); with 6 echoes each, TR = 18 ms, TA = 3:48 min (B/E); both with acceleration in phase encoding direction (factor 2), and with additional 3D acceleration factor 2, whereas TA = 2:02 min (C/F); MT-weighted images with 6 echoes, TR = 37 ms, TA = 7:48 min (A/B/D/E) with acceleration in phase encoding direction (factor 2), and with TA = 4:09 min due to additional acceleration as for T_1 /PD-weighted acquisition (C/F).

4.1.4 High-resolution functional mapping of primary cortical areas at 7T

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Developments of new MR sequences and high-performance RF coils for ultra-high field MRI during the last decade enable the non-invasive investigation of human brain function at sub-millimeter resolution. Among other techniques, an MR sequence developed in the Department of Neurophysics (Heidemann et al., 2012, Magn Reson Med 68, 1506–1516) produced robust maps of BOLD (Blood Oxygen Level Dependent) activation at 0.75-mm isotropic resolution—as for instance in the visual motion area V5 and the primary motor cortex M1 (Figure 4.1.4.1).

Combined with sophisticated analysis techniques for parcellating and contouring the cortex, such acquisition techniques make fMRI a potential tool to map cortical layers and columns. Comparison between cortical activation profiles in M1 revealed different BOLD response amplitudes for different cortical depths, corresponding to cortical layers V and VI, dependent on whether fingers were actually moved or if the movement was only imagined (Trampel et al., 2012, Proc Int Soc Magn Reson Med 20, p663; Turner, 2016, Philos Trans R Soc Lond B Biol Sci 371). Layer-specific fMRI may be used to distinguish input into and output from cortical areas. Thus, it facilitates assigning directionality of information transfer in studies of the human connectome. The observed layer-specific effects are small and easily obscured by the gradient in the BOLD signal amplitude across the cortex due to draining veins. To reduce this confound, we have been developing and applying acquisition methods that are less sensitive to this unspecific effect. For instance, functional changes in cerebral blood volume (CBV) may localise changes in neural activity better than conventional BOLD fMRI though with a lower SNR, since they are more closely linked to capillary responses. Therefore, in upcoming studies of brain function at the level of cortical layers and columns we will employ a CBV-based method which was also developed at MPI CBS (Huber et al., 2014, NeuroImage, 97, 349-362) (for pilot data see Figure 4.1.4.3). The method, SS-SI-VASO (Slice-Saturation Slab-Inversion VAscular Space Occupancy), was optimised for use at 7T and was already shown to be less affected by unspecific vascular effects than BOLD-based fMRI (Huber et al., 2015, NeuroImage, 107, 23-33).



Figure 4.1.4.1 Examples for high resolution BOLD-based fMRI. Left: Coronal section showing the activated visual motion area V5 due to being stimulated with a moving starfield paradigm (moving starfield vs static starfield). Right: Axial section showing the "hand knob" in primary motor cortex M1 activated by finger tapping (finger tapping vs rest).



Figure 4.1.4.2 Differentiating input from output in the cortex. Mean BOLD signal difference between motor imagery, finger tapping, finger moving (finger tapping without touching the thumb), and "rest", respectively, for the different cortical laminae. The dashed circle emphasises the smaller ratio between "middle lamina 2", approximating cortical layer V, and "deep lamina", approximating cortical layer VI, for motor imagery compared to actual motor performance. This is expected because cortical layer V projects to the cortical spinal tract and should therefore be "silent" during motor imagery but active during motor performance. BOLD signal "draining" from cortical layer VI, however, masks this effect, making it necessary to analyse the ratio between cortical layers V and VI.



Figure 4.1.4.3 Example for VASO-based fMRI at a voxel resolution of $1.0 \times 1.0 \times 1.8 \text{ mm}^3$. Axial section showing the visual motion area V5 activated by a moving starfield (vs static starfield).

Development and optimisation of methods for real-time fMRI 4.1.5 neurofeedback

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Real-time fMRI neurofeedback allows for learning selfregulation of local and network brain activity and studying its behavioural consequences (Weiskopf et al., 2012, NeuroImage, 62, 682–692; Figure 4.1.5.1). To facilitate the learning, speed, sensitivity, and specificity of fMRI need to be optimised. Thus, our goals as part of the Braintrain project on neurofeedback (funded by EU FP7) are to optimise image acquisition and image reconstruction (1) for high BOLD sensitivity (BS) and (2) for high acquisition speed.

(1) A frequent issue in fMRI is the loss of BOLD sensitivity in basal brain areas due to susceptibility-induced static magnetic field (B0) distortion. To allow for improved rtfMRI neurofeedback from basal brain areas, we optimised echo-planar imaging (EPI) sequence protocols for high BS based on numerical simulations on a large database of magnetic field maps. The optimised parameters included compensating z-shimming gradient moments, phase encoding gradient polarity of the EPI readout, and

slice tilt (Figure 4.1.5.2). The advantage of our approach is the flexibility of optimising the BS in selected brain areas for arbitrary EPI protocols (e.g. different principal slice orientation, spatial resolution), because it does not require expensive measurements compared to previous approaches (Weiskopf et al., 2006, NeuroImage, 33, 493-504). Numerical optimisations were compared to experiment-based optimisations with good agreement. (2) A high acquisition speed is of importance for realtime fMRI, since it enables a better suppression of physiological noise and more rapid feedback. Ultra-fast fMRI sequences like accelerated 3D EPI and multi-band 2D EPI allowing whole-brain coverage with sub-second acquisition times are available, however, image reconstruction is time-intensive and usually not available on the standard scanner hardware. A custom-made image reconstruction pipeline was established for a 3D EPI sequence (whole-brain coverage, isotropic resolution of 3 mm and TR of 1.3 s) with 2 x 3 parallel imaging acceleration by

Real-time data nal computer and using the open analysis (TBV) source software Gadgetron (Hansen et al., 2012, MRM, 69, 6, 1768-1776) Image acquisition and reconstruction Real-time data export Feedback Stimulation (TBV, Cogent) presentation Shim gradient moment BS gain

for image reconstruction. The next step is to extend this concept to other ultra-fast fMRI sequences like multi-band EPI and compressed sensing, and prove the real-time applicability.

sending the raw data to an exter-

Figure 4.1.5.1 Typical real-time fMRI neurofeedback setup modularising image acquisition, reconstruction, processing, and feedback presentation.

Slice angulation/rotation



Figure 4.1.5.2 Optimised parameters for EPI protocols with axial (top row) and sagittal (oblique) slice orientation (bottom row)

Toward estimates of specific absorption rates (SAR) in individuals

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Most regulatory and standardisation organisations require determination of the specific absorption rate (SAR) for safety assessments of MRI radio-frequency (RF) coils. SAR is not easily determined experimentally for human subjects *in vivo*. Thus, it is typically derived from numerical electromagnetism (EM) simulations. The quality of EM simulations is currently limited by the shortage of anatomically accurate human models. Most available human models are discretised voxel-based geometries without ensuring electrical contact between anatomically connected parts of tissues.

We explored the impact of an improved anatomical model of cerebrospinal fluid (CSF) by investigating the influence of modified CSF dimensions on transmit performance measures, the influence of the CSF electrical properties on SAR estimates, and the limits of the high-resolution human model 3D EM simulations.

The 7T RF coil arrays developed at our Institute were simulated using the surface-based ANSYS (ANSYS

Inc., Canonsburg, PA) human body model, and the VHP model v2.2 developed by NEVA Electromagnetics (Massachusetts, USA). When CSF was simulated accurately as a single electrically connected object, it partially shielded the brain from array RF radiation, resulting in reduced transmit and safety excitation efficiencies.

If possible, our model is grouped into encapsulated sets of objects, for example, CSF, grey matter, white matter, and ventricles so that only one enclosed surface exists between each pair of objects. Such a model can be more readily imported into 3D EM simulation tools that can handle models with implicit geometrical Boolean subtraction, for instance, ANSYS HFSS.

While these high-resolution meshes currently require very long geometry pre-processing and generation time of a frequency domain solver, the test case we have simulated shows the potential for providing subject-specific SAR estimates.



Figure 4.1.6.1 7T 3D EM simulation results.(A) and (B): B_{j+} slices for model without CSF; (C) and (D) SAR10g slices for model without CSF; (E) and (F) B_{j+} slices for model with CSF; (G) and (H) SAR10g slices for model with CSF.



Figure 4.1.6.2 The high-resolution brain geometry model. (A) Geometry cross section of high-resolution brain model. (B) SAR map of the high-resolution brain model excited by a plane wave at 300 MHz.



The development of unified biophysical models is central for successful imaging of the brain's micro-organisation. They effectively integrate and leverage the wide range of contrasts (e.g. diffusion, relaxometry, magnetisation transfer contrasts) for inferring the underlying microstructure from MRI, even when the microstructural features are smaller than the nominal voxel size (Figure 4). The models are additionally informed by a-priori known aspects of structural and functional micro-organisation, for example layers, tangential and radial fibres in the cortex. The multiple contrasts will improve the micro-organisation estimates from MRI, since they offer different perspectives of the underlying microstructure and improve the conditioning of the notoriously difficult model inference.

An example of a model including anatomical prior information is the description of diffusion MRI signal in the cortex (see 4.2.2), taking into account the canonical orientation of efferent/afferent or collateral fibres (radial or tangential to the cortical surface). A mesoscopic unified model formally combining MR parameters is the linear model of the longitudinal relaxation rate R_1 (see 4.2.3), which describes the interdependence of longitudinal, transverse relaxation effects and magnetisation transfer in brain tissue. Our most recent work goes beyond the mesoscopic view by considering the precise microscopic distribution of iron as a contrast mechanism (see 4.2.4) by simulations based on iron maps measured with advanced quantitative histological methods.

The different unified biophysical models require accurate mesoscopic and macroscopic anatomical information combined with the multi-contrast MRI data in a common space. Thus, image processing methods are being developed that accurately register images with different resolutions, can handle exceptionally large datasets, and account for various instrumental and physiological artefacts (e.g. open CBS tools; see 4.2.1).

4.2.1 High-resolution cortical analysis with CBS Tools

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High field MRI requires dedicated image processing and analysis methods to handle and leverage the leap in resolution, new contrasts of interest such as quantitative MR parameter maps, and the increased level of precision achieved with 7T imaging to fully benefit neuroscientific experiments. Our team (different subsets of the authors in the following) has been building advanced computational tools for 7T image analysis (Bazin et al., 2014, NeuroImage, 93, 2, 201–209), with a particular emphasis on methods to precisely align cerebral cortices (Tardif et al., 2015a), model cortical depth and layers (Wähnert et al., 2014, NeuroImage, 93, 2, 210-220 and Wähnert et.al., 2016, NeuroImage, 125, 94–107), and study intracortical T_1 distributions and their relationship to myeloarchitecture (Dinse et al., 2015; Rowley et al., 2015). We demonstrated that careful inter-subject cortex alignment driven by intracortical contrast and anatomically consistent modelling of depth produces highly detailed group average maps of T_1 with varying patterns across cortical layers. Moreover, we demonstrated that a generative model of T_1 values based on myelo- and cyto-architecture can differentiate primary sensorimotor areas on the basis of ultra-high resolution maps of T_1 acquired at 0.5-mm isotropic resolution. We submitted this dataset and others to open repositories (Forstmann et al., 2014, Sci Data, 1, 140050; Gorgolewski et al., 2015, Sci Data, 2, 140054; Tardif et al., 2015b) in order to foster 7T analysis methods development. We are now exploring the use of these methods combined with multi-modal, quantitative MRI in the context of learning-induced brain plasticity (Tardif et al., 2015c). We are also developing new methods for the segmentation of vasculature and the estimation of oxygenation in quantitative susceptibility maps (Bazin et al., 2016). All the analysis methods developed have been integrated into a freely available neuroimaging software package, the CBS Tools (http://www.nitrc.org/projects/ cbs-tools/) and the development code from many of the tools is openly shared on Github (http://www.github. com/piloubazin/cbstools/).



Figure 4.2.1 (A) High-resolution map of intra cortical T_1 at multiple depths in four layers of equidistant depth obtained with an equi-volume model (top: using a single range of T_1 times, bottom: restricting the T_1 ranges per layer to enhance local variations, adapted from Tardif et al., 2015a); (B) Individual maps of Brodmann areas 4, 3b, 1, and 2 estimated from a generative model of T_1 cortical profiles measured at 0.5-mm resolution (adapted from Dinse et al., 2015); (C) Maps of venous vasculature and oxygenation fraction extracted from quantitative susceptibility mapping at an isotropic resolution of 0.6 mm (adapted from Bazin et al., 2016).

4.2.2

Relating diffusion MR contrast to the fibre structure of human neocortex

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Brain diffusion MR contrast is sensitive to the anisotropic hindrance and restriction of water due to neurites—axons and dendrites—and thus, when combined with the use of appropriate biophysical models, can be interpreted in terms of microstructural anatomy at the sub-voxel level. We have developed a biophysical model intended to capture the known tangential- and radial-fibre structure of human neocortex (Edwards, et al., 2016) with the aim of studying afferent/efferent and collateral fibre distributions *in vivo*.

Our diffusion model captures radial fibres as sticks aligned in the radial direction, and tangential fibres as sticks isotropically distributed in the tangential plane (perpendicular to the radial direction). In total there are three compartments: extra-neurite water, intra-radialfibre water, and intra-tangential-fibre water. In order to regularise model fitting, instead of estimating the radial orientation of each cortical voxel from the diffusion data, we estimate this orientation separately from a non-diffusion weighted image collected alongside the diffusion data. The cortical ribbon is segmented from this image, and then the geometry of this ribbon is used to generate equivolume surfaces between the pial surface and the WM/GM border-surface (Wähnert, et al., 2014, 93, 2, 210–220). The normal to these surfaces is taken to be the radial orientation.

In order to validate the model, we have fitted it to a 5-shell diffusion dataset of *ex vivo* human primary visual cortex (V1) from Kleinnijenhuis (Kleinnijenhuis et al., 2013, Cortex, 49, 9, 2569–2582). Figure 4.2.2 shows that the fitted parameters give rise to cortical profiles representative of those found in classical histological stains of V1, implying that the model indeed captures the fibre structure of cortex *ex vivo*. Work is ongoing to directly compare the model estimates in both this sample (and those from other distinct neocortical areas) with histology, and to apply the method *in vivo*.

Figure 4.2.2 (A) Classical myelin stain of human V1 from Vogt & Vogt (J. Psychol. Neurol., 1919) showing cortical fibre structure (labels denote different cortical layers), with fibres seen to be mainly radial (r) or tangential (t). Notable is the stria of Gennari (SoG), a prominent feature of human V1, and the layer of tangential neurites near the pial surface (PS). (B) Volume fractions of the intra-radial fibre and intra-tangential fibre water compartments, showing correspondence with classical histology. These fractions were estimated by fitting the present cortical diffusion model to diffusion data from a human V1 specimen. The volume fractions are means over bins of cortical-equivolume depth, and error bars show the standard deviation within each bin. The position of the SoG is slightly offset from histology because equivolume depth is not linearly related to cortical depth.



4.2.3 Linear relaxometry modelling and synthetic quantitative MRI

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Quantitative MRI (gMRI) provides standardised measures of specific physical parameters that are sensitive to the underlying tissue microstructure. Recently, an interdependence of physical parameters was demonstrated for brain tissue in the form of a linear dependence of the longitudinal relaxation rate (R_1) on the magnetisation transfer saturation (MT, acting as a myelin marker) and the effective transverse relaxation rate $(R_2^*, acting$ as an iron marker; Callaghan et al., 2015, Mag Res Med, 73, 3, 1309–1314). Thus, maps of fundamentally different physical properties can be synthesised by exploiting this principled linear biophysical model. In conjunction with multi-parameter mapping (MPM) (of R_1 , proton density, MT, R_2^*), the interdependence introduces redundancy in the measured parameters that can be exploited in several ways. We demonstrate that synthetic qMRI maps,

particularly synthetic MT maps (Figure 4.2.3), can be calculated from R_1 and R_2^* maps (Callaghan et al., 2016). This may reduce the need for MT-weighted acquisitions (in MPM), which is appealing because these are difficult to acquire at 7T due to their high specific absorption rates (SAR) demands. We have also shown that if a subset of MPM data are affected by motion artefacts, synthetic maps free of artefacts can be synthesised (Figure 4.2.3). The linear relaxometry model exemplifies how the information from multiple MRI contrasts can be effectively combined in a robust way, which is an integral part of our strategy to achieve *in vivo* histology using MRI. Future investigations will further assess the potential for artefact correction, synthetic MT mapping at 7T and compare results to histological standards.



Figure 4.2.3 (A) Multiple axial slices through a motion-corrupted MT map, (B) Synthetic MT map generated using the linear relaxometry model (modified from Callaghan et al., 2016). Note that the synthetic MT map offers exquisite contrast in the subcortical areas, as established for acquired MT maps.

4.2.4 More than simply iron: Iron distribution at the mesoscopic and cellular level determines MR contrast

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Iron is a major source of MR contrast in the brain. Aiming at methodological breakthroughs like *in vivo* Brodmann mapping or MR-based iron quantification, significant theoretical and experimental efforts were devoted to the understanding of iron-induced MR contrast (Fukanaga et al., 2010, PNAS, 107, 8, 3834–3839, Stüber et al., 2014, NeuroImage, 93,1, 95–106). Yet, due to a lack of knowledge about the cellular and subcellular iron distribution, the impact of the brain iron distribution on the MR contrast is poorly understood. We took the first steps to address these open questions by combining state-of-theart quantitative 7T MRI with histological quantitative iron mapping on post-mortem brain samples. Quantitative maps of transverse, effective transverse, and longitudinal relaxation rates $(R_2, R_2^*, R_1, respectively)$ as well as magnetic susceptibility maps were acquired for samples of human grey matter (GM), white matter (WM), and substantia nigra (SN). Laser Ablation Inductively Coupled Mass Spectroscopic Imaging (LA ICP MSI) was used for quantitative iron and myelin mapping with a submillimeter resolution, while proton beam microscopy provided quantitative iron maps with a resolution down to 1 μ m. These techniques demonstrated that iron is inhomogenously distributed. The different spatial scales of inhomogeneity influence the MR contrast in the different tissue types. In GM, sparsely distributed iron-rich fibres, and small glia cells contain most of the iron. In WM matter, however, oligodendrocytes and iron-rich fibres contain most of the iron. In addition, patches of enhanced iron concentration around small vessels with a typical size of 0.2 mm significantly impact R_2^* and QSM and their orientation dependence in WM (Figure 4.2.4.1). A different contrast mechanism prevails in SN, where densely packed iron loaded neurons dominate the MR contrast (Figure 4.2.4.2). These tissue-specific differences demonstrate that characterisation of the meso- and microstructural iron distribution is an essential step towards a quantitative understanding of iron-induced MR contrast.



Figure 4.2.4.1 Iron-induced contrast in the white matter. Iron in the white matter appears in patches with a characteristic size of 0.1-0.2 mm. The patches are observed in classical Perls's and Turnbull's iron stains as well as in quantitative iron maps obtained with LA ICP MSI. They induce substantial intra-voxel frequency dispersion and therefore contribute substantially to R_2^* in white matter (top right).



Figure 4.2.4.2 Iron-induced contrast in substantia nigra as compared to grey matter. In cortical grey matter (upper row), iron hotspots are localised in sparsely-distributed oligodendrocytes and astroglia. Neurons contain little iron. In SN (bottom row), densely packed iron-rich neurons contain most of the iron and dominate the MR contrast. Simulation of local resonance frequency shifts (right column) sheds light on iron-induced R_2^* mechanism in grey matter and SN.

Neuroscientific Proof-of-Concept and Validation Studies Newly developed micro-organisation imaging methods require careful validation. We pursue a three-pronged validation approach that consists of proof-of-concept studies in well characterised neuronal systems, *in vivo* cross-validation between functional and structural measures (e.g. in the visual system as part of the ERC-funded hMRI project), and comparison of micro-organisation estimates and *ex vivo* histology.

To achieve this, we apply and develop advanced histological methods that address the lack of quantification in standard histology and the issue of histological slices providing incomplete information of 3D brain structures. An example is our work on superficial white matter contrast that capitalises on mass spectroscopy imaging and proton-induced X-ray emission (PIXE; see 4.3.3; inc. collaborations with Paul Flechsig Institute (PFI) and Faculty of Physics and Earth Sciences, University of Leipzig). Preliminary experiments using tissue clearing indicate the feasibility of combined CLARITY and *ex vivo* MRI experiments preserving 3D tissue information (see. 4.3.1; in collaboration with PFI).

We anticipate that the *in vivo* micro-organisation mapping methods will allow for detailed studies of the structure–function relationship at the microstructural level. Our work on predicting magnetoencephalography (MEG) responses (see 4.3.2) and functional neuroanatomy from MRI-based R1 cortical myelin maps (Dick et al., 2012, JNeurosc 32, 46, 16095–16105) are early examples of how the information can be leveraged.

4.3.1 Combining optical and MRI microscopy in 3D using CLARITY: A new method for validation of MRI-based histology

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MRI-based histology is a new cutting-edge technology that relies on recent breakthroughs in ultra high-field MRI combined with the development of biophysical models linking tissue microstructure with macroscopic quantitative MR-parameters (Weiskopf et al., 2015). As an emerging method, it requires extensive validation by independent methods. Comparing MRI of post-mortem human tissue with classical histology is the mainstay of such a validation (Geyer, Turner 2013). However, this potentially very powerful approach is limited, because standard histological methods are not quantitative and rely on 2D slices obscuring the important 3D characteristics of tissue. In particular, the substructure of the cortex and its intracortical fibres, indispensable for understanding of neuronal function, cannot be reliably delineated in thin 2D histological slices.

We propose a novel approach to overcome these challenges by a combination of the quantitative MRI with 3D brain microscopy method CLARITY (Chung et al,

2013, Nat Methods, 10, 6, 508-513) on large post-mortem human brain tissue samples. In a pilot experiment, clearing of the large (7-mm thick) human post-mortem temporal lobe tissue sample was accompanied by quantitative ultra-high resolution structural MRI (Figure 4.3.1.1). MRI at different stages allowed for tracking tissue deformation during the clearing process and the monitoring of remaining lipid and iron fractions in the sample. Immunohistochemical stains for cells (HuC/D), myelin (myelin basic protein), and neurofilaments (SMI) were successfully applied to the cleared sample (Figure 4.3.1.2), allowing investigation of cortical architecture and potentially intracortical fibre tracking as deep as 2 mm into the sample. Optical imaging of deeper layers was limited by slow antibody penetration during immunohistochemical staining as well as the remaining light scattering in tissue.

This approach promises to close the methodological gap between MRI-based and optical microscopy in 3D, and enable the further development of MRI-based *in vivo* histology, which we anticipate to transform neuroimaging in research and clinics (Weiskopf et al., 2015).



Figure 4.3.1.1 Quantitative maps of longitudinal relaxation time T_1 (top row) and effective transverse relaxation rate R_2^* (bottom row) before (left column) and after (right column) CLARITY. MR contrast between grey and white matter almost completely disappeared after lipid removal in line with the large contribution of myelin to T_1 and T_2^* contrasts.

Figure 4.3.1.2 Immunohistochemical stains for (A) myelin basic protein and (B) cell marker HuC/D in the cortex after CLARITY. High contrast of the stains revealed preserved protein composition of the sample despite lipid loss due to intensive clearing.

Investigating microstructure-function relationships by combining magnetoencephalography (MEG) with MR-based myelin mapping

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Different quantitative MR parameters are sensitive to myelination in grey and white matter. Since (1) cortical myelin density estimates correlate with cell density, and (2) the electrophysiological signals measured by MEG are predominately generated by the synchronised activity of pyramidal cells, we postulate that myelin estimates predict the magnitude of MEG responses. In line with this prediction, a proof-of-principle study (Helbling et al., 2015, NeuroImage, 108, 377–385) demonstrated that MR-based myelination estimates correlate positively with source-reconstructed dipole moment magnitudes of evoked responses in an auditory pitch perception paradigm. The locally specific correlations do not only allow for characterising non-invasive microstructure–function relationships but promise to improve the MEG source reconstruction of neuronal activity by providing microstructural priors.

In an ongoing follow-up study we aim to generalise our findings to other sensory modalities using data from a visuomotor experiment acquired as part of the UK MEG Partnership normative database project. Volunteers were scanned using custom-made 3D-printed headcasts to minimise head movement and increase co-registration accuracy (Troebinger et al., 2014, NeuroImage, 86, 583–



Figure 4.3.2 Quantitative MRI-based myelin estimates predict the strength of functional MEG measures: Dipole moment magnitudes estimated from a variational Bayesian source reconstruction approach (A) and myelin density estimates across a set of anatomically and functionally defined auditory areas of interest (B) show significant positive correlations (C) (adapted from Helbling et al., 2015, NeuroImage, 108, 377–385).

591). In early visual areas, preliminary findings indicate that both the magnitude of source-reconstructed visual evoked responses and the strength of oscillatory gamma band activity in the MEG show a positive correlation with myelin estimates, suggesting a general relationship between myelination and electrophysiological responses. We are currently improving the specificity of our cortical myelin estimates by sampling MR parameter values along cortical depth profiles gathered from anatomically motivated cortical models (Waehnert et al., 2014, NeuroImage, 93, 2, 210–220). These methodological developments will improve the reliability of myeloarchitecture estimates across cortical areas and might enable us to estimate layer-specific electrophysiological activity in humans non-invasively and for the whole brain.

