Novel approaches to dynamics, development and dysfunction of attention networks

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The presentations in this symposium, chaired by Kimmo Alho, will elucidate how recent methodological advances have enabled novel approaches to dynamics, development and dysfunction of attention networks in the human brain.

The first presentation will be given by Mohsen Alavash and it is titled "Network identification of the attentive listening brain". Selective listening to one of concurrent talkers, classically known as the 'cocktail party problem', has been the topic of extensive research for nearly six decades. While selective listening clearly marks a large-scale neural process, the functional network organization implementing auditory selective attention is not yet completely understood. Novel approaches in network neuroscience provide the opportunity to identify cortical nodes and functional connections that shape the network substrate of selective listening. Mohsen Alavash will argue that one way to achieve this network identification is to study how the brain network makeup at rest changes as it gets engaged in selective listening. He will present the results from a large-scale neuroimaging study in which the aforementioned network identification framework has provided new insights into the cortical organization of selective listening. In this study, an age-varying cohort of 156 healthy adults participated in a two-talker selective listening task, and their brain activity was recorded by means of functional magnetic resonance imaging (fMRI) and electroencephalography (EEG) in separate sessions. Functional brain networks were constructed based on correlation between brain hemodynamic responses or power-envelopes of oscillatory neural sources, respectively. The fMRI results provide evidence in support of a fronto-temporal auditory-control network whose modular reconfiguration from rest to listening was predictive of individuals' listening success. In parallel, source-EEG results reveal a beta-tuned frontoparietal network enabling the flexible adaptation to attentive listening state, and an alpha-tuned posterior cortical network supporting attention to speech. Collectively, these results provide large-scale brain network accounts of attentive listening, and speak to their potential in explaining inter-individual differences in auditory attentional control.

Patrik Wikman and Kimmo Alho, in turn, will give a presentation on "Modulation of brain activity during attentive processing of speech in life-like settings". Technical advances have now enabled use naturalistic audiovisual (AV) stimuli to study the brain mechanisms underlying attention to particular speakers in the presence of irrelevant voices. Wikman and colleagues have conducted a line of studies using videos of dialogues between two speakers during fMRI and EEG. The AV quality of the dialogues was modulated from good (i.e., fully comprehensible) to poor (i.e., virtually incomprehensible) using masking and noise-vocoding. To increase attentional demands, in addition to the AV dialogue a concurrent irrelevant voice was delivered in the background. The participants perform different tasks, namely 1) AV Speech Task: selectively attend to and memorize the dialogue; 2) Phonological Task: selectively attend to the dialogue and detect all phonemes /r/ in it; 3) Shadowing Task: selectively attend to the dialogue and repeat it overtly; 4) Visual Control Task: ignore the dialogue and count rotations of a visually presented cross. They have also modulated the semantic cohesiveness of the dialogues using shuffling. They expected attentive processing of AV speech to modulate activations a network consisting in the auditory cortical regions. They also expected the AV quality to interact with attention-related activity modulations in this network and that top-down information related to the cohesiveness of the dialogues would modulate superior temporal gyrus (STG) activations. Using a combination of univariate- and multivariate-decoding analyzes on both the fMRI and EEG data and combined fMRI-EEG data they found that 1) Attention to AV speech modulates neural activity in STG and superior temporal sulcus (STS) regions, as well as in frontal and medial cortical regions the magnitude of these effects being immense (e.g., some regions showed an above 80% decoding accuracy between the two tasks), 2) semantic context modulates attentional processes in the lateral STG, but also in Heschl's gyrus, suggesting that semantic information feeds back to the lower levels in the speech processing hierarchy, and 3) the magnitude of attentional modulations of brain activity changes during the span of AV attention with different brain regions having distinct temporal attention profiles. Taken together, their findings suggest that attentional mechanisms in speech are more complex than previously thought.

Next, Juha Salmi will give a presentation titled "Attention network dynamics in ADHD: Developments in task-based and naturalistic approaches". He will present findings related to several novel brain imaging approaches developed for research on attention deficit hyperactivity disorder (ADHD). Using a wide variety of different attention conditions Salmi and colleagues have clarified