4.3.3 Superficial white matter imaging: Distinct contrast mechanisms and whole-brain U-fibre mapping

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Superficial white matter (SWM) is the thin layer of white matter just below the cortical sheet. It contains short association fibres, or U-fibres, playing a central role in cortico-cortical connectivity. Despite their importance, U-fibres are poorly characterised in humans due to the lack of reliable and non-invasive SWM imaging methods. Ultra high-resolution magnetic resonance imaging (MRI) measuring the transverse relaxation rates (R_2, R_2^*) and local frequency shifts provide a promising tool for characterising SWM non-invasively (Deistung et al., 2013, NeuroImage, 65, 299-314; Bagnato et al., 2011, Brain, 134, 3602–3615). However, the MR contrast mechanisms in SWM are not well understood, limiting the specificity of current imaging methods. We addressed this issue by characterising multiple MR contrasts in SWM in vivo and post-mortem and comparing MR parameters to classic histology, mass spectroscopy imaging (Scharlach et al., 2016, Journal of Biomedical Nanotechnology, 12, 5, 1001–1010), proton beam microscopy (Morawski et al., 2005, Nuclear Instruments and Methods in Physics Research, 231, 1, 224-228), and by applying tissue deironing. R_2 , R_2^* , and magnetic susceptibility maps show distinct values for SWM different to both deep white and grey matter in Figure 4.3.3.1. These types of contrasts are almost completely driven by the high iron content in the somata of oligodendrocytes and the myelin sheath (Figure 4.3.3.2B). Since the iron concentration in SWM is significantly higher than in the deep white matter (Figure 4.3.3.2A), the standard white matter contrast models based on myelination are not applicable to SWM. Using cellular resolution iron maps, we have developed and validated a novel susceptibility model specific for SWM (Figure 4.3.3.2C, D). When the specificity of the metric is fully established, it will allow for investigations into SWM distribution, development, inter-individual differences, and the structure-function relationship in humans. In the first step, we demonstrated that SWM contrast is not uniform across the brain. Instead, SWM contrast appears anticorrelated with cortical myelin measures and potentially reflects variations in local U-fibre densities.



Figure 4.3.3.1 High-resolution *in vivo* 7T MRI reveals SWM in quantitative QSM, R_2^* and R_2 maps. (A) R_2^* (left top) and magnetic susceptibility maps (left bottom) of a representative participant. The maps are overlaid with estimates of the cortical grey matter ribbon based on the segmentation of quantitative T_1 maps. Thin strips of SWM (highlighted by white arrows) just below the cortex show elevated R_2^* and χ . (B) R_2^* (right top) and R_2 (right bottom) maps obtained from another participant show the same increases of R_2^* and R_2 in SWM.



Figure 4.3.3.2 Elevated iron levels in myelinated fibres and oligodendrocyte somata determine MR contrast in SWM. (A) macroscopic quantitative iron map obtained with Laser Ablation Mass Spectrocopic Imaging reveals higher iron concentration in SWM as compared to deep white matter; (B) microscopic quantitative maps of iron concentration obtained with proton beam microscopy show iron-rich fibres and hotspots of iron concentration in somata of oligodendrocytes; (C) simulated map of microscopic distortion of magnetic field perturbations resulting from the iron distribution shown in (B); (D) water MR line shapes resulting from magnetic field distortions induced by iron-rich fibres and oligodendrocytes overlaid with fit using Gaussian and Lorentzian line shapes, respectively.

4.3.4 Intensity standardisation of 7T MR images for intensity-based segmentation of the human hypothalamus

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The use of 7T MRI can identify subtle volume changes in brain structures, providing potential biomarkers of mental disorders. Most volumetric approaches, however, require that similar intensity values represent similar tissue categories across different subjects. Unfortunately, the high measurement accuracy achieved by high-resolution imaging may be compromised by inter-individual image intensity variation.

We scanned 84 normal subjects (51 women, age 39 \pm 13 [standard deviation, SD] years) with a 7T scanner (Siemens) and an MP2RAGE sequence (Margues et al., 2010, NeuroImage, 49, 2, 1271–1281; voxel size 0.7-mm isotropic). We corrected the T_1 -weighted scans for B_1 field inhomogeneities (native scans) and processed them with the Medical Image Processing and Visualisation (MIPAV) software (Mc Auliffe, 2001, Proc 14th IEEE Symp Computer-Based Medical Systems, 381-386) and the CBS High-Resolution Brain Tools (Bazin et al., 2014, NeuroImage, 93, 201–209). We segmented the scans into grey matter (GM), white matter (WM), and cerebrospinal fluid (CSF), estimated the median intensities of the GM and WM tissue classes, and selected a reference scan with representative GM and WM intensities and 20 scans with intensities in the upper or lower deciles as target scans. We then analysed the performance of five intensity standardisation techniques: (1) mode-based piecewise linear standardisation (based on Nyúl et.al., 1999, Magn Res Med, 42, 6, 1072-1081), (2) a modification, termed



mode-based non-linear standardisation, (3) cumulative histogram matching from the MIPAV software package, (4) region of interest (ROI)-based linear standardisation based on precise ROIs of the hypothalamic GM and surrounding WM, and (5) segmentation-based standardisation that piecewise linearly matched the means of GM, WM, and CSF.

Focusing on the hypothalamic region, we performed a multi-level evaluation and examined the intensity histograms of the ROIs from method (4) and the voxelwise intensity difference within these ROIs. We semi-automatically determined the intensity of the hypothalamic boundary and evaluated its variability. As a fourth criterion, we required that the original biological variance (i.e. the correlation between whole-brain tissue volume and age) be preserved during intensity standardisation.

Only method (4) proved successful across all criteria: It improved the histogram alignment as indicated by reduced average absolute errors and maximum absolute errors between target and reference histograms. The voxelwise intensity differences between target and reference ROIs were strongly reduced compared with those of the native T_1 -weighted target scans. In the native target scans the intensity of the hypothalamic boundary varied by SD = 5.3% of the intensity range. This variation was more than halved by method (4). Finally, before standardisation, we found a medium-sized negative correlation between whole-brain GM volume and subject age that remained stable after standardisation. Mixed results were obtained for methods (1) - (3) and (5), which sometimes came at the cost of a reduced correlation between whole-brain GM volume and subject age.

The results of this study provide the groundwork for the precise structural analysis of a larger, high-resolution MR dataset of psychiatric patients. In the near future we will present volumetric data of the hypothalamus and adjoining third ventricle in patients with depression and bipolar disorder.

Figure 4.3.4 Coronal views of the basal forebrain (subject #1 and #2): T_{1-} weighted scans before (left column) and after ROI-based linear standardisation (method 4, right column), which improved comparability across subjects.

Congresses, Workshops, and Symposia

2015.

 Weiskopf, N. (November). Joint MPI CBS – UCL WTCN Retreat 2015. Retreat. Harnack-Haus Berlin, Germany.

2016.

- Möller, H. E. & Weiskopf, N. (June). Quantitative MRI for characterizing brain tissue microstructure. Workshop. Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.
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Degrees

PhD Thesis

2015 -

 Freund, N. Entwicklung eines 7 Tesla-MRT-Algorithmus zur farbkodierten Volumetrie der Mamillarkörper in vivo bei bipolarer Störung – Eine Pilotstudie. University of Leipzig, Germany.

Appointments

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Weiskopf, N. Honorary Professorship. Faculty of Physics and Earth Sciences, University of Leipzig, Germany.

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Kozlov, M., & Möller, H. E. (2016). 300MHz 8-channel dual-row arrays for MRI loaded by a patient with subgaleal hematome. In *Proceedings of the 2015 IEEE Conference on Antenna Measurements & Applications (CAMA)* (pp. 1–4). Piscataway: IEEE. doi: 10.1109/CAMA.2015.7428145 Kozlov, M., Bazin, P.-L., Möller, H. E., & Weiskopf, N. (2016). Influence of cerebrospinal fluid on specific absorption rate generated by 300 MHz MRI transmit array. In *Proceedings of 10th European Conference on Antennas and Propagation (EuCAP)* (pp. 1–5). Piscataway: IEEE. doi:10.1109/EuCAP.2016.7481666.

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Kozlov, M., Lucano, E., & Angelone, L. (2016). Effects of tuning conditions on near field of MRI transmit birdcage coil at 64 MHz. In *Proceedings of the 38th Annual International Conference of the IEEE Engineering in Medicine and Biology Society* (pp. 6242– 6245). Piscataway: IEEE.

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5.1 Max Planck Research Group "Adaptive Memory"



Research Group Leader

Dr Roland G. Benoit

Postdoc

Ruud Berkers

PhD Students

Ann-Kristin Meyer Philipp C. Paulus (19)

(Commenced July 2016)

5.2 Max Planck Research Group "Early Social Cognition"

Research Group Leader

PD Dr Stefanie Hoehl

Postdocs

Dr Christine Michel Ezgi Kayhan (14)

(Commencing January 2017)

- (14) German Research Foundation (DFG)
- (19) IMPRS NeuroCom, Leipzig, Germany
- (63) Erasmus Mundus Student Exchange Network in Auditory Cognitive Neuroscience, European Commission
- (77) ERC Consolidator Grant

(*) Left the Institute during 2014–2016



5.3 Max Planck Research Group "Neural Mechanisms of Human Communication"

Research Group Leader

Professor Dr Katharina von Kriegstein

Scientific Researchers and Postdocs

Dr Louise Kauffmann Dr Corrina Maguinness Dr Brian Mathias (63) Dr Katja Mayer (*) Dr Paul Glad Mihai Dr Sonja Schall (*) (in cooperation with Humboldt University Berlin) Dr Nadja Tschentscher (77)

PhD Students

Kamila Borowiak (in cooperation with Berlin School of Mind and Brain) Jing Jiang (in cooperation with Berlin School of Mind and Brain) Christa Müller-Axt Claudia Roswandowitz (19) Stefanie Schelinski (14)

MD Students

Claudia Kappes (*) (in cooperation with University of Leipzig) Leona Sureth (in cooperation with University of Leipzig) Carolin Otto (*) (in cooperation with University of Jena) Dr Philipp Riedel (*) (MD since 02/2016)

Personal and Scientific Assistants

Liane Dörr (77)

Technical and Administrative Assistants

Claudia Pelke

Guest Researchers

Dr Manuela Macedonia	(Johannes Kepler University Linz, Austria)
Dr Hame Park	(Technical University of Dresden, Germany)

Former Researchers and Postdocs

Dr Katja Mayer	Traineeship psychotherapist	
Dr Sonja Schall	Maternity leave	(Commenced August 2009)



5.4 Max Planck Research Group "Neuroanatomy & Connectivity"



Research Group Leader

Dr Daniel S. Margulies

Scientific Researchers and Postdocs

Dr Joachim Böttger (*) Melissa Ellamil, PhD (*) Dr Marcel Falkiewicz Dr Chris Gorgolewski (*) Dr Alexandros G. Goulas (*) Dr Manousos A. Klados (*)

PhD Students

Blazej Baczkowski (19) Seyma Bayrak Johannes Golchert (47) Philipp Haueis (in coop. with Berlin School of Mind and Brain) Julia M. Huntenburg (43) Estrid Jakobsen (19) (*) Mark E. Lauckner Vaia Marou (*) David Moreno-Dominguez (47) (*) Katharina Ohrnberger (in coop. with Berlin School of Mind and Brain) Sabine Oligschläger (19) (in coop. with University of Leipzig)



5.5 Minerva Research Group "EGG (Emotion & neuroimaGinG) Lab"

Research Group Leader

PD Dr Julia Sacher

Scientific Assistant	PhD Student	
Alyson Buchenau	Claudia Barth	
Technical Assistant	MD Students (in cooperation with University of Leipzig)	
Ulrike Scharrer	Nathalie Beinhölzl Inga Burmann (*) (MD since 01/2015)	
(Commenced January 2015)	Matthias Heinrich	

Personal and Scientific Assistants

Dr Natacha Mendes Sarah Krause (31)

Guest Researchers

Dr Josh Berson Dr Franziskus Liem

Former Researchers and Postdocs

Dr Joachim Böttger	Freelance software developer
Melissa Ellamil, PhD	Department of Psychology, University of British Columbia,
	Vancouver, Canada
Dr Chris Gorgolewski	Stanford Center for Reproducible Neuroscience, USA
Dr Alexandros G. Goulas	Center for Experimental Medicine, Medical Center Hamburg- Eppendorf (UKE), Germany
Dr Manousos A. Klados	Lifespan Developmental Neuroscience, Technical University Dresden, Germany
Former PhD Students	
Estrid Jakobsen	Montréal Neurological Institute and Hospital, Canada
Vaia Marou	Completion period
Dr David Moreno-Dominguez	Head of Neuroimaging at Mint Labs, Barcelona, Spain

(Commenced January 2012)

$5.6~^{\rm Otto}$ Hahn Group "Neural Bases of Intonation in Speech and Music"



Research Group Leader

Dr Daniela Sammler

PhD Students

Roberta Bianco (19) Nele Hellbernd Pei-Ju Chien (19)

(Commenced July 2013)

(19) IMPRS NeuroCom, Leipzig, Germany

- (31) Volkswagen Foundation, Germany
- (43) German National Academic Foundation
- (47) FAZIT Foundation, Germany

(*) Left the Institute during 2014–2016

5.1 Max Planck Research Group "Adaptive Memory"

Humans possess the remarkable capacity to vividly remember a plethora of events from their lives. They can voluntarily reminisce about cherished moments but also be haunted by intrusive memories of unpleasant experiences. At the heart of the research in the *Adaptive Memory Group* is the insight that memory is not merely a passive capacity but a constructive process. On one hand, memories are thus susceptible to change and disruption. On the other hand, they can therefore be flexibly recombined into simulations of novel experiences. We seek to understand the adaptive nature of memory by using behavioural, neuroimaging, and neuromodulation methods. In particular, we focus on two intertwined research areas:

(i) Memory suppression

When people encounter a reminder of an episode that they would rather not remember, they are motivated to keep the associated memory out of awareness. Previous research indicates that two opposing mechanisms can achieve such memory suppression (Benoit & Anderson, 2012, Neuron, 76, 450–460): one by effectively inhibiting hippocampal retrieval processes (i.e. direct suppression) and the other by guiding hippocampal retrieval towards the recollection of alternative memories that then keep the unwanted memory out of awareness (i.e. thought substitution). Both of these mechanisms not only regulate temporary awareness of the unwanted memory, but can also cause forgetting.

The Adaptive Memory Group examines how these mechanisms are adaptively recruited to purge intrusive memories from consciousness (see Benoit, Hulbert, Huddleston, & Anderson, 2015, J Cogn Neurosci, 27, 96–111), and how suppression deteriorates neural memory traces. We aim to extend this research agenda by the development of more ecologically valid procedures and further investigations into the efficacy of direct suppression and thought substitution.

The goal of this research is to gain a comprehensive understanding of suppression as an adaptive process for controlling unwanted memories. It will provide important steps towards elucidating whether a disruption of this process may contribute to the deficiency in controlling intrusive memories that sometimes develop in the aftermath of traumatic experiences.

(ii) Episodic simulation

Recent years have seen a strong interest in our ability to vividly imagine possible future episodes. This interest has been fostered by the observation that such episodic simulation has much in common with episodic memory. For example, the same core network of brain regions is involved in recollecting the past and imagining the future (Benoit & Schacter, 2015, Neuropsychologia, 75, 450–457). We aim to deconstruct the functional contributions of the network's individual nodes, with an emphasis on the medial prefrontal cortex (Benoit, Szpunar, & Schacter, 2014, Proc Natl Acad Sci USA, 111, 16550–16555). This work also seeks to elucidate the mechanisms by which imagining the future can bias decisions towards more far-sighted outcomes (Benoit, Gilbert, & Burgess, 2011, J Neurosci, 31, 6771–6779). However, despite the clear

adaptive value of episodic simulations, dwelling too much on the future may also have aversive consequences. We try to understand whether, in such situations, the mechanisms involved in memory suppression may also be engaged to effectively stop future imaginings. Taken together, research in the *Adaptive Memory Group* aims at elucidating the cognitive and neural processes that are fundamentally involved in controlling the contents of our memories and the mental creation of our future.

Appointments

2016

Benoit, R. G. Max Planck Research Group Leader (W2), Max Planck Society, Germany.

Publications

Journal Articles

Benoit, R. G., Davies, D. J., & Anderson, M. C. (2016). Reducing future fears by suppressing the brain mechanisms underlying episodic simulation. *Proceedings of the National Academy of Sciences of the USA*. doi:10.1073/pnas.1606604114.

(spanning reporting period, but published prior to joining MPI CBS:)

Benoit, R. G., Hulbert, J. C., Huddleston, E., & Anderson, M. C. (2015). Adaptive top-down suppression of hippocampal activity and the purging of intrusive memories from consciousness. *Journal of Cognitive Neuroscience*, *27*(1), 96–111. doi:10.1162/jocn_a_00696.

Benoit, R. G., & Schacter, D. L. (2015). Specifying the core network supporting episodic simulation and episodic memory by activation likelihood estimation. *Neuropsychologia*, *75*, 450–457. doi:10.1016/j.neuropsychologia.2015.06.034.

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Bergström, Z. M., Vogelsang, D. A., Benoit, R. G., & Simons, J. S. (2015). Reflections of oneself: Neurocognitive evidence for dissociable forms of self-referential recollection. *Cerebral Cortex, 25*(9), 2648–2657. doi:10.1093/cercor/bhu063.

Fawcett, J. M., Benoit, R. G., Gagnepain, P., Salman, A., Bartholdy, S., Bradely, C., Chan, D.-K.-Y., Roche, A., Brewin, C. R., & Anderson, M. C. (2015). The origins of repetitive thought in rumination: Separating cognitive style from deficits in inhibitory control over memory. *Journal of Behavior Therapy and Experimental Psychiatry*, 47, 1–8. doi:10.1016/j.jbtep.2014.10.009. Küpper, C. S., Benoit, R. G., Dalgleish, T., & Anderson, M. C. (2014). Direct suppression as a mechanism of controlling unpleasant memories in daily life. *Journal of Experimental Psychology: General*, *143*(4), 1443–1449. doi:10.1037/a0036518.

Schacter, D. L., Benoit, R. G., de Brigard, F., & Szpunar, K. K. (2015). Episodic future thinking and episodic counterfactual thinking: Intersections between memory and decisions. *Neurobiology of Learning and Memory, 117*, 14–21. doi:10.1016/j. nlm.2013.12.008.

Szpunar, K. K., Jing, H. G., Benoit, R. G., & Schacter, D. L. (2015). Repetition-related reductions in neural activity during emotional simulations of future events. *PLoS One, 10*(9): e0138354. doi:10.1371/journal.pone.0138354.

5.2 Max Planck Research Group "Early Social Cognition"

Human infants are curious and highly social beings. They depend on contact and interaction with other people to form relationships and develop affect regulation. Crucially, they also depend on caregivers to foster their cognitive development and learning. The Early Social Cognition group focuses on infants' development of social cognitive skills and the importance of social learning in early years. We explore the development of fundamental functions such as action understanding, imitation, and social attention in the first years of life. At the core of our research lies the question of what affects social learning in early childhood and how we can promote it. To gain insights into early cognitive development, we employ a multi-method approach using measures of brain activity such as EEG and fNIRS as well as eye tracking and behavioural observations.

Since social interactions play such a crucial role in infants' and children's learning experiences, we will move beyond conventional research paradigms that put infants and children in highly artificial experimental situations, typically by showing them pictures of other people and then measuring their reactions. Social interactions are dynamic, reciprocal, and multimodal experiences. We will therefore develop more ecologically valid paradigms and consider infants and children as active interactional partners in our research. In the central research project of the group, we will assess synchronisation between infants, children, and adults both on the behavioural and on the neural level during live social interactions. When people communicate, they unconsciously synchronise their behaviour, expressions and gestures, and—as recent research shows—their rhythmic brain activities. Being "in tune" with each other seems to be essential for effective communication. It is less clear whether this is also the case in early development. Is there mutual attunement on the neural and behavioural level between children and adults and does this predict whether the child is able to learn something in the interaction? By measuring brain activities simultaneously from adults and children, we seek to find out more about the mechanisms underlying social learning in early development. The ability of infants and adults to mutually tune in may be one of the main prerequisites of language acquisition and social learning, for instance, about object functions and valences, in early development. Simultaneous recording of brain activities from several persons, often referred to as "hyperscanning", will thus yield important new information on how infants' and adults' brains connect during live social interactions.

Appointments

2016 _

 Hoehl, S. Max Planck Research Group Leader (W2), Max Planck Society, Germany.

Publications

(spanning reporting period, but published prior to joining MPI CBS:)

Journal Articles

Hoehl, S. (2015). How do neural responses to eyes contribute to face-sensitive ERP components in young infants? A rapid repetition study. *Brain and Cognition*, *95*, 1–6. doi:10.1016/j. bandc.2015.01.010.

Hoehl, S. (2016). The development of category specificity in infancy – What can we learn from electrophysiology? *Neuropsychologia*, *83*, 114–122. doi:10.1016/j.neuropsychologia.2015.08.021.

Hoehl, S., Michel, C., Reid, V.M., Parise, E., & Striano, T. (2014). Eye contact during live social interaction modulates infants' oscillatory brain activity. *Social Neuroscience*, *9*(3), 300–308. doi: 10.1080/17470919.2014.884982.

Hoehl, S. & Pauen, S. (in press). Do infants associate spiders and snakes with fearful facial expressions? *Evolution and Human Behavior*.

Hoehl, S., Wahl, S., & Pauen, S. (2014). Disentangling the effects of an adult model's eye gaze and head orientation on young infants' processing of a previously attended object. *Infancy*, *19*(1), 53–64. doi: 10.1111/infa.12035.

Hoehl, S., Zettersten, M., Schleihauf, H., Grätz, S., & Pauen, S. (2014). The role of social interaction and pedagogical cues for eliciting and reducing overimitation in preschoolers. *Journal of Experimental Child Psychology*, *122*, 122–133. doi:10.1016/j. jecp.2013.12.012.

Marinovic, V., Hoehl, S., & Pauen, S. (2014). Neural correlates of human-animal distinction: An ERP-study on early categorical differentiation with 4- and 7-month-old infants and adults. *Neuropsychologia*, *60*, 60–76. doi:10.1016/j.neuropsychologia.2014.05.013.

Michel, C., Hoehl, S., & Striano, T. (2014). The influence of familiarity on explicit eye gaze judgment in preschoolers. European Journal of Developmental *Psychology*, *11*, 344–355. doi: 10.1080/17405629.2013.832670.

Michel, C., Stets, M., Parise, E., Reid, V.M., Striano, T., & Hoehl, S. (2015). Theta and alpha-band EEG activity in response to eye gaze cues in early infancy. *NeuroImage*, *118*, 576–583. doi: 10.1016/j.neuroimage.2015.06.042.

Nordt, M., Hoehl, S., Weigelt, S. (2016). The use of repetition suppression paradigms in developmental cognitive neuroscience. *Cortex*, *80*, 61–75. doi:10.1016/j.cortex.2016.04.002.

Pauen, S., Traeuble, B., Hoehl, S., & Bechtel, S. (2015). Show me the world. Object categorization and socially-guided object learning in infancy. *Child Development Perspectives*, *9*(2), 111–116. doi: 10.1111/cdep.12119.

Peykarjou, S., Pauen, S., & Hoehl, S. (2014). How do 9-monthold infants categorize human and ape faces? A rapid repetition ERP study. *Psychophysiology*, *51*(9), 866–878. doi: 10.1111/ psyp.12238.

Peykarjou, S., Pauen, S., & Hoehl, S. (2016). 9-month-old infants recognize individual unfamiliar faces in a rapid repetition ERP paradigm. *Infancy*, *21*(3), 288–311. doi:10.1111/infa.12118.

Schleihauf, H., Grätz, S., Pauen, S., & Hoehl, S. (in press). Contrasting social and cognitive accounts on overimitation: The role of causal transparency and prior experiences. *Child Development*.

5.3 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.

Communication signals are complex signals on fast time scales, in multiple modalities, and have to be computed online, often under adverse conditions. Over the past few years we have shown that auditory and visual sensory processing interact much more and at earlier stages in the human brain than previously thought. These interactions might explain how the brain, in communication, can achieve its speed, accuracy, and robustness. One of our current main hypotheses is that there are also many more and earlier *within* modality interactions, that is, between the cerebral cortex and the subcortical sensory pathways. We expect that these interactions can explain core features of two highly prevalent communication disorders, that is, developmental dyslexia and autism spectrum disorder.

To test our hypotheses, we acquire behavioural and neuroimaging data and employ neurostimulation techniques. We develop novel communication models based on findings in neurotypicals, and test model predictions on populations with developmental communication difficulties and patients with brain lesions. In the following, the first three abstracts exemplify our recent work on sensory processing in communication deficits. The fourth abstract describes a novel paradigm for testing different neuroscientific models of eye-contact—an important feature of communication.

In the long-term our research programme will provide an integrated view on the communication abilities of our brain. It will provide a basis for understanding the mechanisms of developmental communication deficits, namely autism spectrum disorder, dyslexia, and person recognition deficits. Our research will also lead to useful applications such as projects aimed at improving communication functions with behavioural interventions and the translation of evidence-based training regimes to educational and clinical practice.
Reduced structural connections between left visual thalamus and area V5/MT in developmental dyslexia

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To date, most neuroimaging research on the neuroanatomical basis of developmental dyslexia has focused on the cerebral cortex. However, findings from animal models and post-mortem studies in humans indicate that developmental dyslexia is also associated with structural alterations in the thalamic nuclei of the visual and auditory sensory pathways. Whether these alterations are accompanied by reduced structural connections of the early sensory pathways in developmental dyslexia is currently unknown.

To address this question, here we used ultra-high resolution 7 Tesla structural MRI (magnetic resonance imaging), 3 Tesla diffusion MRI, and probabilistic tractography to investigate the structural connections of the visual sensory pathway in dyslexia *in vivo*. We specifically targeted the left-hemispheric connections between the visual thalamus (LGN) and primary visual cortex (V1) and the direct left-hemispheric connections between the LGN and middle temporal area V5/MT, an area which has frequently been implicated in dyslexia in the context of dorsal visual stream dysfunction (for review, see Skottun, 2015, Brain Cogn, 95, 62–66).

We discovered that individuals with developmental dyslexia (N=12), in contrast to controls (N=12), have sig-

nificantly reduced structural connections between the left LGN and left middle temporal area V5/MT, but not between the LGN and V1 (Fig. 5.3.1; ANOVA; one-tailed post hoc t-test; p=.005). The same pattern of results was replicated using both a probabilistic and an independent surface-based approach for the structural definition of cortical regions of interest. In addition, we found that the strength of left-hemispheric V5/MT-LGN connections in dyslexics was correlated with rapid-naming abilities for letters and numbers (one-tailed Pearson's correlation; r = -.59, p=.022), which are known to be highly predictive of reading fluency (for review, see Norton and Wolf, 2012, Annu Rev Psychol, 63, 427–452).

Our findings provide the first evidence of structural alterations in the connections between the sensory thalamus and cortex in developmental dyslexia. The specificity of the reduction in direct left-hemispheric LGN-V5/MT connections as well as its behavioural relevance for rapid-naming abilities in dyslexics suggests that the function of this pathway might be key for explaining dyslexia symptoms. These results indicate that dyslexia may be best explained in a comprehensive cortico-subcortical framework that takes the role of specific dysfunctional cortico-thalamic interactions into account.





5.3.1

5.3.2 Developmental phonagnosia: Linking neural mechanisms with the behavioural phenotype

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Human voice recognition is critical for many aspects of social communication. Recently, four cases of developmental phonagnosia, which describes the inability to recognise a speaker's voice, were discovered (Garrido et al., 2009, Neuropsychologia, 47, 123–131; Roswandowitz et al., 2014, Curr Biology, 24, 2348–2353; Xu et al., 2015, Brain Lang, 149, 106–117). The aim of the present study was to investigate the neural mechanisms for developmental phonagnosia.

Standard two-system models of person recognition contain a so-called core system (i.e. modality-specific sensory analysis) and an extended system (i.e. semantic information storage), which are interconnected (Haxby et al., 2000, Trends Cogn Sci, 4, 223–233; Blank et al., 2014, Neurosci & Biobehav Reviews, 47, 717–734). These models predict that dysfunction in the core system or disconnection between the core and the extended system can cause person recognition deficits.

To test this hypothesis, we used two fMRI experiments to investigate brain function in two behaviourally distinct cases of developmental phonagnosia: AS has apperceptive phonagnosia, namely difficulties with acoustic voice analysis and intact association of semantic information to the voice. SP has associative phonagnosia, namely difficulties in semantic voice association and intact acoustical voice processing. As hypothesised, we found distinct



Figure 5.3.2 FMRI results of the phonagnosia cases AS and SP and their respective controls ($C_{AS'}C_{SP}$). (A/B) Reduced blood oxygen level dependent (BOLD) response and effective connectivity in phonagnosia cases compared to controls reflect malfunctional brain regions. (A) In apperceptive phonagnosia (AS), regions of the core-voice system responded less in comparison to controls in both experimental paradigms. (B) In associative phonagnosia (SP), the core-voice and extended system showed lower effective connectivity during speaker versus speech recognition in SP than in matched controls. (C/D) Increased BOLD responses might reflect compensatory mechanisms for the voice recognition deficits and are present in the extended system for apperceptive phonagnosia (C) and in the core-voice system for associative phonagnosia (D). Results are significant at $p \le 0.001$ uncorrected.

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malfunctioned brain mechanisms in AS and SP matching their behavioural profiles. In apperceptive phonagnosia, the core-voice system showed lower response than in matched controls ($n_{AS} = 16$) for vocal versus non-vocal sounds and for speaker versus speech recognition (Figure 5.3.2A). In associative phonagnosia, the connectivity between the core-voice system and extended system was reduced in comparison to matched controls ($n_{SP} = 16$) during speaker versus speech recognition (Figure 5.3.2B). Additionally, both cases recruited distinct potential compensatory mechanisms (Figure 5.3.2C,D). Our results support current two-system models: They provide the first evidence that dysfunction of the core-voice system and impaired connectivity between core-voice and extended system regions can selectively contribute to developmental person recognition deficits.

Deficits in vocal pitch perception might contribute to vocal emotion recognition difficulties in autism spectrum disorder (ASD)

5.3.3

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People with ASD have difficulties with vocal emotion perception. Currently it is unclear whether these difficulties are associated with deficits in perceiving basic acoustic features of voices that are relevant for emotion perception. A key acoustic feature of vocal emotion perception is the fundamental frequency of the voice which is perceived as vocal pitch.

Here, we tested whether vocal emotion perception abilities are associated with perception abilities for vocal and non-vocal pitch and vocal timbre in a group of adults with high-functioning ASD (n = 16) and pairwise matched typically developed individuals (n = 16). There were three key findings: (i) The ASD group performed worse than typically developed individuals in tests on vocal emotion recognition and on vocal pitch perception (Figure 5.3.3A); the ASD group had, however, intact nonvocal pitch (Figure 5.3.3A) and vocal timbre perception. (ii) Vocal emotion recognition abilities correlated with vocal pitch perception abilities in typically developed individuals, but not in ASD (Figure 5.3.3B) (iii). Lower vocal emotion recognition ability was associated with higher extents of autistic traits in typically developed individuals and showed a trend to an association with higher symptom severity in ASD.

The findings give novel insights into possible underlying mechanisms of the vocal emotion recognition deficit in ASD. A previous study suggested that vocal emotion perception difficulties in ASD must be of non-perceptual nature (Globerson et al., 2015, Autism Res, 8, 153–163), because people with ASD usually have unimpaired pitch processing (O'Connor, 2012, Neurosci & Biobehav Reviews, 36(2), 836–854). However, in that study only



Figure 5.3.3 Results of the vocal emotion recognition test and tests on pitch perception. (A) The ASD group performed worse compared to typically developed individuals (control group) in recognising vocal emotion and discriminating vocal pitch. Both groups performed equally well in non-vocal pitch perception. (B) In the control group, performance in the vocal pitch discrimination test correlated negatively with performance accuracy in the vocal emotion recognition test, implicating that better vocal pitch discrimination abilities were associated with better vocal emotion recognition abilities. There was no such correlation in the ASD group. Error bars represent +/- 1 SE; **p < 0.005; *p < 0.05; n.s. = not significant; TD = typically developed individuals; ASD = autism spectrum disorder; JND = just noticeable difference.

non-vocal pitch perception was measured. In contrast, our results suggest that difficulties in vocal pitch but not in non-vocal pitch perception might underlie difficulties in vocal emotion recognition in ASD. Our findings reopen the possibility that the difficulties with vocal emotion recognition in ASD are based on perceptual difficulties with a basic acoustic feature of the voice-vocal pitch.

5.3.4 Neural mechanisms of eye contact when listening to another person talking

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Eye contact is an important feature of face-to-face verbal communication. However, so far no study has explored the neural mechanisms underlying eye contact when it is accompanied by spoken language. In this study we developed a novel approach, fixation-based eventrelated (FIBER) functional magnetic resonance imaging (fMRI), to simulate the listener making eye contact with a speaker in verbal communication. Participants were freely viewing a pre-recorded speaker talking while their eye movements and fMRI data were recorded simultaneously (Figure 5.3.4.1). We used the fixations obtained from the eye tracking data to define three type of events for the fMRI analyses, that is "eye contact" events when the participants were fixating on the eyes of the speakers, "mouth fixation" events when participants were fixating on the mouth of the speaker, and "off fixation" events when

participants were looking elsewhere. We found that during eye contact the responses in visual cortical areas (cuneus, calcarine sulcus), brain regions related to theory of mind/intentionality processing (temporoparietal junction, posterior superior temporal sulcus, medial prefrontal cortex) and the dorsolateral prefrontal cortex were increased as compared to mouth fixations. Furthermore, enhanced effective connectivity was found between these regions for eye contact in contrast to mouth fixations (Figure 5.3.4.2). The results provide first evidence for neural mechanisms underlying eye contact when watching and listening to another person talking and partly support an influential neuroscientific model on eye contact processing—the fast-track modulator model (Senju & Johnson, 2009, Trends Cogn Sci, 13, 127–134).



Figure 5.3.4.1 Set-up of the simultaneous eye tracking and fMRI data acquisition.



Figure 5.3.4.2 Summary of findings for the eye contact vs. mouth events contrast and comparison to predictions from the fast-track modulator model (adapted from Senju and Johnson, 2009). The fast-track modulator model proposes that eye contact is processed via rapid subcortical (blue frame and arrows) and slow cortical (black frame and arrows) information processing routes that project to brain regions of the so-called "social brain network" (grey zone). The regions of the social brain network are assumed to be modulated by the dorsolateral prefrontal cortex (dIPFC) according to task demands and social context (green frame and arrows). Brain areas that we found responsive in the eye contact vs. mouth events contrast are marked with a yellow background. Note that the early visual areas were not predicted by the model, but showed highly significant responses in the eye contact vs. mouth fixation contrast. Solid arrows represent connectivity found in the effective connectivity analyses (psy-chophysiological interactions, PPI) that were predicted by the fast-track modulator model. Dashed arrows represent connectivity predicted in the model, but not found in our results. Pink and cyan solid arrows represent connectivity found in the current study, but not predicted by the model. Results were considered significant at p < 0.05 (FWE corrected). Cun, cuneus; SC, superior colliculus; Pulv, pulvinar; Amy, amygdala; LOC, lateral occipital cortex; FFA, fusiform face area.

Congresses, Workshops, and Symposia

2015

 Glad Mihai, P. (June). NeuroBureau Art Exhibition at the OHBM. Hawaii, USA

Degrees

Doctoral Theses

2014

Schall, S. The face in your voice - How audiovisual learning benefits vocal communication. Humboldt University, Berlin, Germany.

2016.

 Riedel, P. Der visuelle Kortex in der rein auditorischen Sprachwahrnehmung – ein Neurostimulationsansatz. Technical University of Dresden, Germany.

Awards

2016.

- Kauffmann, L. PhD award of the French Society of Magnetic Resonance in Biology and Medicine 2016.
- Riedel, P. Carl Gustav Carus Award 2016 for doctoral dissertation, Technical University of Dresden, Germany.

- 2016
- Glad Mihai, P. (June). NeuroBureau Art Exhibition at the OHBM. Geneva, Switzerland.
- Kreitewolf, J. Neural and behavioral interactions in the processing of speech and speaker information. Humboldt University, Berlin, Germany.

- Schelinski, S. Travel Award for the 9th Congress of the Society for Autism Spectrum Disorders (WTAS), Freiburg, Germany.
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5.4 Max Planck Research Group "Neuroanatomy & Connectivity"

What are the spatial trends underlying the organisation of the cerebral cortex, and what are their functional implications? Our research agenda focuses on describing these topographic principles of cortical organisation. We recently characterised a principal axis of cortical connectivity, which relates to cortical geometry and describes gradients in function (5.4.1), connectivity distance (5.4.2), and cortical microstructure (5.4.3). Our future research expands on this axis of connectivity to establish a coordinate system with the aim of differentiating cognitive states (5.4.4), investigating inter-individual variance in brain-behaviour relationships (e.g. 5.4.5), and mapping individual cortical anatomy (e.g. 5.4.6).

5.4.1 A principal gradient of macroscale cortical organisation

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Understanding how the structure of cognition arises from the topographical organisation of the cortex is a primary goal in neuroscience. Previous work has described local functional gradients extending from perceptual and motor regions to cortical areas representing more abstract functions, but an overarching framework for the association between structure and function is still lacking. Here, we show that the principal gradient revealed by the decomposition of connectivity data in humans and the macaque monkey is anchored by, at one end, regions serving primary sensory/motor functions and at the other end, transmodal regions that, in humans, are known as the default-mode network (DMN) (Figure 5.4.1A/B). These DMN regions exhibit the greatest geodesic distance along the cortical surface—and are precisely equidistant—from primary sensory/motor morphological landmarks (Figure 5.4.1C). The principal gradient also provides an organising spatial framework for multiple large-scale networks (Figure 5.4.1D) and characterises a spectrum from unimodal to heteromodal activity in a functional meta-analysis (Figure 5.4.1E). Together, these observations provide a characterisation of the topographical organisation of the cortex and indicate that the role of the DMN in cognition might arise from its position at one extreme of a hierarchy, allowing it to process transmodal information that is unrelated to immediate sensory input.



Figure 5.4.1 (A) The principal gradient of connectivity in the human and macaque monkey. (B) The first two gradients in human cortical connectivity capture similarly organised connectivity patterns previously hypothesised from the macaque monkey tract-tracing literature. (C) End-points of the principal gradient are geometrically equidistant. (D) Canonical large-scale networks are organised along the principal gradient. (E) Functions are organised along the principal gradient from sensory and motor towards increasing integration and abstraction.

Gradients of connectivity distance are anchored in primary cortex

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Connectivity between distant cortical areas is a valuable yet costly feature of cortical organisation and is predominantly found between regions of heteromodal association cortex. Our prior work demonstrated the importance of long-distance weak connections in the topology of connectivity within the macaque monkey cerebral cortex (Goulas et al., 2015, Brain Struct Funct, 220, 2939–2951). Here we investigate how the spatial distribution of connectivity distances relates to the topography of the human cortex. The recently proposed "tethering hypothesis" describes the emergence of longdistance connections in the association cortex as a function of their spatial separation from primary cortical regions. We examined this possibility by characterising the distance between functionally connected areas along the cortical surface. We found a systematic relationship between an area's characteristic connectivity distance and its distance from primary cortical areas. Specifically, the further a region is located from primary sensory-motor regions, the more distant its functional connections 5.4.2

with other areas of the cortex. The measure of connectivity distance also captured major functional subdivisions of the cerebral cortex: unimodal, attention, and higherorder association regions. Our findings provide evidence for the anchoring role of primary cortical regions in establishing the spatial distribution of cortical properties that are related to functional specialisation and differentiation. Future work aims to extend this line of research to processing hierarchies and directed connectivity using openly available data from the macaque monkey.



Figure 5.4.2 (A) Group-level distance-to-connected-areas follows a consistent topographical pattern: shortest in primary cortex and longest within association cortex. (B) Distance precisely delineated primary cortical regions. (C) With further distance from primary regions the distance-to-connected-areas increases (Spearman's r = 0.7, p = < .01, slope = .6). These findings show that the spatial distribution of distance-to-connected-areas is anchored in locations of primary cortex.

5.4.3 A systematic relationship between functional connectivity and intracortical myelin in human cerebral cortex

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Research in the macaque monkey suggests that cortical areas with similar microstructure are more likely to be connected. Here we examine this link in the human cerebral cortex using two magnetic resonance imaging (MRI) measures: quantitative T1 maps, which reflect intracortical myelin content and provide an *in vivo* proxy for cortical microstructure, and resting-state functional connectivity. Making use of ultra-high resolution MRI at 7 Tesla



Figure 5.4.3 Intracortical myelin content (top row) and the principal component of functional connectivity (bottom row) are systematically related across the cortex (right).

(Gorgolewski et al., 2015; Tardif et al., 2016, NeuroImage, 124, 1143–1148) and dedicated image processing tools (Bazin et al., NeuroImage, 93, 201–209), we demonstrate a systematic relationship between intracortical myelin content and functional connectivity. This effect is independent of the proximity of areas. We employ nonlinear dimensionality reduction to characterise connectivity components and identify specific aspects of functional connectivity that are linked to myelin content. Our re-

sults reveal a consistent spatial pattern throughout different analytic approaches. While functional connectivity and myelin content are closely linked in unimodal areas, the correspondence is lower in transmodal areas, especially in the posteromedial cortex and the angular gyrus. Our findings are in agreement with comprehensive reports linking histologically assessed microstructure and connectivity in different mammalian species and extend to the human cerebral cortex *in vivo*.

Mapping cortical function using a connectivity coordinate system

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Gradients in patterns of connectivity capture functional trends—as we previously demonstrated for the first two connectivity dimensions (Figure 5.4.4). Here we elaborate this intrinsic connectivity-defined coordinate space

(CCS), and evaluate its functional relevance for discriminating functional brain states. The CCS provides a template space where each axis describes a dimension of variance in connectivity. A functional connectivity matrix



Figure 5.4.4 (A) First three dimensions of the connectivity coordinate space. (B) Spatial regression of dimensions on individual volumes. (C) 50-subject average time course of third dimensions during a working memory task. (D) Task conditions in the connectivity coordinate space. Dots represent three task conditions for each individual. (E) Prediction of task performance in an independent dataset using dimensions 3, 4, 5, and 6.

5.4.4

derived from resting-state fMRI data of 820 participants from the Human Connectome Project is nonlinearly decomposed using diffusion map embedding (Coifman & Lafon, 2006). Each dimension is then used to reconstruct individual fMRI volumes during a working memory task, and the coordinates are averaged over time within each condition (fixation, 0-back, and 2-back task). The first three dimensions were sufficient to achieve 90% accuracy in predicting task condition, and four dimensions were sufficient to explain 40% variance in performance during the 2-back task. These results demonstrate the viability of a CCS derived from resting-state functional connectivity to predict task state and behavioural performance. In ongoing research we expand this approach to the mapping of diverse experimental contexts.

5.4.5 Individual variation in intentionality in the mind-wandering state is reflected in the integration of the default-mode, fronto-parietal, and limbic networks

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Mind-wandering has a controversial relationship with cognitive control. Existing psychological evidence supports the hypothesis that episodes of mind-wandering reflect a failure to constrain thinking to task-relevant material, as well the apparently alternative view that control can facilitate the expression of self-generated mental content. We assessed whether this apparent contradiction arises because of a failure to consider differences in the types of thoughts that occur during mind-wandering, and, in particular, the associated level of intentionality. Using multi-modal magnetic resonance imaging (MRI) analysis, we examined the cortical organisation that underlies inter-individual differences in descriptions of the spontaneous or deliberate nature of mind-wandering. Cortical thickness as well as functional connectivity analyses implicated regions relevant to cognitive control and regions of the default-mode network for individuals who reported high rates of deliberate mind-wandering. In contrast, higher reports of spontaneous mind-wandering were associated with cortical thinning in parietal and posterior temporal regions in the left hemisphere (which are important in the control of cognition and attention) as well as heightened connectivity between the intraparietal sulcus and a region that spanned limbic and default-mode regions in the ventral inferior frontal gyrus. Finally, we observed a dissociation in the thickness of the retrosplenial cortex/lingual gyrus, with higher reports of spontaneous mind-wandering being associated with



Figure 5.4.5 (A) Whole-brain cortical thickness and (B) functional connectivity analyses with respect to measures of deliberate and spontaneous mind-wandering (MW). L IFS, left inferior frontal sulcus; L IPS, left intraparietal sulcus; R IPS, right intraparietal sulcus.

thickening in the left hemisphere, and higher reports of deliberate mind-wandering with thinning in the right hemisphere. These results suggest that the intentionality of the mind-wandering state depends on integration between the control and default mode networks, with more deliberation being associated with greater integration between these systems. We conclude that one reason why mind-wandering has a controversial relationship with control is because it depends on whether the thoughts emerge in a deliberate or spontaneous fashion.

Connectivity-based parcellation of Broca's area on the individual level

5.4.6

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Broca's region is composed of two adjacent cytoarchitectonic areas, 44 and 45, which have distinct connectivity to superior temporal and inferior parietal regions in both macaque monkeys and humans (Margulies & Petrides, 2013, J Neurosci, 33, 16846–16852). This project aimed to make use of prior knowledge of sulcal anatomy and resting-state functional connectivity, together with a novel visualisation technique, to manually parcellate areas 44 and 45 in individual brains *in vivo* (Jakobsen et al., 2016, Europ J Neurosci, 43, 561–571), followed by establishing an automated pipeline for application to novel datasets (Jakobsen et al., 2016, NeuroImage). In the first study, the left hemisphere from 101 resting-state fMRI imaging datasets from the Human Connectome Project were manually parcellated using glyph visualisation tools in brainGL (Böttger et al., 2014) (Figure 5.4.6). Areas 44 and 45 could be clearly distinguished from each other in all individuals, and the manual segmentation method showed high test-retest reliability. Group-level probability maps of areas 44 and 45 showed spatial consistency across individuals, and corresponded well to cytoarchitectonic probability maps. In a subsequent study, an automated observer-independent and anatomy-informed parcellation pipeline with comparable precision to the manual labels at the individual level was developed and applied to two open-source datasets. While the current study focuses on Broca's region, the method is adaptable to parcellate other cortical regions with distinct connectivity profiles.



Figure 5.4.6 Functional connectivity glyphs with examples of connectivity patterns distinguishing areas 44 and 45.

Congresses, Workshops, and Symposia

2014

 Margulies, D. S. (June). Max Planck Group Leaders Annual Meeting. Berlin, Germany

2015.

Margulies, D. S. (January). International Max Planck Research School (IMPRS). Advanced Lectures on Connectivity. Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.

2016.

 Haueis, P. (April) Book Symposium: Articulating the World: Intentionality – Language – Nature. Free University Berlin, Germany.

Appointments

2014

 Margulies, D. S. Associate Director, Hubbub Group, first interdisciplinary project in residence at The Hub. Wellcome Collection, UK.

Publications

Books & Book Chapters

Haueis, P., & Slaby, J. (2015). Brain in the shell: Assessing the stakes and the transformative potential of the human brain project. In J. De Vos, & E. Pluth (Eds.), *Neuroscience and critique: Exploring the limits of the neurological turn* (pp. 117–140). London: Routledge.

Journal Articles

Alderson-Day, B., Diederen, K., Fernyhough, C., Ford, J. M., Horga, G., Margulies, D. S., McCarthy-Jones, S., Northoff, G., Shine, J. M., Turner, J., van de Ven, V., van Lutterveld, R., Waters, F., & Jardri, R. (2016). Auditory hallucinations and the brain's resting-state networks: Findings and methodological observations. *Schizophrenia Bulletin, 42*(5), 1110–1123. doi:10.1093/schbul/ sbw078.

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- Margulies, D. S. (June) OHBM Hackathon. 20th Annual Meeting of the Organization for Human Brain Mapping. Berlin, Germany.
- Haueis, P. (December). Workshop on Patterns in Science, Berlin School of Mind and Brain, Germany.
- Haueis, P. (April) Vital Brains: The Making and Use of Brain Models in Neuroscience and Psychiatry. Free University Berlin, Germany.

Böttger, J., Schäfer, A., Lohmann, G., Villringer, A., & Margulies, D. S. (2014). Three-dimensional mean-shift edge bundling for the visualization of functional connectivity in the brain. *IEEE Transactions on Visualization and Computer Graphics*, *20*(3), 471–480. doi:10.1109/TVCG.2013.114.

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5.5 Minerva Research Group "EGG (Emotion & neuroimaGinG) Lab"

Cultural norms and society have a profound influence on the perception and expression of mental illness. Yet underneath these social constructs lie biological processes that can be measured, understood, and treated in a systematic and scientific way.

The central aim of the research in the EGG (Emotion & neuroimaGinG) Lab is to understand the unique vulnerabilities of women to detrimental depressive symptoms, and the relation in which sex hormones affect depression and mood. Statistically, women are nearly twice as susceptible to depressive illnesses than men. While this does suggest that sex hormones play a key role in depression, the mechanisms behind how sex hormones affect mood are not yet fully understood. In the EGG lab, we use multimodal neuroimaging methods (Positron Emission Tomography & functional Magnetic Resonance Imaging) to study temporal changes in the female brain during hormonal transition periods to better understand how this relates to emotional processing.

Three interwoven lines of work have developed from this central research question: (1) Using the menstrual cycle

as a model, we are able to gather further insight into how subtle hormonal changes impact brain and behaviour (abstract Barth). (2) Supported by the Society in Science, we further explore how monoaminergic changes affect the brain with a specific emphasis on the serotonergic system (abstract Beinhölzl). (3) Finally, we study several vulnerability factors for depression that display sexual dimorphism, such as the change of abdominal fat distribution in mid-life, during the perimenopause (abstract Heinrich).

Nested within the department of Neurology, the EGG lab closely collaborates with the Day Clinic of Neurology to test the hypothesis that serotonergic drugs can enhance neuroplasticity during learning and recovery after lesions, which offers a new perspective for motor rehabilitation and psychotherapy.

In vivo dynamics of the human hippocampus across the menstrual cycle

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Ovarian hormones fluctuate during the menstrual cycle. Evidence from rodent studies suggests similar subtle fluctuations in hippocampal structure (Galea, L. A. et al., 2008, Can J Exp Psychol, 62, 247–260; Lee & McEwen, 2001, Annu Rev Pharmacol Toxicol, 41, 569–591), predominantly linked to oestrogen. Considering the prominent sexual dimorphism seen in many neuropsychiatric disorders, such as major depressive disorder (Kessler,



Figure 5.5.1 Estrogen-modulated FA differences and time course across the menstrual cycle in the bilateral hippocampus. Threshold-Free Cluster Enhancement voxel-wise FA correlation with respective estrogen levels in hippocampal masks (left (panel A) and right (panel B) hippocampi) are displayed. Red voxels, outlined in black and superimposed on respective t-values, correspond to significant FWE-corrected results (p < 0.05). In panel C, FA (left) and RD (right) values from significant clusters, respective peak voxel, are extracted and plotted versus estrogen levels (in red) across the menstrual cycles assessed.

5.5.1

2003, J Affect Disord, 74, 5-13), endogenous sex hormones may play an essential role in modulating human brain states via hippocampal neuroplasticity. Yet, the potential impact of subtle sex hormone fluctuations on human hippocampal structure in health is unclear. We tested the feasibility of longitudinal neuroimaging in conjunction with rigorous menstrual cycle monitoring to evaluate potential changes in hippocampal microstructure associated with physiological sex hormone changes. Thirty longitudinal diffusion weighted imaging scans of a single, healthy female subject were acquired across two full menstrual cycles. We calculated hippocampal fractional anisotropy (FA), a measure sensitive to changes in microstructural integrity, and investigated potential correlations with oestrogen. We observed a significant positive correlation between FA values and oestrogen in the hippocampus bilaterally (Fig. 5.5.1), revealing a peak in FA closely paralleling ovulation. This

exploratory, single-subject study demonstrates the feasibility of a longitudinal DWI scanning protocol across the menstrual cycle and is the first to link subtle endogenous hormonal fluctuations to changes in FA in vivo. In light of recent attempts to neurally phenotype single humans, our findings highlight menstrual cycle monitoring in parallel with highly sampled individual neuroimaging data to address fundamental questions about the dynamics of plasticity in the adult brain. We are currently extending this approach to a larger subject sample by utilising ultra-high-field whole-brain magnetisation-prepared 2 inversion-contrast rapid gradient-echo (7T MP2RAGE) and diffusion-weighted imaging (DWI) to (1) investigate a potential contribution of myelin to changes in hippocampal white matter across the menstrual cycle using high-resolution myelin-sensitive T1 maps; and to (2) pinpoint oestrogen-mediated structural changes in the hippocampus to specific subfields.

5.5.2 Acute effects of serotonin reuptake inhibitors (SSRIs) on intrinsic functional connectivity, emotional and perceptual interplay, and motor plasticity

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Serotonin functions as an essential neuromodulator that serves a multitude of roles, most prominently balancing mood (Frazer & Hensler, 1999, Serotonin Involvement in Physiological Function and Behavior, Sixth Edition, Philadelphia: Lippincott-Raven). Serotonergic challenge has been observed to reduce intrinsic functional connectivity in brain regions implicated in mood regulation (McCabe & Mishor, 2011, NeuroImage, 57, 1317-1323; McCabe et al., 2011, Mol. Psychiatry, 16, 592-594; van de Ven et al., 2013, PLoS One, 8, e68355). However, the full scope of serotonergic action on functional connectivity in the human brain has not been explored. Here, we show evidence that a single dose of a serotonin reuptake inhibitor dramatically alters functional connectivity throughout the whole brain in healthy subjects (n = 22, Fig. 5.5.2.1). Our network centrality analysis reveals a widespread decrease in connectivity in most cortical and subcortical areas (Fig. 5.5.2.1). In the cerebellum and thalamus, however, we find localised increases (Fig. 5.5.2.1). These rapid and brain-encompassing connectivity changes linked to acute serotonin transporter occupan-

cy suggest a key role for the serotonin transporter in the modulation of the functional macroscale connectome. In a subsequent study, we tested the acute effects of a serotonergic challenge on the neural network underlying attention-management during emotional distraction in a placebo-controlled, randomised cross-over design. We found an attenuated BOLD response in the right insula, right amygdala, and the left orbito-frontal cortex following SSRI versus placebo for negative stimuli in low compared to high load (whole brain, cluster-level uncorr. p<0.001, FWE-cluster-corr. p<0.001-0.01, Fig. 5.5.2.2). Post-hoc PSC-analysis showed significantly decreased activation following SSRI-intake for the comparison of load during negative distraction in all ROIs, most prominently in bilateral insula (left $t_{(20)}$ =11.41, p=0.0008, right t₍₂₀₎=11.22, p=0.0008, Bonferroni corr., Fig. 5.5.2.3). While we did not find any significant relationship between escitalopram levels and mood changes, we show a positive correlation between SSRI-induced BOLD-change in the right insula and changes in mood assessed with the Hamilton Depression Scale (r=0.53, p<0.028, Bonferroni



Figure 5.5.2.1 Comparison of Average Degree Centrality Baseline versus Placebo and Escitalopram. Sagittal slices of mean degree centrality of three conditions: (A) baseline, (B) placebo, and (C) escitalopram (20 mg), superimposed on a T1-anatomical standard template. Orange colours indicate higher centrality. Baseline and placebo condition show more similar centrality patterns, whereas degree centrality analysis reveals a global signal change following the administration of the SSRI.

Signal Change in Degree Centrality Induced by a Single Dose of Escitalopram Contrasted with Placebo. Sagittal slices show the contrast of degree centrality between placebo and escitalopram condition superimposed on a T1-anatomical standard MNI template. Orange colours indicate increased centrality; blue colours decreased centrality following SSRI administration compared to placebo. Dark lines indicate significant clusters (p < 0.01, corrected for multiple comparisons). Significant increases in degree centrality are located in the thalamus and the cerebellum; decreases in degree centrality were found throughout the neocortex. Position of sagittal slices is shown in one axial slice. Table S1 provides a comprehensive overview of all significant clusters in the escitalopram versus placebo condition. Figure S3 depicts the contrast at a range of thresholds (r > 0.10, r > 0.15, r > 0.20).



Figure 5.5.2.2 Neural responses to negative distraction with varying cognitive challenge. Tri-planar view of the activation maps contrasting valence (negative picture) and load (low load, 2 letters > high load, 6 letters), focused on the amygdala, in placebo (A) and SSRI (B) condition. There was significant BOLD activation in the insula, inferior frontal gyrus (IFG), amygdala/hippocampus and orbitofrontal cortex (OFC) in the placebo condition. A single oral dose of escitalopram, however, substantially attenuated the BOLD responses in these brain regions. The colour bar shows the corresponding t-values (whole brain, p < 0.001, uncorr.).

corr., Fig. 5.5.2.4). These results emphasise that the management of attentional resources to negative stimuli during varying stages of cognitive challenge could represent a key mechanism of action during SSRI treatment. Accumulating evidence also suggests that SSRI treatment improves motor rehabilitation in stroke patients-even in the absence of depression (Chollet et al., 2011, Lancet Neurol, 10(2), 123-130; Chollet et al., 2014, Ann Phys Rehabil Med, 57(8), 509-519). In rodent models, SSRIs induced plasticity in aberrant neural circuits, which were paralleled by functional recovery when combined with appropriate rehabilitation (Maya Vetencourt et al., 2008, Science, 320(5874), 385-388). Our next project within this line of work will test this network hypothesis of antidepressant action, which claims that SSRIs act by inducing activity-dependent plasticity in relevant networks (Castren et al., 2005, Nat Neurosci, 6(3), 241-246; Castren et al., 2013, JAMA Psych, 70(9), 983-989) in a double-blind, randomised, placebo-controlled trial in healthy subjects in combination with a sequential motor learning task.



Figure 5.5.2.3 Percent signal change analysis. Extracted percent signal change in anatomically defined regions of interest for each treatment condition at the individual subject level. Significant decrease of task-specific activation in all regions of interest induced by SSRI relative to placebo is shown. The upper row indicates the left hemisphere and the bottom row the right hemisphere. IFG=inferior frontal gyrus; OFC=orbito frontal cortex.



Figure 5.5.2.4 Relationships between escitalopram plasma levels, BOLD signal and mood in healthy subjects. Panel (A) depicts a positive correlation between escitalopram plasma levels and SSRI-induced BOLD signal. There was no significant relationship between escitalopram plasma levels and mood changes assessed with the Hamilton Depression Scale (HAM-D) (B). Panel (C) shows a positive correlation between SSRI-induced BOLD change and SSRI-induced mood changes (HAM-D score changes).

A perimenopausal vulnerability model for obesity-related brain damage

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Perimenopause, the early stage of menopause in midlife, elevates the vulnerability of women to depression and cognitive decline, an increased risk that is likely associated with the fluctuations of oestrogens (Georgakis et al., 2016, JAMA Psych, 73(8), 874-875; Barth et al., 2015). Fluctuations in 17-ß-estradiol (E2) during perimenopause have also been associated with higher visceral adipose tissue (VAT), a decisive risk factor for inflammation, diabetes, and dementia. However, the mechanisms underlying these changes are unknown. Evidence from in vivo magnetic resonance imaging (MRI) suggests a relationship between changes in brain structure and connectivity and midlife obesity, specifically with visceral fat accumulation (Debette et al., 2010, Ann Neurol, 68(2), 136–144; Veit et al., 2014, NeuroImage Clin6, 307–311). Yet, we know remarkably little about how perimenopausal visceral fat accumulation relates to brain structure and function and potentially mediates the increased vulnerability for depression and cognitive decline, as we lack (a) the data for the interplay between perimenopausal psychosocial, metabolic, and neural stress; and (b) the appropriate methods to investigate these processes. This gap in knowledge hinders the advancement of tailored strategies that promote stress resilience of the mind and the body. Through a combination of neuroimaging and psychoneuroimmunology, we aim to fill this gap: Using a large population-based cohort study (Loeffler et al., 2015, BMC Public Health, 15:691), we show first evidence supporting the hypothesis that the perimenopause is a crucial time point for the interaction between visceral abdominal fat (VAT) and grey matter structural networks (Fig. 5.5.3). By complementing this cross-sectional design with a longitudinal cohort assessing (1) brain structure and function, (2) central serotonin transporter availability, (3) abdominal fat distribution, and (4) inflammation and stress markers throughout the perimenopausal transition period, we aim to test this perimenopausal vulnerability model. By identifying how sex hormone fluctuations relate to measures of metabolic risk and susceptibility to depression, we hope to lay the foundation for optimally timed strategies that maintain female mental health and well-being through midlife.





Figure 5.5.3 Higher visceral adipose tissue (VAT) volumes associated with lower gray matter volume in a network of multimodal regions (IC1: A, B, C). (A) Colours indicate positive (red/yellow) or negative (blue/light-blue) covariations within the network (volume: z > 15; thickness and pial surface: z > 4), maps are drawn on a standard brain. (B & C) Scatter plots show the individual's loading on the network, log transformed VAT volume and linear fit in two subgroups (under and over 40 years) separated by sex. Significant negative correlation between visceral adipose tissue (log) and load on independent component 1 (IC1) detected for males aged < 40 years (R2 = 0.116/p < 0.001) and > 40 years (R2 = 0.133 /p < 0.001) and for females aged > 40 years (R2 = 0.116 /p < 0.001)(C). No significant correlation was found in the female subgroup < 40 years (R2 = 0.009 / p = 0.293)(B).

Congresses, Workshops, and Symposia

2014.

- Sacher, J. (May). Sex-Hormone Fluctuations as a Risk Model for Postpartum Mood Disorders. Joint Symposium. 69th Meeting of the Society of Biological Psychiatry (SOBP). New York City, USA.
- Sacher, J. (June). Sex Hormones, Serotonin & Society in Science. Symposium: Society in Science Site Visit Prof. Chen. Leipzig, Germany.

2015.

 Sacher, J. (November). Timing of Serotonin Reuptake Inhibitors Revisited. Society in Science Symposium. Zurich, Switzerland.

2016 _

- Sacher, J., Pletzer, B., Derntl, B. (May). Sex Hormones & Social Cognition. Joint Symposium. The European Society for Cognitive and Affective Neuroscience (ESCAN) conference. Porto, Portugal.
- Sacher, J. & Keil, J. (September). Gender Prospects in Medicine (GPmed). Symposium. University of Leipzig, Germany.
- Sacher, J. (November). In-vivo dynamics of the human hippocampus across the menstrual cycle. Society in Science Symposium. Zurich, Switzerland.

Degrees

MD Thesis 2015

Burmann, I. A single dose of oral escitalopram decreases resting-state functional connectivity. University of Leipzig, Germany.

Appointments

2014.

 Sacher, J. W2 Minerva Research Group Leader. Max Planck Institute for Human Brain and Cognitive Sciences, Leipzig, Germany.

Awards

2016.

- Beinhölzl, N. Award Medical Doctoral Thesis Proposal: Functional connectivity during steady state of selective serotonin reuptake inhibitor (SSRI) escitalopram. Medical Faculty, University of Leipzig, Germany.
- Sacher, J. NARSAD Young Investigator Award. Brain & Behavior Research Foundation, USA.

Habilitation Thesis

- 2016 ____
- Sacher, J. Modulators of individual responses to psychopharmacological intervention. University of Leipzig, Germany

2015.

- Sacher, J. Faculty member of the International Max Planck Research School on Neuroscience of Communication: Function, Structure, and Plasticity (IMPRS NeuroCom). Max Planck Institute for Human Brain and Cognitive Sciences, Leipzig, Germany.
- Sacher, J. "Sign Up! Careerbuilding". Max Planck Society, Germany.

Publications

Journal Articles

Arélin, K., Mueller, K., Barth, C., Rekkas, P. V., Kratzsch, J., Burmann, I., Villringer, A., & Sacher, J. (2015). Progesterone mediates brain functional connectivity changes during the menstrual cycle: A pilot resting state MRI study. *Frontiers in Neuroscience*, *9*: 44. doi:10.3389/fnins.2015.00044.

Barth, C., Steele, C., Mueller, K., Rekkas, V. P., Arelin, K., Pampel, A., Burmann, I., Kratzsch, J., Villringer, A., & Sacher, J. (2016). Invivo dynamics of the human hippocampus across the menstrual cycle. *Scientific Reports, 6*: 32833. doi:10.1038/srep32833.

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Ihme, K., Sacher, J., Lichev, V., Rosenberg, N., Kugel, H., Rufer, M., Grabe, H.-J., Pampel, A., Lepsien, J., Kersting, A., Villringer, A., & Suslow, T. (2014). Alexithymia and the labeling of facial emotions: Response slowing and increased motor and somatosensory processing. *BMC Neuroscience*, *15*: 40. doi:10.1186/1471– 2202–15–40.

Lichev, V., Sacher, J., Ihme, K., Rosenberg, N., Quirin, M., Lepsien, J., Pampel, A., Rufer, M., Grabe, H.-J., Kugel, H., Kersting, A., Villringer, A., Lane, R. D., & Suslow, T. (2015). Automatic emotion processing as a function of trait emotional awareness: An fMRI study. *Social Cognitive and Affective Neuroscience*, *10*(5), 680-689. doi:10.1093/scan/nsu104.

Mueller, K., Arelin, K., Möller, H. E., Sacher, J., Kratzsch, J., Luck, T., Riedel-Heller, S., Villringer, A., & Schroeter, M. L. (2016). Serum BDNF correlates with connectivity in the (pre)motor hub in the aging human brain: A resting-state fMRI pilot study. *Neurobiology of Aging, 38*, 181–187. doi:10.1016/j.neurobiolaging.2015.11.003. Rekkas, P.V., Wilson, A. A., Lee, V.W. H., Yogalingam, P., Sacher, J., Rusjan, P., Houle, S., Stewart, D. E., Kolla, N. J., Kish, S., Chiuccariella, L., & Meyer, J. H. (2014). Greater monoamine oxidase a binding in perimenopausal age as measured with carbon 11–labeled harmine positron emission tomography. *JAMA Psychiatry*, *71*(8), 873–879. doi:10.1001/jamapsychiatry.2014.250.

Sacher, J., Rekkas, V. P., Wilson, A. A., Houle, S., Romano, L., Hamidi, J., Rusjan, P., Fan, I., Stewart, D. E., & Meyer, J. H. (2015). Relationship of monoamine oxidase - A distribution volume to postpartum depression and postpartum crying. *Neuropsychopharmacology*, *40*(2), 429–435. doi:10.1038/ npp.2014.190.

Schäfer, A., Burmann, I., Regenthal, R., Arélin, K., Barth, C., Pampel, A., Villringer, A., Margulies, D. S., & Sacher, J. (2014). Serotonergic modulation of intrinsic functional connectivity. *Current Biology, 24*(19), 2314–2318. doi:10.1016/j. cub.2014.08.024.

Schroeter, M. L., Mueller, K., Arhroe, K., Sacher, J., Holiga, S., Kratzsch, J., Luck, T., Riedel-Heller, S., & Villringer, A. (2015). Serum neuron-specific enolase is related to cerebellar connectivity: A resting-state functional magnetic resonance imaging pilot study. *Journal of Neurotrauma*, *32*(17), 1380–1384. doi:10.1089/ neu.2013.3163.

Tittmann, M., Guenther, T., Sacher, J; Himmerich, H., Villringer, A., Hegerl, U., & Schoenknecht P. Structural brain changes in early-onset and late-onset depression: An update of volumetric MRI findings. *International Journal of Imaging Systems and Technology*, *24*(2), 149–160. doi:10.1002/ima.22089.

5.6 Otto Hahn Group "Neural Bases of Intonation in Speech and Music"

It don't mean a thing if it ain't got that swing - Duke Ellington -

Our auditory world is populated with melodies-modulations of pitch over time—that influence our lives more diversely than we might think. Just imagine a world without melodies: no perfect fourth of fire engines that signals us to instantly clear the road, no music that inspires us to sing, and no tone in a speaker's voice that makes us feel welcomed (or not) and shapes our interpersonal reaction. The Otto Hahn Group investigates the various functions of melodies in our everyday lives, with particular focus on speech and music. Our specific research goals are to (i) describe the neurocognitive mechanisms that enable listeners to make sense of others' melodic signals, to (ii) identify principles of higher-order motor control that allow performers to produce melodically meaningful signals, and to (iii) specify how the use of melody and intonation is shaped by (cultural) convention, training, or disorder.

The past three years saw the group interrogating the neural bases of intonation with various psychoacoustic, electrophysiological, and neuroimaging techniques in healthy adults, professional musicians, and actors. The following four projects exemplify our approach to melody in speech and music, perception and action. In the speech domain, we explored communicative "conventions" in the expression of intentions through prosody (5.5.1) and shed light on the neural networks (fMRI, PPI) that underlie the comprehension of interpersonal prosodic meaning, irrespective of linguistic content (5.5.2). In the music domain, we scrutinised the neural networks of multi-level action planning in pianists during music performance (5.5.4) and explored the tuning of these processes under classical and jazz conventions (EEG, fMRI) (5.5.3). Overall, the combined data make a strong case for the power of melody and intonation in driving human behaviour, be it receptive or active.

5.6.1 Prosody conveys speakers' intentions: Acoustic cues for speech act perception

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During conversation, recognition of others' communicative intentions is key to successful interpersonal interaction. Yet, despite elaborate linguistic abilities, speakers do not always code their intentions literally. The present study investigated whether and how prosody—the tone of voice—contributes to the identification of "unspoken" intentions. Single (non-)words were spoken by four native German speakers with different intonations meant to express criticism, doubt, naming, suggestion, warning, and wish. This corpus was acoustically analysed by means of discriminant analyses, and behaviourally evaluated in two experiments involving a 6-alternative forced choice task and intention ratings subjected to multiple regression analyses. The combined results show characteristic prosodic feature configurations for different intentions that were reliably recognised by listeners and used to identify a speaker's intention. Interestingly, identification of intentions was not contingent on context (we used single words), lexical information (we found similar results for words and non-words), and recognition of the speaker's emotion (results held after parcelling out valence and arousal of the stimuli). Overall, the data demonstrate that prosodic cues are powerful indicators of a speaker's intentions beyond the overt lexical meaning and argue in favour of conventionalised acoustic feature configurations that connote communicative concepts.



Figure 5.6.1 (A) Stimulus examples: spectrograms of the six intentions expressed by a female speaker. (B) Discriminant analyses on the acoustic features classified the stimuli with high accuracy of 92%. (C) Likewise, the confusion matrix of participants' speech act categorisation in a 6-AFC task indicates good recognition of the prosodic intentions.

Neural networks for intention understanding through prosody

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Research on the recognition of others' intentions often reports abstract interpersonal reasoning to infer the actor's intent. Extending our first investigations on communicative intentions in speech, the current project explored the neurocognitive mechanisms of intention understanding in listeners through prosody. Single words, intoned to express criticism, doubt, and suggestion, were acoustically morphed to create 7-step prosodic continua, one for each intention pair. During fMRI scanning, participants categorised the intention of each stimulus in a 2-alternative forced choice task. Comprehension of CLEAR (outer morph steps) contrasted with AMBIGUOUS prosodies (middle morph steps) induced stronger activations in neural networks associated with acoustic template matching (Heschl's gyrus, planum temporale),

theory of mind (mPFC, angular gyrus, precuneus, MTG), as well as social relevance (amygdala, hippocampus). The opposite contrast showed higher activations in the salience network, comprising ACC, anterior insula, and IFG, which has been associated with decision-making. PPI analyses showed that the amygdala functionally integrated auditory-prosodic as well as decision-making processes when people heard clear, socially relevant intentional prosodies. In sum, prosody allows for successful comprehension of the speaker's intent through interactions between complementary neural networks—from auditory-prosodic and socio-cognitive processing to more explicit decision-making mechanisms when the signal becomes ambiguous.



Figure 5.6.2 (A) Clear prosodies activated auditory-prosodic as well as socio-cognitive brain areas. Green borders indicate areas activated in a ToM localiser. (B) Ambiguous prosodies activated areas in the salience network. (C) PPI analysis. Bilateral amygdala showed increased connectivity with auditory-prosodic as well as salience regions during recognition of clear (compared to ambiguous) prosodies. Thresholds: voxel p < .001, cluster p < .05 FWE-corrected.

5.6.3 Genre-specific EEG signatures of musical action planning in classical and jazz pianists

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Music production, from spontaneous jazz improvisations to rehearsed classical concert interpretations, requires action planning at multiple levels. Relative high-level plans specify the appropriate ordering of discrete acts into musically meaningful sequences, while lower-level plans specify optimal movement parameters for execution of each single act. Whether and how musicians adaptively tune these levels of action planning to master genre-specific demands remains little explored. The present EEG study tested classical and jazz pianists in a real-time imitation task asking them to execute 5- and 2-chord progressions (without sound) that assessed (i) structure-based planning of the action sequence by manipulating its conformity with Western tonal harmony (congruent/incongruent), and (ii) parameter specification of single acts by manipulating the fingering used to play the chords (correct/incorrect). Beyond similar hierarchical core principles of action planning in both groups,





behavioural, ERP, and spectral power measures (Fig. 5.6.3) show (i) that jazz pianists were more flexible in revising high-level structure-based plans in face of harmonic incongruities, while (ii) classical pianists were more sensitive to accurately set fingering parameters to structural

features. Overall, we show that core processes of action planning are shaped by the specific musical genre pianists master, which paves the way to understanding the exceptionality of individual performance.

Neural networks for harmonic structure in music perception and action

5.6.4

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The ability to predict upcoming structured events based on long-term knowledge and contextual priors is a fundamental principle of both perception and action. Whether pianists can motorically represent harmonic structures in chord sequences regardless of auditory feedback and whether motor and auditory structure-based predictions can be dissociated in the brain remains largely unknown. To fill this gap, classical pianists were presented with harmonically congruent or incongruent chord progressions, either as musical actions that they were required to watch and imitate without sound, or in an auditory format that they listened to without playing. By combining task-based functional magnetic resonance imaging (fMRI) with functional connectivity at rest (Fig. 5.6.4), we identified distinct subregions in the right inferior frontal gyrus (rIFG) interconnected with parietal and temporal areas for processing action and audio sequences, respectively. These networks are likely to provide the infrastructure that allows frontal areas to keep track of structural relationships in sequential information via dynamic exchange with progressively lower-level modality-specific systems of knowledge. Importantly, the absence of auditory activation in the action task demonstrates that pianists can flexibly decouple motor from auditory images of the forthcoming chord in the sequence, and that structural knowledge of music can be grounded in the musicians' visual-motor control system.



Figure 5.6.4 (A) Imitating (without sound) or (B) listening to (without acting) harmonically incongruent > congruent chord sequences both recruit subregions of rIFG and task-specific parietal and temporal areas, respectively. (C) Dorsal action (BA 44) and (D) ventral audio-related (BA 45) subregions in rIFG (black circles) are functionally connected to these posterior parietal regions along the dorsal stream and temporal regions along the ventral stream, respectively.

Congresses, Workshops, and Symposia

2015.

 Sammler, D. (August). The Melodic Mind. Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany Hellbernd, N. (December). OpenCon Satellite Event. Satellite event for OpenCon conference. Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.

Awards

2014.

 Hellbernd, N. IMPRS NeuroCom Summer School Poster Competition Award. London, UK.

Publications

Journal Articles

Alonso, I., Sammler, D., Valabrègue, R., Dinkelacker, V., Dupont, S., Belin, P., & Samson, S. (2014). Hippocampal sclerosis affects fMR-adaptation of lyrics and melodies in songs. *Frontiers in Human Neuroscience*, *8*: 111. doi:10.3389/fnhum.2014.00111.

Besson, P., Dinkelacker, V., Valabrègue, R., Thivard, L., Leclerc, X., Baulac, M., Sammler, D., Colliot, O., Lehéricy, S., Samson, S., & Dupont, S. (2014). Structural connectivity differences in left and right temporal lobe epilepsy. *NeuroImage, 100*, 135–144. doi:10.1016/j.neuroimage.2014.04.071.

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Bianco, R., Novembre, G., Keller, P. E., Scharf, F., Friederici, A. D., Villringer, A., & Sammler, D. (2016). Syntax in action has priority over movement selection in piano playing: An ERP study. *Journal of Cognitive Neuroscience, 28*(1), 41–54. doi:10.1162/jocn_a_00873.

Hellbernd, N., & Sammler, D. (2016). Prosody conveys speaker's intentions: Acoustic cues for speech act perception. *Journal of Memory and Language, 88*, 70–86. doi:10.1016/j. jml.2016.01.001.

Maffongelli, L., Bartoli, E., Sammler, D., Koelsch, S., Campus, C., Olivier, E., Fadiga, L., & D'Ausilio, A. (2015). Distinct brain signatures of content and structure violation during action sequence observation. *Neuropsychologia*, *75*, 30–39. doi:10.1016/j.neuropsychologia.2015.05.020. Merrill, J., Bangert, M., Sammler, D., & Friederici, A. D. (2016). Classifying song and speech: Effects of focal temporal lesions and musical disorder. *Neurocase*. doi:10.1080/13554794.2016.1 237660.

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Figure 5.6.1

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Figure 5.6.4

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Methods & Development Groups

6.1 Methods and Development Group "Nuclear Magnetic Resonance"



PhD Students

Dr Cornelius Eichner (*) (PhD since 08/2015) Jakob Georgi Maria Guidi (8, 19) Dr Laurentius Huber (*) (PhD since 04/2015) Ahmad Seif Kanaan (8, 19, 37) (in cooperation with Hannover Medical School) Tobias Lenich (37) Kathrin Lorenz (19) Henrik Marschner (37) Miguel Martínez Maestro (8) Riccardo Metere (8, 19) Dr Manoj Shrestha (*) (PhD since 09/2016) Dr Steffen von Smuda (*) (PhD since 02/2015)

Head

Professor Dr Harald E. Möller

Senior Researchers and Postdocs

Dr Štefan Holiga (22, 39) (*) Dr Kristin Ihle Marta Kaczmarczyk (*) Dr Anna Kosatschek Dr Christian Labadie (37) (*) Dr Leonie Lampe (22) (**) (in cooperation with University of Leipzig) Dr Jöran Lepsien Dr Jöran Lepsien Dr Toralf Mildner Professor Dr Karsten Mueller Dr habil. André Pampel Dr Daniel-Paolo Streitbürger (22) (*)

Secretarial and Technical Staff

Nancy Muschall Reiner Hertwig (*) Manuela Hofmann Mandy Jochemko Anke Kummer Roland Müller Nicole Pampus (*) Torsten Schlumm Simone Wipper
Visiting Research Fellows and Guest Researchers

Professor Dr Robert Jech	Department of Neurology and Center of Clinical Neuroscience, 1 st Faculty of Medicine and General Teaching Hospital, Charles University Prague, Czech Republic
Tomáš Pšorn	Faculty of Electrical Engineering and Communication, Faculty of Information Technology, Brno University of Technology, Czech Republic
Dr Filip Růžička	Department of Neurology and Center of Clinical Neuroscience, 1 st Faculty of Medicine and General Teaching Hospital, Charles University Prague, Czech Republic
Dr Tomáš Sieger	Department of Neurology and Center of Clinical Neuroscience, 1 st Faculty of Medicine and General Teaching Hospital, Charles University Prague, Czech Republic, and Faculty of Electrical Engineering, Czech Technical University, Prague, Czech Republic
Olivia Viessmann	FMRIB Centre, Nuffield Department of Clinical Neurosciences, John Radcliffe Hospital, University of Oxford, United Kingdom

Former Researchers and Postdocs

Dr Štefan Holiga	F. Hoffmann-La Roche Ltd., Basel, Switzerland
Marta Kaczmarczyk	Clinic and Outpatients' Clinic for Gynaecology and Obstetrics, Carl Gustav Carus University Hospital Dresden, Germany
Dr Christian Labadie	Berlin Center for Advanced Neuroimaging (BCAN), Charité University Medicine Berlin, Germany
Dr Leonie Lampe	Department of Neurology, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany
Dr Daniel-Paolo Streitbürger	EWERK Consulting GmbH, Leipzig, Germany

Former PhD Students

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Dr Manoj Shrestha	Brain Imaging Center (BIC), Center for Imaging in Neuroscience, University Hospital Frankfurt, Goethe University Frankfurt/Main, Germany
Dr Steffen von Smuda	Lucht Probst Associates GmbH, Frankfurt/Main, Germany

- (8) European Union 7th Framework Programme
 (19) IMPRS NeuroCom, Leipzig, Germany
 (22) Leipzig Research Center for Civilization Diseases (LIFE)
- funded by European Union and State of Saxony

(37) Helmholtz Association, Germany

- (39) Parkinson's Disease Foundation (PDF), USA
- (*) Left the Institute during 2014–2016(**) Left the group during 2014–2016

6.2 Methods and Development Group "MEG and Cortical Networks"



Heads

PD Dr habil. Thomas R. Knösche (left) Dr Burkhard Maess (right)

Senior Researchers and Postdocs

Dr Melanie Knorr (13) (*)

PhD Students

Vincent Chien (19) Jae-Hyun Cho (13) Mirco Fuchs (21) Seung-Goo Kim (19) Tim Kunze Dominic Portain (14) (*) Hermann Sonntag Dr Peng Wang (19) (*) (PhD since 03/2016)



Secretarial and Technical Staff

Nancy Muschall Ralph Schurade (*) Yvonne Wolff-Rosier

Visiting Research Fellows and Guest Researchers

Professor Dr Jens Haueisen	Institute of Biomedical Engineering and Informatics, Ilmenau University of Technology, Germany
Mariya Kharaman	Department of Linguistics, University of Konstanz, Germany
Dr Alessandro Tavano	Max Planck Institute for Empirical Aesthetics, Frankfurt/Main, Germany
Dr Konstantin Weise	Advanced Electromagnetics Group, Department of Electrical Engineering and Information Technology, Institute for Information Technology, Ilmenau University of Technology, Germany

Former PhD Students

Dominic Portain	Trianel GmbH, Aachen, Germany
Dr Peng Wang	Department of Electrical and Computer Engineering and Clinical Imaging Research Center, National University of Singapore

$6.3\,$ Methods and Development Group "Databases and IT"



Heads

Dr Roberto Cozatl (DB) (right) Dr Helmut Hayd (IT) (left)

Secretarial and Technical Staff

Nancy Muschall Frank Burkhardt (IT) Heiko Korsawe (IT) Hagen Lipka (IT) Elke Maess (DB) Stephan Moeller (IT) Gabriel Rivera (DB) (11) (*) Markus Then (IT)



- (11) Federal Ministry of Education and Research (BMBF), Germany
- (13) German Federation of Industrial Research Associations (AiF)
- (14) German Research Foundation (DFG)
- (19) IMPRS NeuroCom, Leipzig, Germany
- (21) Leipzig University of Applied Sciences (HTWK), Germany
- (*) Left the Institute during 2014–2016

6.1 Methods and Development Group "Nuclear Magnetic Resonance"

Rooted in magnetic resonance, our research interests range from methods to applications in the neurosciences as shown in the examples given below. They have been further strengthened through fruitful collaborations within the Marie Curie networks "TRANSACT", "HiMR", and "TS-EUROTRAIN", the Helmholtz Alliance "ICEMED", and with colleagues from Tübingen, Magdeburg, Duke, Maastricht, Lausanne, Leipzig, MGH, Sheffield, Prague, and Hannover.

Efforts in radio frequency (RF) technology shifted largely to 7T, continuing joint work with the former Neurophysics Department. A double-row transmit array remains of particular interest. However, preamplifier decoupling and a novel concept of balanced feed lines were also studied. Integration of carbon-wire loops in simultaneous EEG/ fMRI recordings achieved correction of unpredictable movement artefacts. Among pulse-sequence developments, EPI-based cylindrical encoding was employed for cine imaging of blood passing through the cerebral arteries. A fast approach to measure arterial spin labelling efficiencies shows promise for improving perfusion imaging at 7T. Previously limited brain coverage in cerebral blood volume (CBV) based fMRI was addressed by simultaneous multi-slice acquisitions. For microstructural studies, MP2RAGE was optimised to allow simultaneous mapping of T_1 , T_2^* , and magnetic susceptibility, while concepts for magnetisation transfer (MT) imaging were adapted to obtain metabolic information via chemical exchange.

Finally, after almost 19 years of service, the Institute's first 3T scanner was "retired" to make room for a Connectom system with unique gradient capabilities.



3T Magnet of the new Connectom scanner with the installed 300mT/m gradient system including high-power gradient cables and cooling water hoses.

Insights into brain tissue microstructure from magnetisation transfer

6.1.1

Pampel, A.¹, Müller, D. K.¹, Marschner, H.¹, Metere, R.¹, Anwander, A.¹, & Möller, H. E.¹

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

Precise magnetisation transfer (MT) experiments reveal an orientation dependence of the T_2 relaxation time of semi-solid membrane compounds in cerebral white matter as observed through their interaction with water molecules. A quantitative explanation is achieved by a dipolar absorption lineshape that considers the specific geometrical arrangement of lipid bilayers wrapped around an axon. This model reduces the myelin membrane to its lipid constituents, which is in line with previous observations of efficient water cross-relaxation at cholesterol or galactocerebroside sites. The excellent agreement between measured and simulated maps utilising empirical diffusion data (Fig. 6.1.1) further supports suggestions to model the fibre orientations in a voxel as a scaled Bingham distribution.



Figure 6.1.1 Maps of the apparent relaxation time, $T_{2b'}$ of macromolecules obtained with standard MT fitting in two subjects (A, D) and results from semi-empirical forward calculations. Excellent quantitative agreement with the experimental result is achieved assuming $T_{2b} = 13$ µs for subject 1 (B) and 13.5 µs for subject 2 (F), whereas only subtle variations (here, by 4%) lead to distinct offsets (C, E).

Strategies to mitigate the impact of noise in diffusion-weighted MRI

Eichner, C.^{1,2}, Marschner, H.¹, Pampel, A.¹, Turner, R.¹, Setsompop, K.², Wald, L. L.², & Möller, H. E.¹

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

² MGH Martinos Center for Biomedical Imaging, Harvard Medical School, Charlestown, MA, USA

The Rician noise floor is a well-known problem for traditional magnitude-based diffusion-weighted MRI (dMRI) data, leading to biased model fits and inaccurate signal averaging. This bias is eliminated for real-valued dMRI data with zero-mean Gaussian noise. They were obtained by applying a total-variation algorithm for background phase estimation. Comparisons of real- and magnitudevalued data yielded better model fitting and increased

Fig. 6.1.2 (A) For standard magnitude data (left), but not for real-valued data (middle), large values of the fractional anisotropy (FA) are only visible in areas of high SNR, whereas the noise bias reduces FA estimates even in the corpus callosum and corticospinal tract, leading to an artificial shift in the FA histogram towards lower values (right). (B) Fibre-tracking results obtained with a single average of a high-resolution dMRI scan (left) are improved after AWESOME denoising (middle), approaching the quality obtained after standard averaging of six acquisitions (right).



sensitivity to detect secondary fibre directions (Fig. 6.1.2A). Moreover, the phase information can be used for classification of signal and noise contributions in wavelet space. This denoising technique ("AWESOME") permits

averaging of complex-valued images acquired with different gradient directions yielding significantly improved SNR and more reliable tracking results (Fig. 6.1.2B).

6.1.3

Studies of brain function by quantitative mapping of physiologic and metabolic changes at laminar resolution

Huber, L.¹, Guidi, M.¹, Goense, J.^{2,3}, Gauthier, C. J.¹, Turner, R.¹, & Möller, H. E.¹

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

² Max Planck Institute for Biological Cybernetics, Tübingen, Germany

³ Institute of Neuroscience and Psychology, University of Glasgow, United Kingdom

Sub-millimetre resolution fMRI can be used to study effects of different afferents and efferents on activity in specific cortical layers. Here, a vascular space occupancy variant was optimised to capture lamina-dependent CBV changes with minimal partial volume effects. Layer-dependent responses in the ipsilateral hemisphere during unilateral finger tapping showed distinct positive activation in the ipsilateral primary motor cortex, but

negative activation in the ipsilateral primary sensory cortex (Fig. 6.1.3). Further information on evoked oxygen consumption is obtained using an additional calibration step and physiological model. Initial results indicate an uncoupling between BOLD-based fMRI and metabolic changes across cortical depth, while the tight coupling between CMRO₂ and CBV was conserved across cortical layers.



Figure 6.1.3 (A) BOLD and CBV changes during unilateral finger tapping. A positive BOLD response (yellow) and CBV increase (blue) were observed in the primary motor cortex in both hemispheres. In the primary somatosensory cortex (S1), this (excitatory) pattern was only found in the contralateral hemisphere, whereas ipsilateral S1 showed an (inhibitory) negative BOLD response (blue) and CBV decrease (yellow). (B) The cortical CBV profiles in S1 further indicate a spatial shift: The maximal positive response is observed in middle layers, whereas the negative response peaks slightly deeper. (C, D) Results from calibrated BOLD experiments employing the same task show that the calibration parameter *M* (i.e. the maximum possible BOLD change) is largest at the cortical surface, whereas CMRO₂ peaking inside the cortex appears to be more specific to neural tissue.

Altered brain circuitry in Parkinson's disease observed by functional connectivity

Holiga, Š.¹, Möller, H. E.¹, Schroeter, M. L.^{1,2}, Jech, R.³, & Mueller, K.¹

- ¹ Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany
- ² Clinic for Cognitive Neurology, University Hospital Leipzig, Germany
- ³ Department of Neurology and Center of Clinical Neuroscience, 1st Faculty of Medicine, Charles University Prague, Czech Republic

During electrode implantation for deep brain stimulation (DBS), a transitory improvement of motor symptoms, known as "micro-lesion effect" (MLE), is often observed in patients suffering from Parkinson's disease (PD). Here, we used resting-state fMRI to study potentially underlying mechanisms. Penetration of electrodes was associated with increased "connectivity" in the brainstem (Fig. 6.1.4).

Surprisingly, MLE and DBS were associated with anatomically different connectivity changes despite their similar clinical benefit on motor functions. While the DBS acts at the cortical level, suggesting compensatory activation of less affected motor regions, the MLE affects more fundamental circuitry because the dysfunctional brainstem predominates at the beginning of PD.



Figure 6.1.4 Impact of DBS electrode implantation in the subthalamic nucleus. (A) Clinical scores indicating alleviation of motor symptoms in the acute phase of MLE followed by a relapse one month after implantation. Effects from DBS one month and one year after implantation are additionally shown as grey bars. (B) Reorganisation of motor communication due to MLE identifying the brainstem as the central connectivity hub.

Abnormal glutamatergic neurotransmission in Gilles de la Tourette syndrome

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

² Clinic of Psychiatry, Social Psychiatry and Psychotherapy, Hannover Medical School, Germany

Gilles de la Tourette syndrome (GTS) is a neuropsychiatric movement disorder with reported abnormalities in the neurotransmission of dopamine and GABA. In view of the crucial role played by glutamate (Glu) in tonic/ phasic dopaminergic signalling and the interdependent metabolic relationship exhibited between Glu and GABA via glutamine (Gln), we postulated that glutamatergic signalling is related to the pathophysiology of GTS. Consistently, magnetic resonance spectroscopy (MRS) demonstrated reductions in striatal concentrations of Gln and of Glu+Gln (Glx) in GTS patients, which normalised after aripiprazole treatment (Fig. 6.1.5). This suggests an abnormality in the GABA-Glu-Gln cycle in GTS, thus implying perturbations in the subtle balance between excitatory and inhibitory transmission within subcortical nuclei.





Congresses, Workshops, and Symposia

2014.

 Möller, H. E. (January–December). Magnetic Resonance Methods in Brain Research. Seminar. Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.

2015 _

 Möller, H. E. (January–December). Magnetic Resonance Methods in Brain Research. Seminar. Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.

2016 _

- Möller, H. E. (January–December). Magnetic Resonance Methods in Brain Research. Seminar. Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.
- Möller, H. E., & Weiskopf, N. (June). ESMRMB Lectures on MR
 – "Quantitative MRI for Characterizing Brain Tissue Micro-Structure". Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.

Degrees

Doctoral Theses

2014 _

 Streitbürger, D.-P. Investigating brain structure using voxel-based methods with magnetic resonance imaging. University of Leipzig, Germany.

2016 _

Shrestha, M. Application of center-out k-space trajectories to three-dimensional imaging of structure and blood transport in the human brain. University of Leipzig, Germany.

Appointments

2015

 Mueller, K. Adjunct Professorship, University of Leipzig, Germany.

Awards

2014.

- Holiga, Š. Trainee Award. International Society for Magnetic Resonance in Medicine (ISMRM), Milan, Italy.
- Huber, L. Magna cum Laude Merit Award. International Society for Magnetic Resonance in Medicine (ISMRM), Milan, Italy.

Möller, H. E. (April). 17th Educational Course of the German Chapter of ISMRM "Methods and Concepts for fMRI of the Human Brain – Doctoral Training". Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.

 Möller, H. E. (September). ESMRMB 33rd Annual Scientific Meeting. Congress. Messe Wien Exhibition & Congress Center, Vienna, Austria.

2015 _

- Huber, L. Mapping human brain activity by functional magnetic resonance imaging of blood volume. University of Leipzig, Germany.
- Woost, T. Neurale Korrelate des DemTect bei Patienten mit Alzheimer-Krankheit und frontotemporaler Lobärdegeneration [Neural correlates of DemTect in patients with Alzheimer's disease and frontotemporal lobar degeneration]. University of Leipzig, Germany.

- Huber, L. Summa cum Laude Merit Award. International Society for Magnetic Resonance in Medicine (ISMRM), Milan, Italy.
- Huber, L. Trainee Award. International Society for Magnetic Resonance in Medicine (ISMRM), Milan, Italy.

- Huber, L. Trainee Award. ISMRM Workshop on Functional MRI: Emerging Techniques and New Interpretations, Charleston, SC, USA.
- Huber, L. Young Investigator Award. ISMRM Workshop on Functional MRI: Emerging Techniques and New Interpretations, Charleston, SC, USA.
- Labadie, C. 1st Place Poster Award. 5th Annual Scientific Symposium on Ultrahigh Field Magnetic Resonance, Berlin, Germany.

2015 _

- Guidi, M. Summa cum Laude Merit Award. International Society for Magnetic Resonance in Medicine (ISMRM), Toronto, ON, Canada.
- Huber, L. Magna cum Laude Merit Award. International Society for Magnetic Resonance in Medicine (ISMRM), Toronto, ON, Canada.
- Marschner, H. 2 x Magna cum Laude Merit Award. International Society for Magnetic Resonance in Medicine (ISMRM), Toronto, ON, Canada.

2016_

- Huber, L. Otto Hahn Medal. Max Planck Society, Germany.
- Kanaan, A. S. Professor Mary Robertson Award. European Society for the Study of Tourette Syndrome (ESSTS), Warsaw, Poland.

- Metere, R. 2nd Place Poster Award. 5th Annual Scientific Symposium on Ultrahigh Field Magnetic Resonance, Berlin, Germany.
- Martínez-Maestro, M. Magna cum Laude Merit Award. International Society for Magnetic Resonance in Medicine (ISMRM), Milan, Italy.
- Shrestha, M. Magna cum Laude Merit Award. International Society for Magnetic Resonance in Medicine (ISMRM), Milan, Italy.
- Metere, R. 3 x Magna cum Laude Merit Award. International Society for Magnetic Resonance in Medicine (ISMRM), Toronto, ON, Canada.
- Metere, R. Trainee Award. International Society for Magnetic Resonance in Medicine (ISMRM), Toronto, ON, Canada.
- Kanaan, A. S. Best Poster Presentation Award. International Max Planck Research School on Neuroscience of Communication: Function, Structure, and Plasticity (IMPRS NeuroCom), Leipzig, Germany.
- Metere, R. Trainee Award. International Society for Magnetic Resonance in Medicine (ISMRM), Singapore.

Publications

Books & Book Chapters

Kanaan, A. S., & Müller-Vahl, K. (2017). Cannabinoid-based medicines for the treatment of Gilles de la Tourette syndrome. In *Handbook of cannabis and related pathologies: Biology, pharma-cology, diagnosis, and treatment* (pp. 1035–1044). Cambridge, MA: Academic Press.

Journal Articles

Arélin, K., Mueller, K., Barth, C., Rekkas, P. V., Kratzsch, J., Burmann, I., Villringer, A., & Sacher, J. (2015). Progesterone mediates brain functional connectivity changes during the menstrual cycle: A pilot resting state MRI study. *Frontiers in Neuroscience*, *9*: 44. doi:10.3389/fnins.2015.00044.

Barth, C., Steele, C., Mueller, K., Rekkas, V. P., Arelin, K., Pampel, A., Burmann, I., Kratzsch, J., Villringer, A., & Sacher, J. (2016). Invivo dynamics of the human hippocampus across the menstrual cycle. *Scientific Reports, 6*: 32833. doi:10.1038/srep32833.

Cardoso-Leite, P., Waszak, F., & Lepsien, J. (2014). Human perceptual decision making: Disentangling task onset and stimulus onset. *Human Brain Mapping*, *35*(7), 3170–3187. doi:10.1002/ hbm.22393. Kiebel, S. J., & Mueller, K. (2015). The general linear model. In A. W. Toga (Ed.), *Brain mapping: An encyclopedic reference* (pp. 465–469). Amsterdam: Elsevier. doi:10.1016/B978-0-12-397025-1.00317-1.

Dhital, B., Labadie, C., Stallmach, F., Möller, H. E., & Turner, R. (2016). Temperature dependence of water diffusion pools in brain white matter. *NeuroImage*, *127*, 135–143. doi:10.1016/j. neuroimage.2015.11.064.

Eichner, C., Cauley, S. F., Cohen-Adad, J., Möller, H. E., Turner, R., Stesompop, K., & Wald, L. L. (2015). Real diffusion-weighted MRI enabling true signal averaging and increased diffusion contrast. *NeuroImage*, *122*, 373–384. doi:10.1016/j.neuroimage.2015.07.074.

Fan, A. P., Schäfer, A., Huber, L., Lampe, L., von Smuda, S., Möller, H. E., Villringer, A., & Gauthier, C. (2016). Baseline oxygenation in the brain: Correlation between respiratory-calibration and susceptibility methods. *NeuroImage*, *125*, 920–931. doi:10.1016/j.neuroimage.2015.11.007. Forde, N. J., Kanaan, A. S., Widomska, J., Padmanabhuni, S. S., Nespoli, E., Alexander, J., Arranz, J. I. R., Fan, S., Houssari, R., Nawaz, M. S., Zilhão, N. R., Pagliaroli, L., Rizzo, F., Aranyi, T., Barta, C., Boeckers, T. M., Boomsma, D. I., Buisman, W. R., Buitelaar, J. K., Cath, D., Dietrich, A., Driessen, N., Drineas, P., Dunlap, M., Gerasch, S., Glennon, J., Hengerer, B., van den Heuvel, O. A., Jespersgaard, C., Möller, H. E., Müller-Vahl, K. R., Openneer, T., Poelmans, G., Pouwels, P. J. W., Scharf, J. M., Stefansson, H., Tümer, Z., Veltman, D., van der Werf, Y. D., Hoekstra, P. J., Ludolph, A., & Paschou, P. (2016). TS-EUROTRAIN: A European-wide investigation and training network on the aetiology and pathophysiology of Gilles de la Tourette syndrome. *Frontiers in Neuroscience*, *10*: 384. doi:10.3389/fnins.2016.00384.

Gerasch, S., Kanaan, A. S., Jakubovski, E., & Müller-Vahl, K. (2016). Aripiprazole improves associated comorbid conditions in addition to tics in adult patients with Gilles de la Tourette syndrome. *Frontiers in Neuroscience*, *10*: 416. doi:10.3389/fnins.2016.00416.

Guidi, M., Huber, L., Lampe, L., Gauthier, C., & Möller, H. E. (2016). Lamina-dependent calibrated BOLD response in human primary motor cortex. *NeuroImage*, *141*, 250–261. doi:10.1016/j. neuroimage.2016.06.030.

Hellrung, L., Hollmann, M., Zscheyge, O., Schlumm, T., Kalberlah, C., Roggenhofer, E., Okon-Singer, H., Villringer, A., & Horstmann, A. (2015). Flexible adaptive paradigms for fMRI using a novel software package 'Brain Analysis in Real-Time' (BART). *PLoS One, 10*(4): e0118890. doi:10.1371/journal.pone.0118890.

Holiga, S., Mueller, K., Möller, H. E., Urgosik, D., Ruzicka, E., Schroeter, M. L., & Jech, R. (2015). Resting-state functional magnetic resonance imaging of the subthalamic microlesion and stimulation effects in Parkinson's disease: Indications of a principal role of the brainstem. *NeuroImage: Clinical, 9*, 264–274. doi:10.1016/j.nicl.2015.08.008.

Huber, L., Goense, J., Kennerley, A. J., Ivanov, D., Krieger, S., Lepsien, J., Trampel, R., Turner, R., & Möller, H. E. (2014). Investigation of the neurovascular coupling in positive and negative BOLD responses in human brain at 7 T. *NeuroImage*, *97*, 349–362. doi:10.1016/j.neuroimage.2014.04.022.

Huber, L., Goense, J., Kennerley, A. J., Trampel, R., Guidi, M., Ivanov, D., Neef, N., Gauthier, C., Turner, R., & Möller, H. E. (2015). Cortical lamina-dependent blood volume changes in human brain at 7 T. *NeuroImage*, *107*, 23–33. doi:10.1016/j.neuroimage.2014.11.046.

Huber, L., Ivanov, D., Guidi, M., Turner, R., Uludag, K., Möller, H. E., & Poser, B. A. (2016). Functional cerebral blood volume mapping with simultaneous multi-slice acquisition. *NeuroImage*, *125*, 1159–1168. doi:10.1016/j.neuroimage.2015.10.082.

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Ihme, K., Sacher, J., Lichev, V., Rosenberg, N., Kugel, H., Rufer, M., Grabe, H.-J., Pampel, A., Lepsien, J., Kersting, A., Villringer, A., Lane, R. D., & Suslow, T. (2014). Alexithymic features and the labeling of brief emotional facial expressions: An fMRI study. *Neuropsychologia*, *64*, 289–299. doi:10.1016/j.neuropsychologia.2014.09.044.

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Kazan, S. M., Mohammadi, S., Callaghan, M. F., Flandin, G., Huber, L., Leech, R., Kennerly, A., Windischberger, C., & Weiskopf, N. (2016). Vascular autorescaling of fMRI (VasA fMRI) improves sensitivity of population studies: A pilot study. *NeuroImage*, *124*(A), 794–805. doi:10.1016/j.neuroimage.2015.09.033.

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Figure 6.1.1

Pampel, A., Müller, D. K., Anwander, A., Marschner, H., & Möller, H. E. (2015). Orientation dependence of magnetization transfer parameters in human white matter. *NeuroImage, 114*, 136–146. doi:10.1016/j.neuroimage.2015.03.068.

Figure 6.1.2 (A)

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Figure 6.1.4

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Figure 6.1.5

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6.2 Methods and Development Group "MEG and Cortical Networks"

In this group, the work is focussed on the identification of functional and structural networks by means of noninvasive brain imaging methods such as MEG/EEG, functional MRI, and diffusion MRI. Electroencephalography (EEG) and magnetoencephalography (MEG) provide real time fingerprints of brain activity. The measured fields are the direct and immediate consequence of the electrical currents due to neuronal activity. However, as the spatial sensitivity is limited, the methodological challenge consists in the decomposition of the superimposed effects, while taking into account the complex physical structure of the head. Source reconstruction methods seek to solve the associated inverse problem by combining EEG/MEG data with other modalities (e.g. fMRI, diffusion MRI) and sensible assumptions in a meaningful way. We developed and evaluated approaches to reconstruct functional networks in the brain from EEG/MEG data (6.2.1; Cho et al., submitted). In a variational Bayesian framework, we combined MEG data with fMRI and diffusion tractography to obtain more stable and reliable

accounts of functional networks in the brain (Fukushima et al., 2015, NeuroImage, 105, 408–427). In order to elucidate the relationship between the structure of neural networks and cognitive functions such as music and language processing, we use both a correlative approach (6.2.2) and explicit modelling of neural circuits by means of neural mass modelling (6.2.3). Time-frequency analysis and MEG source reconstruction have been further research foci in our group, which have been applied in collaboration projects with other groups at this Institute on various questions of auditory perception (6.2.4, 6.2.5, 6.2.6).

Estimation of human brain connectivity with EEG and MEG source localisation

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We investigated the influence of the head model on source connectivity analysis (Cho, Vorwerk, Wolters, & Knösche, 2015, NeuroImage, 110, 60–77). In both EEG and MEG, neglecting a white and grey matter distinction or CSF causes considerable errors, while in EEG a distinction between spongy and compact bone is of minor relevance, provided that an adequate skull conductivity value is used (Fig. 6.2.1A). Moreover, we showed that the imaginary coherence is a relatively safe connectivity measure with respect to the crosstalk effects caused by imperfect head models, as opposed to the generalised partial directed coherence (GPDC).

We also introduced an improved method of projecting multivariate autoregressive models from sensor to source space for source connectivity analysis (Cho, Aydin, Wolters, & Knösche, submitted). Using that method, Granger causality-based connectivity measures can be used without reconstructing source time courses for a priori selected source locations. In simulation studies, we showed that errors in connectivity analysis were reduced by applying our proposed method. Furthermore, we applied the proposed method to an interictal MEG spike dataset and investigated the changes of information flow over time intervals (Fig. 6.2.1B).



Figure 6.2.1 (A) The relative error of GPDC (3–7 Hz) between the original and reconstructed source time courses for the information flow from source 1 to 2. The location of source 1 is kept fixed (blue circle), while source 2 is positioned at all remaining locations of the source space. (B) Information flow of the GPDC (12–16 Hz) for five different time intervals of the interictal spike events. The locations of the two focal cortical dysplasias are marked with yellow squares.

Myeloarchitecture and intrinsic functional connectivity of auditory cortex in musicians with absolute pitch

6.2.2

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Absolute pitch (AP) is the ability to recognise pitch chroma of any given tonal sound without external reference. Whereas various AP-specific brain structures and functions at the macroscopic level are known (e.g. larger right Heschl's gyrus), microscopic features, which may elucidate underlying mechanisms of AP, have remained

6.2.1

unknown. We investigated myeloarchitecture and functional connectivity of the auditory cortex based on novel techniques of quantitative MRI (Kim, & Knösche, 2016, Hum Brain Mapp, 37(10), 3486–3501). In musicians, we found an area in the right planum polare (PP) (Fig. 6.2.2A) with increased cortical myelin associated with AP, and a nearby but spatially distinct area in the right lateral Heschl's gyrus with an association of myelination with the frequency discrimination ability. This demonstrates the existence of distinctive neural processes for absolute

recognition and relative discrimination of pitch. In a follow-up study (Kim, & Knösche, submitted), spontaneous activities of the right PP and the left PP at rest (as well as other cortical regions) were highly coherent in musicians with AP (Fig. 6.2.2B). The found regions are part of the ventral auditory pathway, which processes spatially invariant information such as object identity and pitch chroma suggesting its involvement in chromatic categorisation processes of AP.





Figure 6.2.2 Relationships of absolute pitch score to cortical myelin and resting-state functional connectivity. (A) T-statistic maps for cortical myelin overlaid to an inflated cortical surface. Black contour: zero-crossings of curvature; white contour: statistical threshold. (B) T-statistic maps for crosscorrelation (upper row) and cross-coherence (lower row) between the seed (i.e. right PP; white patch) and the rest of cortex. Abbreviations: HG, Heschl's gyrus; PP, planum polare; PT, planum temporale; STG, superior temporal gyrus; STS, superior temporal sulcus; TIFG, triangular inferior frontal gyrus; LSTG, lateral STG; ISCI, inferior segment of the circular sulcus of the insula; MOFG, medial orbital frontal cortex; SFG superior frontal gyrus.

6.2.3 Canonical microcircuits constitute structure building computations in cognitive functions

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Compositionality describes the notion that higher brain functions, and eventually cognitive processes, rest upon a combination of basic information processing operations, presumably supported by canonical microcircuits.

We merge findings on the local neurobiological organisation of cortex and neurolinguistic theories to establish mechanistic hypotheses on the implementation of speech processing in the neuronal infrastructure. Using numerical simulations and bifurcation theory, we describe distinct impulse response behaviours—constituting the basic processing operations of signal flow gating and working memory—in a model of a local canonical microcircuit (Kunze, Peterson, Haueisen, & Knösche, submitted). The response behaviours depend nontrivially on the stimulus' intensity and duration (see Fig. 6.2.3) and are examined as a function of network topology and excitation—inhibition balance.

Equipped with the understanding of the local repertoire, we propose a domain-general mechanism for the establishment of spatio-temporal sequences. We demonstrate how a dynamic recruitment of canonical microcircuits might underlie syntax parsing in speech processing and show how the structure build-up fails after a shift in local network balance, for example after drug intake.



Figure 6.2.3 Dependence of the response behaviours on the salience of the stimulus. Nonresponsive behaviour is observed for intensities below 78 s⁻¹ (green region). While longer stimuli exceeding this threshold evoke memory behaviour (orange region), shorter stimuli will lead to transfer response behaviour (grey region). The stripe-like patterns signify a dependency of the behaviour (transfer or memory) on the phase relation between stimulus switch-off time and the intrinsic system oscillation. Plots to the right exemplify time dependence of input (green), response (blue), and firing threshold (red).

Slow-delta phase concentration marks improved temporal expectations based on the passage of time

6.2.4

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Temporal orienting guides the focus of attention to the moment when a target is expected. This leads to facilitated processing. Temporal expectations enhance encoding precision, reflected in improved alignment of slow neural oscillatory phases (i.e. delta range, 0.5–4 Hz). This

study assessed temporal expectations that arise from the passage of time, that is, temporal expectations follow a "hazard rate function".

While undergoing magnetoencephalography, participants performed an auditory-delayed matching-to-sam-



Figure 6.2.4 (A) Correlation of S1-onset time with delta inter-trial phase coherence (ITPC). The upper plot illustrates variations of slow-delta ITPC with S1-onset time for each subject. The thick black line represents the average of all single-subject linear fits. The topographic plot (lower, left) illustrates the distribution of second-level z values averaged across the slow-delta range (0.6 to 0.9 Hz) during the duration of the delta effect (-0.5 to 0.48 s). (B) Rose plots illustrate slow-delta phase distribution during early S1-onset times and late S1-onset times of one representative participant. The red line corresponds to the resultant vector. (C) Correlation of slow-delta ITPC and alpha power on participants.

ple task with two syllables (S1, S2). Critically, S1-onset time varied in the 0.6–1.8-s range corresponding to 0.6–1.7 Hz. S1 had to be maintained in memory for two seconds.

On a neural level, temporal expectations affected the processing of the syllable S1: Correlation analyses between S1-onset time and delta phase coherence revealed that increasing S1-onset times led to increased slow-delta (0.6–0.9 Hz) phase coherence over right frontotemporal sensors during S1 encoding. Moreover, individuals with higher slow-delta coherence showed decreased alpha power (8–13 Hz), an indicator for reduced cognitive effort, during subsequent memory retention.

We interpret this phase effect during stimulus presentation such that temporal expectations facilitated stimulus processing that is also underlined by reduced alpha power during memory retention, indicating reduced memory effort.

6.2.5 Spatiotemporal dynamics of auditory attention synchronise with speech

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Attending and ignoring play fundamental roles in our everyday behaviour in spatially and temporally fastvarying environments. We used magnetoencephalography (MEG) to test whether focused attention to one of two speech streams adapts to these spatiotemporal dynamics (Fig. 6.2.5A). Auditory spatial attention to the left versus right side modulated the power of ~10-Hz alpha oscillations and their lateralisation across the two cerebral hemispheres (Fig. 6.2.5B). This lateralisation of alpha activity was modulated in temporal synchrony with the speech rate and lagged the time course of auditory phase-locking (Fig. 6.2.5C). Higher amplitude of rhythmic alpha power modulation at the speech rate predicted fewer errors in the stream-specific speech comprehension (Fig. 6.2.5D). Results demonstrate that alpha activity acts as a spatiotemporal filter to control the read-out of attended and ignored sensory content.



Figure 6.2.5 (A) The left panel visualises that each ear received one separate speech stream. The right panel shows a response panel from which the to-be-attended digits were selected. (B) α -lateralisation in sensor and in source space. (C) α -lateralisation and 1–5 Hz phase-locking displayed over time. (D) Correlation between the rhythmic α -power modulation and number of errors in attended stream comprehension.

Voice identity recognition: Functional division of the right superior temporal sulcus (STS) and its behavioural relevance

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The human voice carries both identity and speech information. To date, it is unclear at which time point processing for voice identity diverges from speech recognition. Here, we recorded magnetoencephalographic data during a voice identity and a speech recognition task on the same auditory stimulus material. Neural source activity distributions were estimated using cortically constrained distributed source imaging. At about 200 ms after stimulus onset, processing of voice and speech information diverged (Fig. 6.2.6A). The right posterior STS showed increased activity during voice identity recognition (Fig. 6.2.6B) and the left mid STS during speech recognition. In addition, right anterior STS activity correlated positively with voice identity recognition performance (Fig. 6.2.6C–E). The results highlight the right STS as a key area for voice identity recognition. They suggest that 200 ms after stimulus onset marks the time point at which speech-independent processing of vocal sounds occurs in the posterior STS and is successfully mapped to vocal identities in the anterior STS.



Figure 6.2.6 Source analysis results. (A) Time courses of right STS regions. (B) Contrast between both tasks. (C–E) Correlation between voice task performance and STS source strength.

Congresses, Workshops, and Symposia

2014

Haueisen, J., & Knösche, T. R. (March). EEG/MEG Source Reconstruction: High resolution EEG/MEG measurements. Teaching Programme of 30th International Congress of Clinical Neurophysiology (ICCN) of the IFCN, Berlin, Germany.

2016 -

Grigutsch, M., Knösche, T. R., & Maess, B. (July). How can we estimate functional brain connectivity from EEG or MEG data? Workshop. 6th IMPRS NeuroCom Summer School. Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.

Degrees

PhD Theses

2014

- Moreno-Dominguez, D. Whole-brain cortical parcellation: A hierarchical method based on dMRI tractography. Technical University of Ilmenau, Germany.
- Riffert, T. Extraction of structural metrics from crossing fiber models. University of Leipzig, Germany.

2015.

Wang, P. A realistic local cortical circuit model with laminarspecific connections and synaptic plasticity. Technical University of Ilmenau, Germany.

Publications

Books & Book Chapters

Haueisen, J., & Knösche, T. R. (2014). Forward modeling and tissue conductivities. In S. Supek, & C. J. Aine (Eds.), *Magnetoencephalography* (pp. 107–127). Berlin: Springer.

Knösche, T. R. (2015). Chaos, neural population models and. In D. Jaeger, & R. Jung (Eds.), *Encyclopedia of computational neuroscience* (pp. 599–601). New York: Springer.

Knösche, T. R. (2015). Bifurcations, neural population models and. In D. Jaeger, & R. Jung (Eds.), *Encyclopedia of computational neuroscience* (pp. 380–383). New York: Springer.

Knösche, T. R. (2015). Jansen-Rit model. In D. Jaeger, & R. Jung (Eds.), *Encyclopedia of computational neuroscience* (pp. 1463–1466). New York: Springer.

2015

 Haueisen, J., & Knösche, T.R. (August). New Instrumentation for Brain Measurements and Stimulation. 7th International Summer School in Biomedical Engineering, Lutherstadt Wittenberg, Germany.

 Schreiber, J. Plausibility Tracking: A method to evaluate anatomical connectivity and microstructural properties along fiber pathways. Technical University of Ilmenau, Germany.

Moreno-Dominguez, D. (2014). Whole-brain cortical parcellation: A hierarchical method based on dMRI tractography. *MPI Series in Human Cognitive and Brain Sciences: Vol. 161*. Leipzig: Max Planck Institute for Human Cognitive and Brain Sciences.

Schreiber, J. (2014). Plausibility Tracking: A method to evaluate anatomical connectivity and microstructural properties along fiber pathways. *MPI Series in Human Cognitive and Brain Sciences: Vol. 157.* Leipzig: Max Planck Institute for Human Cognitive and Brain Sciences.

Wiebel, A., Müller, C., Garth, C., & Knösche, T. R. (2014). A system for combined visualization of EEG and diffusion tensor imaging tractography data. In *Visualization and processing of tensors and higher order descriptors for multi-valued data* (pp. 325–337). Berlin: Springer.

Journal Articles

Bianco, R., Novembre, G., Keller, P. E., Kim, S.-G., Scharf, F., Friederici, A. D., Villringer, A., & Sammler, D. (2016). Neural networks for harmonic structure in music perception and action. *NeuroImage*. doi:10.1016/j.neuroimage.2016.08.025.

Böttger, J., Schurade, R., Jakobsen, E., Schäfer, A., & Margulies, D. S. (2014). Connexel visualization: A software implementation of glyphs and edge-bundling for dense connectivity data using brainGL. *Frontiers in Neuroscience*, *8*: 15. doi:10.3389/fnins.2014.00015.

Cho, J.-H., Vorwerk, J., Wolters, C. H., & Knösche, T. R. (2015). Influence of the head model on EEG and MEG source connectivity analysis. *NeuroImage*, *110*, 60–77. doi:10.1016/j.neuroimage.2015.01.043.

Eichelbaum, S., Dannhauer, M., Hlawitschka, M., Brooks, D., Knösche, T. R., & Scheuermann, G. (2014). Visualizing simulated electrical fields from electroencephalography and transcranial electric brain stimulation: A comparative evaluation. *NeuroImage*, *101*, 513–530. doi:10.1016/j.neuro-image.2014.04.085.

Fukushima, M., Yamashita, O., Knösche, T. R., & Sato, M.a. (2015). MEG source reconstruction based on identification of directed source interactions on whole-brain anatomical networks. *NeuroImage*, *105*, 408–427. doi:10.1016/j. neuroimage.2014.09.066.

Kim, S.-G., Jung, W. H., Kim, S. N., Jang, J. H., & Kwon, J. S. (2015). Alterations of gray and white matter networks in patients with obsessive-compulsive disorder: A multimodal fusion analysis of structural MRI and DTI using mCCA+jICA. *PLoS One, 10*(6): e0127118. doi:10.1371/journal.pone.0127118.

Kim, S.-G., & Knösche, T. R. (2016). Intracortical myelination in musicians with absolute pitch: Quantitative morphometry using 7-T MRI. *Human Brain Mapping*, *37*(10), 3486–3501. doi:10.1002/hbm.23254.

Knösche, T. R., Anwander, A., Liptrop, M., & Dyrby, T. (2015). Validation of tractography: Comparison with manganese tracing. *Human Brain Mapping, 36*(10), 4116–4134. doi:10.1002/ hbm.22902.

Maess, B., Mamashli, F., Obleser, J. Helle, L., & Friederici, A. D. (2016). Prediction signatures in the brain: Semantic pre-activation during language comprehension. *Frontiers in Human Neuroscience*, 10:591. doi: 10.3389/fnhum.2016.00591.

Maess, B., Schröger, E., & Widmann, A. (2016). High-pass filters and baseline correction in M/EEG analysis-continued discussion. *Journal of Neuroscience Methods, 266*, 171–172. doi:10.1016/j.jneumeth.2016.01.016.

Maess, B., Schröger, E., & Widmann, A. (2016). High-pass filters and baseline correction in M/EEG analysis. Commentary on: "How inappropriate high-pass filters can produce artefacts and incorrect conclusions in ERP studies of language and cognition". *Journal of Neuroscience Methods, 266*, 164–165. doi:10.1016/j.jneumeth.2015.12.003.

Moreno-Dominguez, D., Anwander, A., & Knösche, T. R. (2014). A hierarchical method for whole-brain connectivitybased parcellation. *Human Brain Mapping*, *35*(10), 5000–5025. doi:10.1002/hbm.22528. Nakamura, A., Maess, B., Knösche, T. R., & Friederici, A. D. (2014). Different hemispheric roles in recognition of happy expressions. *PLoS One, 9*(2): e88628. doi:10.1371/journal. pone.0088628.

Ono, K., Nakamura, A., & Maess, B. (2015). Keeping an eye on the conductor: Neural correlates of visuo-motor synchronization and musical experience. *Frontiers in Human Neuroscience*, *9*: 154. doi:10.3389/fnhum.2015.00154.

Pieloth, C., Knösche, T. R., Maess, B., & Fuchs, M. (2014). Online distributed source localization from EEG/MEG data. *International Journal of Computing*, *13*(1), 17–24.

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Ruschel, M., Knösche, T. R., Friederici, A. D., Turner, R., Geyer, S., & Anwander, A. (2014). Connectivity architecture and subdivision of the human inferior parietal cortex revealed by diffusion MRI. *Cerebral Cortex, 24*(9), 2436–2448. doi:10.1093/cercor/bht098.

Schall, S., Kiebel, S. J., Maess, B., & von Kriegstein, K. (2015). Voice identity recognition: Functional division of the right STS and its behavioral relevance. *Journal of Cognitive Neuroscience*, *27*(2), 280–291. doi:10.1162/jocn_a_00707.

Schreiber, J., Riffert, T., Anwander, A., & Knösche, T. R. (2014). Plausibility Tracking: A method to evaluate anatomical connectivity and microstructural properties along fiber pathways. *NeuroImage, 90*, 163–178. doi:10.1016/j.neuro-image.2014.01.002.

Viehweger, A., Riffert, T., Dhital, B., Knösche, T. R., Anwander, A., Stepan, H., Sorge, I., & Hirsch, W. (2014). The Gini coefficient: A methodological pilot study to assess fetal brain development employing postmortem diffusion MR. *Pediatric Radiology*, *44*(10), 1290–1301. doi:10.1007/s00247-014-3002-4.

Vorwerk, J., Cho, J.-H., Rampp, S., Hamer, H., Knösche, T. R., & Wolters, C. H. (2014). A guideline for head volume conductor modeling in EEG and MEG. *NeuroImage*, *100*, 590–607. doi:10.1016/j.neuroimage.2014.06.040.

Widmann, A., Schröger, E., & Maess, B. (2015). Digital filter design for electrophysiological data – A practical approach. *Journal of Neuroscience Methods, 250*, 34–46. doi:10.1016/j.jneumeth.2014.08.002.

Wilsch, A., Henry, M., Herrmann, B., Maess, B., & Obleser, J. (2015). Alpha oscillatory dynamics index temporal expectation benefits in working memory. *Cerebral Cortex, 25*(7), 1938–1946. doi:10.1093/cercor/bhu004.

Wilsch, A., Henry, M., Herrmann, B., Maess, B., & Obleser, J. (2015). Slow-delta phase concentration marks improved temporal expectations based on the passage of time. *Psychophysiology*, *52*(7), 910–918. doi:10.1111/psyp.12413.

Wöstmann, M., Herrmann, B., Maess, B., & Obleser, J. (2016). Spatiotemporal dynamics of auditory attention synchronize with speech. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(14), 3873–3878. doi:10.1073/pnas.1523357113.

Index of Published Figures

Figure 6.2.1

Figure modified from Cho, J.-H., Vorwerk, J., Wolters, C. H., & Knösche, T. R. (2015). Influence of the head model on EEG and MEG source connectivity analysis. *NeuroImage, 110*, 60–77. doi:10.1016/j.neuroimage.2015.01.043.

Figure 6.2.2

Figure modified from Kim, S.-G., & Knösche, T. R. (2016). Intracortical myelination in musicians with absolute pitch: Quantitative morphometry using 7-T MRI. *Human Brain Mapping*, *37*(10), 3486-3501. doi:10.1002/hbm.23254.

Figure 6.2.4

Figure modified from Wilsch, A., Henry, M., Herrmann, B., Maess, B., & Obleser, J. (2015). Slow-delta phase concentration marks improved temporal expectations based on the passage of time. *Psychophysiology*, *52*(7), 910–918. doi:10.1111/ psyp.12413.

Figure 6.2.5

Figure modified from Wöstmann, M., Herrmann, B., Maess, B., & Obleser, J. (2016). Spatiotemporal dynamics of auditory attention synchronize with speech. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(14), 3873–3878. doi:10.1073/pnas.1523357113.

Figure 6.2.6

Figure modified from Schall, S., Kiebel, S. J., Maess, B., & von Kriegstein, K. (2015). Voice identity recognition: Functional division of the right STS and its behavioral relevance. *Journal of Cognitive Neuroscience*, *27*(2), 280–291. doi:10.1162/jocn_a_00707.

6.3 Methods and Development Group "Databases and IT"

Consolidation of XNAT as data management and archiving service tool

6.3.1

Cozatl, R.¹

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

Our local installation of the Extensible Neuroimaging Archive Toolkit (XNAT) has continued to consolidate it-

self as a valuable data management and processing resource at the Institute. XNAT is now used by several



Fig 6.3.1.1 A screenshot of our WebGL-HTML5-based viewer displaying several data type views for a single subject. With this viewer, it is possible to explore the MR data (top right display panel) and at the same time view the results of several quality-assurance parameters. In this case, the bottom right (mean EPI values) and left (fieldmap correction maps) display panels show results of Freesurfer's quality assurance pipelines.

departments and research groups. This open-source imaging informatics platform is used at the Institute for diverse tasks ranging from long-term archiving to data processing and data-sharing in the context of collaborative projects.

During this reporting period, our group has added some features to our local XNAT which are not native to a standard XNAT installation. In this regard, we have developed an uploader that adds non-MRI information such as demographical, cognitive, physiological, and genetics data at group and subject level to XNAT projects. It is often critical to be able to add other study-related information to enrich and contextualise the MR datasets available in XNAT. MRI datasets in XNAT can now be searched and mined using other study-related parameters as search criteria. Another feature of this new uploader is the functionality to create anonymised subject IDs for XNAT projects which can replace (if deemed necessary) the original IDs used at the Institute with project-specific ones. This is achieved via a dedicated back-end server and has the effect of displaying anonymised-only IDs to users of a given project whilst still allowing system administrators

to seamlessly match and keep track of original and anonymised IDs. This system, together with the provision of a defacing pipeline to remove facial features from MRI structural scans, makes our local XNAT installation especially suitable for multi-site studies and data-sharing collaborations in which the usage of anonymised IDs is necessary to ensure that only the research-related and not the personal data of a test subject is made available to data users.

We have also added a new HTML5/WebGL-based viewer to allow scientists to explore MRI data and other data types. This viewer skirts the java and browser-version dependencies which often prevent the native viewer in XNAT from working correctly at the client end. In addition, our viewer offers the possibility to view in parallel MRI data and other data types such as derivate data and reconstruction files. This facilitates work with multimodal studies and enables scientists to perform, for example, post scanning quality assurance tests and checks (see Fig 6.3.1.1). Finally, we have continued our benchmarking efforts to establish XNAT as a formal data repository for MRI data collections. A two-NAS server scalable system

Projects	CBS_MPG_	XNAT currently	contains	47 proj	ects, 10367 subjec	ts, and 3294	45 imaging	sessions.		
+ Recent	Projects	Subjects	MR	PET	ст					
My projects	ID:	44			Name:		0	Description:		
Other projects										
Stored Searches	Keywords	5.			Investigator:					
Data					(SELECT)		*			
	Projects					Rec	ent Data A	Activity	9	ubmit
	Projects			(Rec	ent Data (Activity	S	ubmit
	Projects A high res	volution 7-Tes	la resting	g-state	MRI test-retest	Rec	cent Data A	Activity	S	ubmit
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Fig 6.3.1.2 Our XNAT internet start page showing the two public data collections which can be accessed without logging in. An online interface has been programmed to produce download statistics about these projects. Currently, the average number of registered downloads per month (year 2016) for our two featured public datasets: 1) Evaluation of hardware motion sensors with respect to correction of the Helium artefact and 2) A high resolution 7-Tesla resting-state fMRI test-retest dataset including cognitive and physiologic measurements is 3 and 33, respectively.

with 15 TB capacity is the core storage unit of our XNAT installation. However, an additional 20 TB of storage capacity will be added in 2017 via the Institute's new ZFS system (see next report). The first two scientific papers offering persistent links to their original primary datasets

were deposited in our XNAT in 2015 and 2016. The datasets for these projects are publicly available via our XNAT start site (Fig. 6.3.1.2). Since then, whole-project or partial (specific sessions and experiments) downloads from these collections have taken place regularly.

New data network at the Institute

Hayd, H.¹

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

The new file system ZFS was introduced to offer more powerful file servers for the increasing demands of the Institute with regards to performance and capacity.

ZFS is a powerful combination of a modern file system, with a logical volume manager, a RAID controller, and a collection of compression algorithms. One of the main advantages of this new data network is that data analysis can now be carried out on the file servers directly without having to first copy the data to the local workstations to start the analyses. Another major advantage of the system is that it scales very well on the so-called commodity hardware, that is, devices with components that are relatively inexpensive, widely available, and more or less interchangeable.

In addition to these changes, the core of the Institute's network was replaced by a cloud of switches to have more high speed ports (10 Gigabit-Ethernet) for file and compute servers. The core can now be expanded to all areas of the Institute where a fibre optic cable ends (e.g. a scanner device).

Former Departments and Groups

Department of Neurophysics: Mapping Brain Structures Using MRI Techniques

Director Emeritus

Professor Dr Robert Turner

Research Group Leader

PD Dr Stefan Geyer now Department of Neurophysics (Weiskopf)

Senior Researchers and Postdocs

- Dr Pierre-Louis Bazin now Department of Neurophysics (Weiskopf)
- Claudine J. Gauthier, PhD (14) (*) now Concordia University Montréal, Canada
- Dr Mikhail Kozlov now Department of Neurophysics (Weiskopf)
- Dr Andreas Schäfer (*) now Siemens Healthcare GmbH, Germany
- Dr Jessica Schulz (44) (*) now IHK Saxony, Leipzig, Germany
- Dr Carsten Stüber (*) now Weill Cornell Medical College, New York City, USA
- Christine Tardif, PhD (*) now Douglas Mental Health University Institute, Verdun, Canada
- Dr Robert Trampel now Department of Neurophysics (Weiskopf)

Research Associates

PD Dr Gabriele Lohmann Max Planck Institute for Biological Cybernetics, Tübingen, Germany

MD Students

Friederike Petzold (*) Stephanie Schindler



PhD Students

Dr Juliane Dinse (PhD since 2015) (**) currently on maternity leave

- Dr Cornelius Eichner (PhD since 2015) (*) now Accenture GmbH, Berlin, Germany
- Dr Laurentius Huber (PhD since 2015) (*) now NIHM, Bethesda, USA
- Estrid Jakobsen (19) (*) now Montreal Neurological Institute and Hospital, McGill University, Canada
- Qianwen Miao (42) (*) now Beijing University, China
- Dr Steffen von Smuda (PhD since 2015) (*) now Lucht Probst Associates GmbH, Frankfurt am Main, Germany
- Dr Johannes Stelzer (PhD since 2014) (*) now Max Planck Institute for Biological Cybernetics, Tübingen, Germany
- Dr Barbara Strotmann (19) (PhD since 2014) (*) no longer working in the field

(44) Federal Ministry of Economics and Technology (BMWi), Germany

Dr Miriam Wähnert (PhD since 2014) (*) currently on maternity leave

- (14) German Research Foundation (DFG)
- (19) IMPRS NeuroCom, Leipzig, Germany
- (31) Volkswagen Foundation, Germany
- (42) Max Planck Society and Chinese Academy of Sciences Doctoral Promotion Programme (DPP)
- (66) Siemens Industriekooperation
- (*) left the Institute during 2014–2016
- (**) left the department during 2014–2016

Department of Psychology: Cognition and Action

Director Emeritus

Professor Dr Dr h.c. Wolfgang Prinz

PhD Students

- Dr Andrea Walter (PhD since 2014) (*) now East German Chamber of Psychotherapists, Leipzig
- Dr Anne Keitel (PhD since 2014) (*) now University of Glasgow, UK
- Dr Marie Ragert (née Uhlig) (PhD since 2014) (*) currently on maternity leave
- Dr Maria Christine van der Steen (PhD since 2014) (*) now Catharina Hospital, Eindhoven, NL
- Dr Nadine Pecenka (PhD since 2014) (*) now Clienia Littenheid AG, Externe Psychiatrische Dienste Thurgau Frauenfeld, Schweiz
- Dr Manja Attig (PhD since 2016) (*) now Leibniz-Institut für Bildungsverläufe, Bamberg, Germany
- Dr Barbara Kruse (PhD since 2016) (*) now Abteilung Neurologie des Asklepios Klinikums Harburg, Hamburg, Germany

Max Planck Research Group "Auditory Cognition"

Research Group Leader

Professor Dr Jonas Obleser (*) now Professor of Physiological Psychology and Research Methods, Department of Psychology, University of Lübeck, Germany

Scientific Researchers and Postdocs

- Dr Alex Brandmeyer (*) now Dolby Laboratories Inc., San Francisco, USA
- Molly J. Henry, PhD (*) now University of Western Ontario, Canada
- Dr Sophie Herbst (*) now University of Lübeck, Germany
- Dr Björn Herrmann (*) now University of Western Ontario, Canada
- Sung-Joo Lim, PhD (*) now University of Lübeck, Germany
- Dr Mohsen Alavash Shooshtari (*) now University of Lübeck, Germany

Dunja Kunke, MSc (66) currently on maternity leave





PhD Students

Dr Julia Erb (PhD since 2014) (*) now University of Maastricht, the Netherlands

- Lorenz Fiedler (*) (31)
- now University of Lübeck, Germany
- Dr Antje Strauß (PhD since 2014) (*) now University of Grenoble, France
- Dr Anna Wilsch (PhD since 2015) (*) now University of Oldenburg, Germany
- Dr Malte Woestmann (PhD since 2015) (*) now University of Lübeck, Germany

Max Planck Research Group "Early Social Development"



Group Leader

Professor Dr Tobias Grossmann now Professor of Psychology, Department of Psychology, University of Virginia, USA

Scientific Researchers and Postdocs

- Dr Nicole Altvater-Mackensen (*) now University of Mainz, Germany
- Dr Merle Fairhurst-Menuhin (*) now Institute of Philosophy, University of London, UK
- Dr Sarah Jessen (*) now Research Group Cognitive Neurology, Unievrsity of Lubeck, Germany

PhD Students

Dr Manuela Missana (PhD since 2015) (*)

Dr Purva Rajhans (PhD since 2016) (*) Dr Kathleen M. Krol (19) (PhD since 2016) (*) now Leipzig Research Centre for Early Child Development, University of Leipzig, Germany now Baylor College of Medicine, Houston, Texas, USA now Baby Lab, Department of Psychology, University of Virginia, USA

Max Planck Fellow Group "Cognitive and Affective Control of Behavioural Adaptation"

Max Planck Fellow Professor Dr Hans-Jochen Heinze Group Leader Professor Dr Florian Schlagenhauf (*) now Heisenberg Professor for "Reinforcement learning dysfunction in neuropsychiatric disorders" at Charité University Medicine Berlin, Germany, Scientific Researchers and Postdocs Dr Lorenz Deserno (**) now Department of Neurology, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany (in cooperation with Charité University Medicine Berlin) now Department of Cognitive Psychology, Leiden Zsuzsika Sjoerds, PhD (79) (*) University, the Netherlands Dr Jakob Kaminski (**) now Department of Neurology, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany (in cooperation with Charité University Medicine Berlin) Dr Martin Panitz (**) Currently on parental leave

Minerva Research Group "Brain Modes"

Research Group Leader

- PD Dr Petra Ritter (*)
 - now Group Leader, Clinic for Neurology with Experimental Neurology, Charité University Medicine Berlin, Germany

Scientific Researchers and Postdocs

Dr Gamaliel Rodrigo Sigala Alanis (*) now Clinic for Neurology with Experimental Neurology, Charité University Medicine Berlin, Germany

PhD Students

Sabrina Chettouf (*) Simon Rothmeier (*) Completion period Completion period



- (19) IMPRS NeuroCom, Leipzig, Germany
- (79) Netherlands Organisation of Scientific Networks
- (*) left the Institute during 2014–2016
- (**) left the department during 2014–2016



PhD Students

- Dr Andrea M. F. Reiter (PhD since 2016) (19) (*) now scientific researcher at Chair of Lifespan Developmental Neuroscience, Technical University of Dresden, Germany
- Claudia Gählsdorf (*) Charité University Medicine Berlin, Germany

MD Students

Luise Claaß (**) Carolyn Elizabeth Edwards (**) Annika Hedrich (**) Martin Huss (**) Christoph Radenbach (*) Tilmann Wilbertz (*)

7.1 Department of Neurophysics: Mapping Brain Structures Using MRI Techniques

Degrees

PhD Theses

2014 _

- Stelzer, J. Nonparametric statistical inference for functional brain information mapping, University of Leipzig, Germany.
- Strotmann, B. The human habenula: Structure, function and connectivity. University of Leipzig, Germany.

2015 -

- Dhital, B. Characterizing brain white matter with diffusion-weighted magnetic resonance, University of Leipzig, Germany.
- Dinse, J. A model-based cortical parcellation scheme for high-resolution 7 Tesla MRI data. Otto von Guericke University Magdeburg, Germany.
- Eichner, C. Slice-Accelerated Magnetic Resonance Imaging - Measurements of Blood Perfusion and Water-Diffusion in the Human Brain, University of Leipzig, Germany.

Appointments

2014

 Turner, R. Honorary Professorship, Faculty of Medicine, University of Amsterdam, the Netherlands.

Publications

Books and Book Chapters

Chiao, J. Y., Li, S.-C., Seligman, R., & Turner, R. (Eds.). (2016). *The Oxford handbook of cultural neuroscience*. Oxford: Oxford University Press.

- Wähnert, M. Modelling cortical laminae with 7T magnetic resonance imaging. University of Leipzig, Germany.
- Huber, L. Mapping human brain activity by functional magnetic resonance imaging of blood volume. University of Leipzig, Germany.
- von Smuda, S. Applicability of quantitative functional MRI techniques for studies of brain function at ultra-high magnetic field, University of Leipzig, Germany.

Dinse, J. (2015). A model-based cortical parcellation scheme for high-resolution 7 Tesla MRI data. *MPI Series in Human Cognitive and Brain Sciences: Vol. 168.* Leipzig: Max Planck Institute for Human Cognitive and Brain Sciences. Geyer, S. (2014). Brodmann's areas. In M. J. Aminoff, & R. B. Daroff (Eds.), *Encyclopedia of the neurological sciences* (2nd ed., pp. 550–554). San Diego: Elsevier.

Turner, R. (2015). Myelin imaging. In A. W. Toga (Ed.), *Brain mapping: An encyclopedic reference* (pp. 137–142). Cambridge, MA: Academic Press.

Journal Articles

Bazin, P.-L., Weiss, M., Dinse, J., Schäfer, A., Trampel, R., & Turner, R. (2014). A computational framework for ultra-high resolution cortical segmentation at 7 Tesla. *NeuroImage*, *93*(2), 201–209. doi:10.1016/j.neuroimage.2013.03.077.

Böttger, J., Schäfer, A., Lohmann, G., Villringer, A., & Margulies, D. S. (2014). Three-dimensional mean-shift edge bundling for the visualization of functional connectivity in the brain. *IEEE Transactions on Visualization and Computer Graphics*, *20*(3), 471–480. doi:10.1109/TVCG.2013.114.

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Patents

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7.2 Department of Psychology: Cognition and Action

Degrees

PhD Theses

2014 -

- Walter, A. The role of goal representations in action control. University of Leipzig, Germany.
- Keitel, A. Action perception in development: The role of experience. University of Leipzig, Germany.
- Ragert, M. Cognitive mechanisms underlying perception and production of multi-part music. University of Leipzig, Germany.

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- Attig, M. Handlungsverständnis in den ersten Lebensjahren: Retrospektive und prospektive Verarbeitung. Universität Leipzig, Germany.
- Appointments

2015.

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Publications

Books & Book Chapters

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Pfister, R., Obhi, S. S., Rieger, M., & Wenke, D. (2014). Action and perception in social contexts: Intentional binding for social action effects. *Frontiers in Human Neuroscience*, *8*: 667. doi:10.3389/fnhum.2014.00667.

Prinz, W. (2014). Action representation: Crosstalk between semantics and pragmatics. *Neuropsychologia*, *55*, 51–56. doi:10.1016/j.neuropsychologia.2013.08.015.

Prinz, W. (2016). Explaining consciousness: From correlations to foundations (Commentary on Morsella et al.). *Behavioral and Brain Sciences*, 39, e193. doi:10.1017/S0140525X1500223X.

Prinz, W. (2014). Freiheitsintuitionen: Handlungsurheberschaft zwischen Natur und Kultur. *Monatsschrift für Kriminologie und Strafrechtsreform*, *5/6*, 333–344.

Prinz, W. (in press). Task implementation and top-down control in continuous search (Commentary on Hulleman & Olivers). *Behavioral and Brain Sciences*.

Prinz, W. (2015). Task representation in individual and joint settings. *Frontiers in Human Neuroscience, 9*: 268. doi:10.3389/fnhum.2015.00268.

Rieger, M., Dietrich, S., & Prinz, W. (2014). Effects of angular gain transformations between movement and visual feedback on coordination performance in unimanual circling. *Frontiers in Psychology*, *5*: 152. doi:10.3389/fpsyg.2014.00152.

Rieger, M., Dietrich, S., & Prinz, W. (2014). Effects of angular shift transformations between movements and their visual feedback on coordination in unimanual circling. *Frontiers in Psychology*, *5*: 693. doi:10.3389/fpsyg.2014.00693.

Stenzel, A., Dolk, T., Colzato, L. S., Sellaro, R., Hommel, B., & Liepelt, R. (2014). The joint Simon effect depends on perceived agency, but not intentionality, of the alternative action. *Frontiers in Human Neuroscience*, *8*: 595. doi:10.3389/fnhum.2014.00595.

Zmyj, N., Prinz, W., & Daum, M. M. (2015). Eighteen-montholds' memory interference and distraction in a modified A-not-B task is not associated with their anticipatory looking in a false-belief task. *Frontiers in Psychology*, *6*: 857. doi:10.3389/ fpsyg.2015.00857.

7.3 Max Planck Research Group "Auditory Cognition"

Degrees

PhD Theses

2014.

Erb, J. The neural dynamics of perceptual adaptation to degraded speech. University of Leipzig, Germany.

2015

 Wilsch, A. Neural oscillations in auditory working memory. University of Leipzig, Germany.

Habilitation Thesis

2015 _

Obleser, J. The brain dynamics of comprehending degraded speech. University of Leipzig, Germany.

Appointments

2015

 Obleser, J. W3 Professorship for Physiological Psychology and Research Methods, Department of Psychology, University of Lübeck, Germany.

Publications

Books & Book Chapters

Erb, J. (2014). The neural dynamics of perceptual adaptation to degraded speech. *MPI Series in Human Cognitive and Brain Sciences: Vol. 159.* Leipzig: Max Planck Institute for Human Cognitive and Brain Sciences. Obleser, J. (2015). The brain dynamics of comprehending degraded speech. *MPI Series in Human Cognitive and Brain Sciences: Vol. 164.* Leipzig: Max Planck Institute for Human Cognitive and Brain Sciences.

- Strauß, A. Neural oscillatory dynamics of spoken word recognition. University of Leipzig, Germany.
- Wöstmann, M. Neural dynamics of selective attention to speech in noise. University of Leipzig, Germany.

Strauss, A. (2015). Neural oscillatory dynamics of spoken word recognition. *MPI Series in Human Cognitive and Brain Sciences: Vol. 163.* Leipzig: Max Planck Institute for Human Cognitive and Brain Sciences.

Wilsch, A. (2015). Neural oscillations in auditory working memory. *MPI Series in Human Cognitive and Brain Sciences: Vol. 166.* Leipzig: Max Planck Institute for Human Cognitive and Brain Sciences.

Journal Articles

Bendixen, A., Scharinger, M., Strauss, A., & Obleser, J. (2014). Prediction in the service of comprehension: Modulated early brain responses to omitted speech segments. *Cortex, 53*, 9-26. doi:10.1016/j.cortex.2014.01.001.

Guediche, S., Holt, L. L., Laurent, P., Lim, S.-J., & Fiez, J. A. (2015). Evidence for cerebellar contributions to adaptive plasticity in speech perception. *Cerebral Cortex, 25*(7), 1867-1877. doi:10.1093/cercor/bht428.

Henry, M., & Herrmann, B. (2014). Low-frequency neural oscillations support dynamic attending in temporal context. *Timing* & *Time Perception*, *2*, 62–86.

Henry, M., Herrmann, B., & Obleser, J. (2014). Entrained neural oscillations in multiple frequency bands comodulate behavior. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(41), 14935–14940. doi:10.1073/pnas.1408741111.

Henry, M., Herrmann, B., & Obleser, J. (2016). Neural microstates govern perception of auditory input without rhythmic structure. *The Journal of Neuroscience, 36*(3), 860–871. doi:10.1523/JNEUROSCI.2191-15.2016.

Henry, M., Herrmann, B., & Obleser, J. (2015). Selective attention to temporal features on nested time scales. *Cerebral Cortex*, 25(2), 450–459. doi:10.1093/cercor/bht240.

Herbst, S., & Landau, A. N. (2016). Rhythms for cognition: The case of temporal processing. *Current Opinion in Behavioral Sciences*, *8*, 85–93. doi:10.1016/j.cobeha.2016.01.014.

Herrmann, B., Henry, M., Fromboluti, E. K., McAuley, J. D., & Obleser, J. (2015). Statistical context shapes stimulus-specific adaptation in human auditory cortex. *Journal of Neurophysiology*, *113*(7), 2582–2591. doi:10.1152/jn.00634.2014.

Herrmann, B., Henry, M., Haegens, S., & Obleser, J. (2016). Temporal expectations and neural amplitude fluctuations in auditory cortex interactively influence perception. *NeuroImage*, *124*(Part A), 487–497. doi:10.1016/j.neuroimage.2015.09.019.

Herrmann, B., Henry, M., Johnsrude, I. S., & Obleser, J. (2016). Altered temporal dynamics of neural adaptation in the aging human auditory cortex. *Neurobiology of Aging, 45*, 10–22. doi:10.1016/j.neurobiolaging.2016.05.006.

Herrmann, B., Henry, M., Scharinger, M., & Obleser, J. (2014). Supplementary motor area activations predict individual differences in temporal-change sensitivity and its illusory distortions. *NeuroImage*, *101*, 370–379. doi:10.1016/j.neuroimage.2014.07.026.

Herrmann, B., Parthasarathy, A., Han, E. X., Obleser, J., & Bartlett, E. L. (2015). Sensitivity of rat inferior colliculus neurons to frequency distributions. *Journal of Neurophysiology*, *114*(5), 2941–2954. doi:10.1152/jn.00555.2015.

Wöstmann, M. (2015). Neural dynamics of selective attention to speech in noise. *MPI Series in Human Cognitive and Brain Sciences: Vol. 172.* Leipzig: Max Planck Institute for Human Cognitive and Brain Sciences.

Herrmann, B., Schlichting, N., & Obleser, J. (2014). Dynamic range adaptation to spectral stimulus statistics in human auditory cortex. *The Journal of Neuroscience*, *34*(1), 327–331. doi:10.1523/JNEUROSCI.3974-13.2014.

Keil, J., Timm, J., SanMiguel, I., Schulz, H., Obleser, J., & Schönwiesner, M. (2014). Cortical brain states and corticospinal synchronization influence TMS-evoked motor potentials. *Journal of Neurophysiology*, *111*(3), 513–519. doi:10.1152/ jn.00387.2013.

Lim, S.-J., Fiez, J. A., & Holt, L. L. (2014). How may the basal ganglia contribute to auditory categorization and speech perception? *Frontiers in Neuroscience*, *8*: 230. doi:10.3389/fnins.2014.00230.

Lim, S.-J., Lacerda, F., & Holt, L. L. (2015). Discovering functional units in continuous speech. *Journal of Experimental Psychology: Human Perception and Performance, 41*(4), 1139– 1152. doi:10.1037/xhp0000067.

Lim, S.-J., Wöstmann, M., & Obleser, J. (2015). Selective attention to auditory memory neurally enhances perceptual precision. *The Journal of Neuroscience, 35*(49), 16904–16104. doi:10.1523/JNEUROSCI.2674-15.2015.

Meyer, L., Cunitz, K., Obleser, J., & Friederici, A. D. (2014). Sentence processing and verbal working memory in a white-matter-disconnection patient. *Neuropsychologia*, *61*, 190–196. doi:10.1016/j.neuropsychologia.2014.06.014.

Meyer, L., Henry, M., Gaston, P., Schmuck, N., & Friederici, A. D. (2016). Linguistic bias modulates interpretation of speech via neural delta-band oscillations. *Cerebral Cortex*. doi:10.1093/cer-cor/bhw228.

Obleser, J. (2015). Re-visiting the electrophysiology of language. *Brain and Language*, *148*, 23–24. doi:10.1016/j. bandl.2015.06.001.

Petersen, E. B., Wöstmann, M., Obleser, J., Stenfelt, S., & Lunner, T. (2015). Hearing loss impacts neural alpha oscillations under adverse listening conditions. *Frontiers in Psychology, 6*: 177. doi:10.3389/fpsyg.2015.00177.

Rufener, K. S., Oechslin, M. S., Wöstmann, M., Dellwo, V., & Meyer, M. (2016). Age-related neural oscillation patterns during the processing of temporally manipulated speech. *Brain Topography*, *29*(3), 440–458. doi:10.1007/s10548-015-0464-0.

Sadakata, M., Shingai, M., Sulpizio, S., Brandmeyer, A., & Sekiyama, K. (2014). Language specific listening of Japanese geminate consonants: A cross-linguistic study. *Frontiers in Psychology*, *5*: 1422. doi:10.3389/fpsyg.2014.01422.

Scharinger, M., Bendixen, A., Herrmann, B., Henry, M., Mildner, T., & Obleser, J. (2016). Predictions interact with missing sensory evidence in semantic processing areas. *Human Brain Mapping*, *37*(2), 704–716. doi:10.1002/hbm.23060.

Scharinger, M., & Idsardi, W. (2014). Sparseness of vowel category structure: Evidence from English dialect comparison. *Lingua*, 140, 35–51. doi:10.1016/j.lingua.2013.11.007.

Scharinger, M., Henry, M., Meyer, L., Erb, J., & Obleser, J. (2014). Thalamic and parietal brain morphology predicts auditory category learning. *Neuropsychologia*, *53*, 75–83. doi:10.1016/j.neuropsychologia.2013.09.012.

Scharinger, M., Henry, M., & Obleser, J. (2015). Acoustic cue selection and discrimination under degradation: Differential contributions of the inferior parietal and posterior temporal cortices. *NeuroImage*, *106*, 373–381. doi:10.1016/j.neuroimage.2014.11.050.

Scharinger, M., Herrmann, B., Nierhaus, T., & Obleser, J. (2014). Simultaneous EEG-fMRI brain signatures of auditory cue utilization. *Frontiers in Neuroscience*, *8*: 137. doi:10.3389/fnins.2014.00137.

Strauss, A., Henry, M., Scharinger, M., & Obleser, J. (2015). Alpha phase determines successful lexical decision in noise. *The Journal of Neuroscience*, *35*(7), 3256–3262. doi:10.1523/ JNEUROSCI.3357-14.2015.

Strauss, A., Kotz, S. A., Scharinger, M., & Obleser, J. (2014). Alpha and theta brain oscillations index dissociable processes in spoken word recognition. *NeuroImage*, *97*, 387–395. doi:10.1016/j. neuroimage.2014.04.005.

Strauss, A., Wöstmann, M., & Obleser, J. (2014). Cortical alpha oscillations as a tool for auditory selective inhibition. *Frontiers in Human Neuroscience*, 8: 350. doi:10.3389/fnhum.2014.00350.

Weisz, N., & Obleser, J. (2014). Synchronisation signatures in the listening brain: A perspective from non-invasive neuroelectrophysiology. *Hearing Research, 307*(SI), 16–28. doi:10.1016/j. heares.2013.07.009. Wilsch, A., Henry, M., Herrmann, B., Maess, B., & Obleser, J. (2015). Alpha oscillatory dynamics index temporal expectation benefits in working memory. *Cerebral Cortex*, *25*(7), 1938–1946. doi:10.1093/cercor/bhu004.

Wilsch, A., Henry, M., Herrmann, B., Maess, B., & Obleser, J. (2015). Slow-delta phase concentration marks improved temporal expectations based on the passage of time. *Psychophysiology*, *52*(7), 910–918. doi:10.1111/psyp.12413.

Wilsch, A., & Obleser, J. (2016). What works in auditory working memory? A neural oscillations perspective. *Brain Research*, *1640*(B), 193–207. doi:10.1016/j.brainres.2015.10.054.

Wöstmann, M., Herrmann, B., Maess, B., & Obleser, J. (2016). Spatiotemporal dynamics of auditory attention synchronize with speech. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(14), 3873–3878. doi:10.1073/pnas.1523357113.

Wöstmann, M., Herrmann, B., Wilsch, A., & Obleser, J. (2015). Neural alpha dynamics in younger and older listeners reflect acoustic challenges and predictive benefits. *The Journal of Neuroscience*, *35*(4), 1458–1467. doi:10.1523/JNEUROSCI.3250-14.2015.

Wöstmann, M., Schröger, E., & Obleser, J. (2015). Acoustic detail guides attention allocation in a selective listening task. *Journal of Cognitive Neuroscience*, *27*(5), 988–1000. doi:10.1162/jocn_a_00761.

Zimmerer, F., Scharinger, M., & Reetz, H. (2014). Phonological and morphological constraints on German /t/-deletions. *Journal of Phonetics*, *45*, 64–75. doi:10.1016/j.wocn.2014.03.006.

7.4 Max Planck Research Group "Early Social Development"

Degrees

PhD Theses

2015.

- Missana, M. Infant processing of emotional faces and bodies: Insights from event-related potentials and asymmetrical frontal brain activity. University of Heidelberg, Germany.
- 2016.
- Krol, K. M. Emotion perception in motherhood and infancy: The role of breastfeeding experience and the oxytocin system. University of Heidelberg, Germany.

Appointments

- 2014 _
- Grossmann, T. Assistant Professorship for Psychology, Department of Psychology, University of Virginia, USA.

Publications

Books & Book Chapters

Altvater-Mackensen, N., & Mani, N. (2015). Phonological features mediate object-label retrieval and word recognition in the visual world paradigm. In R. K. Mishra, N. Srinivasan, & F. Huettig (Eds.), *Attention and Vision in Language Processing* (pp. 23–38). Berlin: Springer.

Journal Articles

Altvater-Mackensen, N., & Fikkert, P. (2015). A cross-linguistic perspective on the acquisition of manner of articulation contrasts in the productions of Dutch and German children. *Language Acquisition*, *22*(1), 2–39. doi:10.1080/10489223.2014.892945.

Rajhans, P. A developmental perspective on the importance of context in emotion perception. University of Heidelberg, Germany.

Blakemore, S. J., Cohen Kadosh, K., Sebastian, C., Grossmann, T., & Johnson, M. H. (2014). Social development. In D. Mareschal, A. Tolmie, & B. Butterworth (Eds.), *Educational Neuroscience* (pp. 268–296). Oxford: Wiley-Blackwell.

Altvater-Mackensen, N., & Grossmann, T. (2015). Learning to match auditory and visual speech cues: Social influences on the acquisition of phonological categories. *Child Development*, *86*(2), 362–378. doi:10.1111/cdev.12320.

Altvater-Mackensen, N., & Grossmann, T. (2016). The role of left inferior frontal cortex during audiovisual speech perception in infants. *NeuroImage, 133,* 14–20. doi:10.1016/j.neuroimage.2016.02.061.

Altvater-Mackensen, N., Jessen, S., & Grossmann, T. (2016). Brain responses reveal that infants' face discrimination is guided by statistical learning from distributional information. *Developmental Science*. doi:10.1111/desc.12393.

Altvater-Mackensen, N., Mani, N., & Grossmann, T. (2016). Audiovisual speech perception in infancy: The influence of vowel identity and infants' productive abilities on sensitivity to (mis)matches between auditory and visual speech cues. *Developmental Psychology*, *52*(2), 191–204. doi:10.1037/a0039964.

Altvater-Mackensen, N., Van der Feest, S., & Fikkert, P. (2014). Asymmetries in early word recognition: The case of stops and fricatives. *Language Learning and Development, 10*(2), 149–178. doi:10.1080/15475441.2013.808954.

Fairhurst, M. T., Löken, L., & Grossmann, T. (2014). Physiological and behavioral responses reveal 9-month-old infants' sensitivity to pleasant touch. *Psychological Science*, *25*(5), 1124–1131. doi:10.1177/0956797614527114.

Grossmann, T. (2015). The development of social brain functions in infancy. *Psychological Bulletin, 141*(6), 1266–1287. doi:10.1037/bul0000002.

Jessen, S., Altvater-Mackensen, N., & Grossmann, T. (2016). Pupillary responses reveal infants' discrimination of facial emotions independent of conscious perception. *Cognition*, *150*, 163– 169. doi:10.1016/j.cognition.2016.02.010.

Jessen, S., & Grossmann, T. (2016). The developmental emergence of unconscious fear processing from eyes during infancy. *Journal of Experimental Child Psychology*, *142*, 334–343. doi:10.1016/j.jecp.2015.09.009.

Jessen, S., & Grossmann, T. (2016). Neural and behavioral evidence for infants' sensitivity to the trustworthiness of faces. *Journal of Cognitive Neuroscience, 28*(11), 1728–1736. doi:10.1162/jocn_a_00999.

Jessen, S., & Grossmann, T. (2015). Neural signatures of conscious and unconscious emotional face processing in human infants. *Cortex*, *64*, 260–270. doi:10.1016/j.cortex.2014.11.007.

Jessen, S., & Grossmann, T. (2014). Unconscious discrimination of social cues from eye whites in infants. *Proceedings of the National Academy of Sciences of the United States of America*, 111(45), 16208–16213. doi: 10.1073/pnas.1411333111.

Jessen, S., & Kotz, S. A. (2015). Affect differentially modulates brain activation in uni- and multisensory body-voice perception. *Neuropsychologia*, *66*, 134–143. doi:10.1016/j.neuropsychologia.2014.10.038.

Kamboj, S. K., Krol, K. M., & Curran, H. V. (2015). A specific association between facial disgust recognition and estradiol levels in naturally cycling women. *PLoS One, 10*(4): e0122311. doi:10.1371/journal.pone.0122311.

Koehne, S., Behrends, A., Fairhurst, M. T., & Dziobek, I. (2016). Fostering social cognition through an imitation- and synchronization-based dance/movement intervention in adults with autism spectrum disorder: A controlled proof-of-concept study. *Psychotherapy and Psychosomatics, 85*(1), 27–35. doi:10.1159/000441111.

Krol, K. M., Kamboj, S. K., Curran, V., & Grossmann, T. (2014). Breastfeeding experience differentially impacts recognition of happiness and anger in mothers. *Scientific Reports, 4*: 7006. doi:10.1038/srep07006.

Krol, K. M., Monakhov, M., Lai, P. S., Ebstein, R., & Grossmann, T. (2015). Genetic variation in CD38 and breastfeeding experience interact to impact infants' attention to social eye cues. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(39), E5434-E5442. doi:10.1073/pnas.1506352112.

Krol, K. M., Rajhans, P., Missana, M., & Grossmann, T. (2015). Duration of exclusive breastfeeding is associated with differences in infants' brain responses to emotional body expressions. *Frontiers in Behavioral Neuroscience*, *8*: 459. doi:10.3389/fnbeh.2014.00459.

Marschik, P. B., Bartl-Pokorny, K. D., Tager-Flusberg, H., Kaufmann, W. E., Pokorny, F., Grossmann, T., Windpassinger, C., Petek, E., & Einspieler, C. (2014). Three different profiles: Early socio-communicative capacities in typical Rett syndrome, the preserved speech variant and normal development. *Developmental Neuro rehabilitation*, *17*(1), 34–38. doi:10.3109/17518423.2013.837537.

Missana, M., Atkinson, A. P., & Grossmann, T. (2015). Tuning the developing brain to emotional body expressions. *Developmental Science*, *18*(2), 243–253. doi:10.1111/desc.12209.

Missana, M., Grigutsch, M., & Grossmann, T. (2014). Developmental and individual differences in the neural processing of dynamic expressions of pain and anger. *PLoS One*, *9*(4): e93728. doi:10.1371/journal.pone.0093728.

Missana, M., & Grossmann, T. (2015). Infants' emerging sensitivity to emotional body expressions: Insights from frontal asymmetrical brain activity. *Developmental Psychology*, *51*(2), 151–160. doi:10.1037/a0038469.

Missana, M., Rajhans, P., Atkinson, A. P., & Grossmann, T. (2014). Discrimination of fearful and happy body postures in 8-monthold infants: An event-related potential study. *Frontiers in Human Neuroscience*, *8*: 531. doi:10.3389/fnhum.2014.00531.

Obermeier, C., Kotz, S. A., Jessen, S., Raettig, T., von Koppenfels, M., & Menninghaus, W. (2016). Aesthetic appreciation of poetry correlates with ease of processing in event-related potentials. *Cognitive, Affective and Behavioral Neuroscience, 16*(2), 362–373. doi:10.3758/s13415-015-0396-x.

Ragert, M., Fairhurst, M. T., & Keller, P. E. (2014). Segregation and integration of auditory streams when listening to multi-part music. *PLoS One*, *9*(1): e84085. doi:10.1371/journal.pone.0084085.

Rajhans, P., Altvater-Mackensen, N., Vaish, A., & Grossmann, T. (2016). Children's altruistic behavior in context: The role of emotional responsiveness and culture. *Scientific Reports, 6*: 24089. doi:10.1038/srep24089.

Rajhans, P., Jessen, S., Missana, M., & Grossmann, T. (2016). Putting the face in context: Body expressions impact facial emotion processing in human infants. *Developmental Cognitive Neuroscience, 19*, 115–121. doi:10.1016/j.dcn.2016.01.004.

Rajhans, P., Missana, M., Krol, K. M., & Grossmann, T. (2015). The association of temperament and maternal empathy with individual differences in infants' neural responses to emotional body expressions. *Development and Psychopathology, 27*(4), 1205–1216. doi:10.1017/S0954579415000772.

Schreiner, M. S., Altvater-Mackensen, N., & Mani, N. (2016). Early word segmentation in naturalistic environments: Limited effects of speech register. *Infancy*, *21*(5), 625–647. doi:10.1111/infa.12133.

Vaish, A., Grossmann, T., & Woodward, A. (2015). Personcentred positive emotions, object-centred negative emotions: 2-year-olds generalize negative but not positive emotions across individuals. *British Journal of Developmental Psychology*, 33(3), 391–397. doi:10.1111/bjdp.12093.

7.5 Max Planck Fellow Group "Cognitive and Affective Control of Behavioural Adaptation"

Degrees

2014 _

Deserno, L. Cognitive deficits in schizophrenia: A model-based functional imaging study on working memory and flexible behavioural adaptation. Charité University Medicine Berlin, Germany.

Publications

Journal Articles

Boehme, R., Deserno, L., Gleich, T., Katthagen, T., Pankow, A., Behr, J., Buchert, R., Roiser, J., Heinz, A., & Schlagenhauf, F. (2015). Aberrant salience is related to reduced reinforcement learning signals and elevated dopamine synthesis capacity in healthy adults. *The Journal of Neuroscience, 35*(28), 10103–10111. doi:10.1523/JNEUROSCI.0805-15.2015.

Charlet, K., Schlagenhauf, F., Richter, A., Naundorf, K., Dornhof, L., Weinfurtner, C. E. J., König, F., Walaszek, B., Schubert, F., Müller, C. A., Gutwinski, S., Seissinger, A., Schmitz, L., Walter, H., Beck, A., Gallinat, J., Kiefer, F., & Heinz, A. (2014). Neural activation during processing of aversive faces predicts treatment outcome in alcoholism. *Addiction Biology*, *19*(3), 439–451. doi:10.1111/ adb.12045.

Deserno, L., Beck, A., Huys, Q. J. M., Lorenz, R. C., Buchert, R., Buchholz, H.-G., Plotkin, M., Kumakara, Y., Cumming, P., Heinze, H.-J., Grace, A. A., Rapp, M. A., Schlagenhauf, F., & Heinz, A. (2015). Chronic alcohol intake abolishes the relationship between dopamine synthesis capacity and learning signals in ventral striatum. *European Journal of Neuroscience*, *41*(4), 477–486. doi:10.1111/ejn.12802. 2016 _

Reiter, A. Out of control behaviors? Investigating behavioral control in alcohol-addiction, binge eating disorders, and associated risk factors. University of Leipzig, Germany.

Deserno, L., Huys, Q. J. M., Boehme, R., Buchert, R., Heinze, H.-J., Grace, A. A., Dolan, R., Heinz, A., & Schlagenhauf, F. (2015). Ventral striatal dopamine reflects behavioral and neural signatures of model-based control during sequential decision making. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(5), 1595–1600. doi:10.1073/pnas.1417219112.

Deserno, L., Wilbertz, T., Reiter, A., Horstmann, A., Neumann, J., Villringer, A., Heinze, H. J., & Schlagenhauf, F. (2015). Lateral prefrontal model-based signatures are reduced in healthy individuals with high trait impulsivity. *Translational Psychiatry, 5*: e659. doi:10.1038/tp.2015.139.

Friedel, E., Koch, S. P., Wendt, J., Heinz, A., Deserno, L., & Schlagenhauf, F. (2014). Devaluation and sequential decisions: Linking goal-directed and model-based behavior. *Frontiers in Human Neuroscience*, *8*: 587. doi:10.3389/fnhum.2014.00587.

Friedel, E., Schlagenhauf, F., Beck, A., Dolan, R. J., Huys, Q. J., Rapp, M. A., & Heinz, A. (2015). The effects of life stress and neural learning signals on fluid intelligence. *European Archives of Psychiatry and Clinical Neuroscience, 265*(1), 35–43. doi:10.1007/s00406-014-0519-3.

Garbusow, M., Schad, D. J., Sommer, C., Juenger, E., Sebold, M., Friedel, E., Wendt, J., Kathmann, N., Schlagenhauf, F., Zimmermann, U. S., Heinz, A., Huys, Q. J. M., & Rapp, M. A. (2014). Pavlovian-to-instrumental transfer in alcohol dependence: A pilot study. *Neuropsychobiology*, *70*(2), 111–121. doi:10.1159/000363507.

Gleich, T., Deserno, L., Robert, L., Boehme, R., Pankow, A., Buchert, R., Kühn, S., Heinz, A., Schlagenhauf, F., & Gallinat, J. (2015). Prefrontal and striatal glutamate differently relate to striatal dopamine: Potential regulatory mechanisms of striatal presynaptic dopamine function? *The Journal of Neuroscience*, *35*(26), 9615–9621. doi:10.1523/JNEUROSCI.0329-15.2015.

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7.6 Minerva Research Group "Brain Modes"

Publications

Journal Articles

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Neuroscience of Communication: Function, Structure, and Plasticity

International Max Planck Research School

The International Max Planck Research School on Neuroscience of Communication: Function, Structure, and Plasticity (IMPRS NeuroCom) is an interdisciplinary PhD programme. The school is based at MPI CBS and the University of Leipzig (UL) and also involves the Max Planck Institute for Evolutionary Anthropology (MPI EVA) in Leipzig, and the Institute of Cognitive Neuroscience (ICN) at UCL, UK. The IMPRS NeuroCom is funded by the Max Planck Society, the MPI CBS, and the UL. Currently the school is in its second funding period (2015–2021). We have more than 300 applicants yearly among whom we choose 10–15 outstanding doctoral students. The graduate school strengthens the already existing, close working relationship between all participating institutions.



Group photo IMPRS NeuroCom, 30 May, 2016

PhD students and projects

Module I: Language and Communication¹

Student	Project	Project Stage
Beese, Caroline	Oscillatory processes during sentence comprehension in the aging population	progressed
Bianco, Roberta	What is beyond a pianist's hand? Syntactic-based prediction of forthcoming musical motor acts	submitted
Chien, Pei-Ju	Cross-cultural recognition of speaker's intentions from prosody - universals and misunderstandings	orientation
Dr Fengler (née Hubert), Anja	Recursion during language development	completed
Goranskaya, Dariya	Neural basis of grammar learning	progressed
Graessner, Astrid	The development of understanding nested structures in language and action	orientation

¹ Formerly named: Verbal Communication: Language

Hellbernd, Nele	The neural bases of prosody in speech acts	progressed
Dr Knierim, Iris Nicola	Rules don't come easy: Investigating feedback-based learning of rules in the language domain	completed
Dr Kraft, Indra	Predicting developmental dyslexia at a preliterate age by combining behavioral assessment with structural MRI	completed
Krause, Carina Denise	Who did what to whom? - The differential roles of syntactic complexity and verbal working memory capacity in sentence comprehension	final
Kroczek, Leon	Topdown influences during language processing	progressed
Marzecová, Anna	Temporal expectancy, auditory cognition, and cognitive control	submitted
Qi, Ting	The relationship between the functional and structural language conncetome in brain development	progressed
Roswandowitz, Claudia	Voice and speech recognition abilities in patient and control groups	final
Schell, Marianne	Neuroanatomical correlates for syntactic and semantic composition on a fundamental level	final
Stuckenberg (née Erfort), Maria	Bimodal interaction mechanisms	progressed
Vassileiou, Benedict	Description of the spatiotemporal network dynamics subserving working memory resources involved in sentence comprehension	progressed
Winkler, Marina	Learning complex grammar from simple tones: Young in- fants' and adults' processing of nested dependencies measured by EEG and fNIRS	progressed
Dr Wöstmann, Malte	Neural dynamics of selective attention to speech in noise	completed
Xiao, Yaquiong	Resting-stage functional connectivity in the brain and its relation to language development in preschool children	submitted

Module II: Non-Verbal Communication: Action and Interaction (2009–2012)²

Student	Project	Project Stage
Dr Goltz, Dominique	Sustained spatial attention in touch: Underlying brain areas and their interaction	completed
Dr Ragert (née Uhlig), Marie	Cognitive meachnisms underlying perception and production of polyphonic music	completed

² For reasons of faculty member retirement or relocation, the structure and research focus of Module II, in particular, has changed considerably. This was formerly named "Non-verbal Communication: Action and Interaction" but it is now "Social, Cognitive and Affective Neuroscience".

Student	Project	Project Stage
Jakobsen, Estrid	Functional neuroanatomy of the human somatomotor cortex: Microstructural and functional mapping with ultra-high-field magnetic resonance imaging	submitted
Dr Krol, Kathleen M.	Emotion perception in motherhood and infancy: The role of breastfeeding experience and the oxytocin system	completed
Linz, Roman	Investigating the effects of mental training on stress	progressed
Lumma, Anna-Lena	Neurophenomenology: The integration of first- and third- person methods in the study of effects of meditation practices and the self	final
Oligschläger, Sabine	Investigating the spatial organization of the human cortex using connectivity distance	progressed
Paulus, Philipp C.	Schematic representations in vmPFC	orientation
Puhlmann, Lara	Changes of health related markers after mental training	progressed
Valk, Sofie L.	The structural architecture of social cognitive networks	final
Zinchenko, Artyom	Affective control and prediction formation in multisensory integration	progressed

Module II: Social, Cognitive and Affective Neuroscience

Module III: Neuroscience: Basic and Clinical

Student	Project	Project Stage
Albrecht, Franziska	Neural Correlates of Parkinsonian Syndromes	progressed
Baczkowski, Blazej	Subcortical contributions to intrinsic cortical dynamics	progressed
Ballarini, Tommaso	The role of brain connectivity signatures in neurodegen- erative disorders. From diagnosis to the assessment of treatment outcomes	progressed
Dr Freigang, Claudia	Processing of auditory objects in older adults in the acoustic free field	completed
Hardikar, Samyogita	A genetic approach to gustatory processing	final
Dr Hoyer (née Rambow), Jana	Peripheral physiological responses to distinct stressors: Associations with behavioral and neural measures	completed
Polyakova, Maryna	Neural correlates of affective and cognitive dysfunctions	progressed
Dr Reiter, Andrea M.F.	Behaviours running out of control – failure of behavioural adaptation in psychopathology	completed

Sarrou, Mikaella	Auditory motion perception	final
Schaare, Herma Lina	Neurocognition of vascular risk factors	final
Shih, Pei-Cheng	Neuronal and behavioral characteristics of mirror- and non-mirror-symmetrical upper limb movements	progressed
Dr Strotmann, Barabara	The human habenula: Structure, function, and connectivity	completed
Uhlig, Marie	Where is the peak of the inverted U shape? A multisystem investigation of the benefit and burden of stress	orientation

Module IV: Neuroimaging Physics and Signal Processing³

Student	Project	Project Stage
Attar, Mohavedian Fakhereh	Identification and characterization of superficial white mat- ter structures using non-invasive MRI	orientation
Chien, Shih-Cheng	The Relationship between auditory sequence learning and mismatch negativity	progressed
Guidi, Maria	High-resolution fMRI	progressed
Kalloch, Benjamin	Individualized therapy through computer simulation	progressed
Kanaan, Ahmad Seif	Neurochemical and network based analysis of the patho- physiological mechanisms of Tourette Syndrome	progressed
Kim, Seung-Goo	Myeloarchitectonic and functional organizations of audi- tory cortex in musicians with absolute pitch	submitted
Lorenz, Kathrin	Parameters of the human cerebral blood supply observed by arterial spin labelling techniques	progressed
Metere, Riccardo	The biophysical basis of MR signals	progressed
Rose, Daniel	Informing neuronal network models by MRI-based in-vivo histology	orientation
Dr Teichmann, Christoph	Improving Bayesian methods for unsupervised natural lan- guage structure induction	completed
Vaculčiaková, Lenka	Ultra high resolution mapping of cortical myelination us- ing quantitative MRI	orientation
Dr Wang, Peng	Parameter estimation of neural mass model	completed
Waschke, Johannes	Analysis of histological data	orientation
Zarubin, Georgy	Identification and characterization of superficial white matter	progressed

³ Formerly named "Methods: Physics of Neuroimaging and Computational Neuroscience"

Faculty

Module I: Language and Communication

Professor B. Comrie (2009–2015)	Professor J. Obleser (2012–2015)
MPI EVA, Dept. of Linguistics (now University of	MPI CBS, MPRG "Auditory Cognition" (now University of
California, Santa Barbara, USA)	Lübeck, Germany)
Professor A. D. Friederici (since 2009)	Professor T. Pechmann (2009–2016)
MPI CBS, Dept. of Neuropsychology	UL, Dept. of Linguistics
Dr G. Hartwigsen (since 2016) MPI CBS, RG "Modulation of Language Networks"	Dr D. Sammler (since 2013) MPI CBS, OHG "Neural Bases of Intonation in Speech and Music"
PD Dr S. Hoehl (since 2016)	Professor D. Saur (since 2016)
MPI CBS, MPRG "Early Social Cognition"	UL, Dept. of Neurology
Professor J. Jescheniak (since 2009)	Professor E. Schröger (since 2009)
UL, Dept. of Cognitive Psychology	UL, Dept. of Cognitive and Biological Psychology
Professor S. A. Kotz (2009–2016) MPI CBS, Dept. of Neuropsychology, University of Manchester, UK (now Maastricht University, the Netherlands)	Professor K. von Kriegstein (since 2012) MPI CBS, MPRG "Neural Mechanisms of Human Communication"

Module II: Social, Cognitive and Affective Neuroscience

Dr R. G. Benoit (since 2016) MPI CBS, MPRG "Adaptive Memory"	Professor D. Haun (since 2016) UL, Dept. of Early Development and Culture
Professor J. Call (2012–2016) MPI EVA, Wolfgang Köhler Primate Research Center, University of St Andrews, United Kingdom	Dr D. S. Margulies (since 2012) MPI CBS, MPRG "Neuroanatomy & Connectivity"
Professor M. Carpenter (2012–2016) MPI EVA, Dept. of Developmental and Comparative Psychology, University of St Andrews, United Kingdom	PD Dr J. Sacher (since 2016) MPI CBS, Branco Weiss Fellowship Group - EGG (Emotions & neuroimaGinG)-Laboratory
Dr V. Engert (since 2016) MPI CBS, Dept. of Social Neuroscience	Professor M. L. Schroeter (since 2012) UL, Day Clinic of Cognitive Neurology, and MPI CBS, Dept. of Neurology
Professor T. Grossmann (2012–2015) MPI CBS, MPRG "Early Social Development" (now University of Virgina, USA)	Professor T. Singer (since 2012) MPI CBS, Dept. of Social Neuroscience

Module III: Neuroscience: Basic and Clinical

Professor I. Bechmann (since 2012)	Professor R. Rübsamen (since 2009)
UL, Institute for Anatomy	UL, Dept. of General Zoology and Neurobiology
Professor J. Claßen (since 2012)	Dr F. Schlagenhauf (since 2012)
UL, Dept. of Neurology	MPI CBS, Dept. of Neurology
PD Dr S. Geyer (since 2009) MPI CBS, RG "Anatomical Analysis of the Organization of the Human and Non-Human Primate Brain"	Professor P. Schönknecht (since 2009) UL, Clinic and Polyclinic of Psychiatry
Professor U. Hegerl (since 2009)	Professor M. Schönwiesner (since 2016)
UL, Clinic and Polyclinic of Psychiatry	UL, Dept. of General Zoology and Neurobiology
Professor H. Obrig (since 2009) UL, Day Clinic of Cognitive Neurology, and MPI CBS, Dept. of Neurology	Professor A. Villringer (since 2009) MPI CBS, Dept. of Neurology
Professor P. Ragert (since 2016)	Professor K. von Klitzing (since 2009)
UL, Dept. Movement and Training, and MPI CBS,	UL, Clinic and Polyclinic of Children and Youth
Dept. of Neurology	Psychiatry

Module IV: Neuroimaging Physics and Signal Processing

Professor M. Bogdan (since 2012) UL, Dept. of Computer Engineering	Dr B. Maess (since 2009) MPI CBS, Methods and Development Group "MEG and Cortical Networks"
Professor J. Haase (since 2009) UL, Dept. of Magnetic Resonance of Complex Quantum Solids	Professor H. E. Möller (since 2009) MPI CBS, Methods and Development Group "Nuclear Magnetic Resonance"
Professor G. Heyer (2009–2014) UL, Dept. of Automatic Language Processing	Professor K. Mueller (since 2009) MPI CBS, Methods and Development Group "Nuclear Magnetic Resonance"
Professor M. Hlawitschka (since 2012) UL, Dept. of Scientific Visualisation	Professor G. Scheuermann (since 2009) UL, Dept. of Image Processing
Professor D. Huster (2012–2016) UL, Dept. of Medical Physics and Biophysics	Professor R. Turner (2009–2014) MPI CBS, Dept. of Neurophysics
Professor S. J. Kiebel (2012–2015) MPI CBS, Dept. of Neurology, and Dept. of Neurology, University Clinics Jena (now Technical University of Dresden)	Prof N. Weiskopf (since 2016) MPI CBS, Dept. of Neurophysics
PD Dr T. R. Knösche (since 2009) MPI CBS, Methods and Development Group "MEG and Cortical Networks"	

Note. MPRG = Max Planck Research Group; OHG = Otto Hahn Group

IMPRS NeuroCom

The IMPRS NeuroCom focuses on the functional, structural, and neural plasticity foundations of the neuroscience of communication through an integrative and interdisciplinary approach. The overriding goal of this programme is to train PhD students in the multidisciplinary aspects of cognition, psychology, and neuroscience involved in different levels of communicative action, and to introduce specific research themes within this broad area of academic endeavour. Besides introducing behavioural methodology, the programme draws on powerful modern neuroimaging techniques such as functional and structural MRI, EEG, MEG, NIRS, and TMS, with the aim of understanding the brain in its complexity and functionality. There is permanent exchange between neuroscientific methodologies and cognitive science, which is supported by the school's infrastructure and facilities. PhD projects, teaching, and supervision are organised in the following four modules:

- Module I: Language and Communication
- Module II: Social, Cognitive, and Affective Neuroscience
- Module III: Neuroscience: Basic and Clinical
- Module IV: Neuroimaging Physics and Signal Processing

Following the recommendation of the IMPRS Evaluation Committee in 2013, the IMPRS NeuroCom applied for a second funding period. The application for extension has been evaluated positively so that the IMPRS NeuroCom is now in its second funding period, lasting from 2015– 2021. Starting with the new funding period, the IMPRS NeuroCom changed its structure from a triennial to an annual recruitment of new PhD candidates. Accordingly, the structure of the curriculum has been adapted so that courses are now offered every year.

For the third recruitment period of doctoral students in 2015, we received 273 applications. For the fourth call for applications in 2016 we received 315 applications, an increase of 15% compared to 2015. In 2015 eight new PhD students started at the IMPRS, and in 2016 15 students started their PhD at our school. These numbers show that admission to the school was highly competitive, with less than 5% of applicants receiving an offer for a position. The wide variety of the students' professional backgrounds enables them to benefit from shared knowledge and resources.

Another important aspect of the new structure of the IMPRS is that the IMPRS NeuroCom Summer School takes place annually instead of twice every three years. Every third year the Summer School takes place in London at our partner institute, the Institute of Cognitive Neuroscience at the UCL. The overall topic of the most recent Summer School, which took place from 4-6 July, 2016 at MPI CBS in Leipzig was "What makes us human?" We were very happy to host outstanding international experts who supported the school with excellent lectures and workshops. There were three days of exciting sessions on Language, Artificial Intelligence & Machine Learning, Consciousness and Comparative Psychology, as well as scientific workshops and poster sessions. Around 200 participants had the opportunity to discuss their research projects with peers and experts, gain experience, get ideas, and establish contacts for possible future research collaborations. Excellent lectures, courses, and



Lecture, 6th IMPRS NeuroCom Summer School, 4–6 July, 2016, Leipzig



Workshop, 6th IMPRS NeuroCom Summer School, 4–6 July, 2016, Leipzig

workshops offered participants the chance to immerse themselves in the neurosciences and to experience scientific expertise on a high level.

The PhD curriculum combines opportunities for outstanding research with excellent teaching to ensure that students are highly qualified for a successful career in relevant areas of Neuroscience. Courses held in 2014–2016 included modules on Neuroscience, Physics of Neuroimaging, Language and Communication, Connectivity, and Social Neuroscience. Lectures were conducted by the IMPRS faculty from all involved institutions in Leipzig as well as by external guest speakers. In addition, the IMPRS NeuroCom organised a workshop on data visualisation. In order to assist students in developing and broadening essential research skills, the IMPRS NeuroCom offered transferable skills seminars, such as a workshop on time and project management, as well as a workshop on scientific writing. To support and assist PhD students in their future career planning, IMPRS NeuroCom also organised a workshop on career planning, including a session with MPI CBS and IMPRS NeuroCom Alumni as guests. Furthermore, international students were encouraged and financially supported to participate in German language courses.

Spokesperson

Professor Arno Villringer (since 2013)

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Coordinator

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Katja Kirsche (September 2014–September 2015)

Dr Antje Niven (January 2009–September 2014)

Assistant

Susann Glasewald (as of January 2017)



Poster session, 6th IMPRS NeuroCom Summer School, 4–6 July, 2016, Leipzig



New PhD students of the 4th cohort, 30 September, 2016

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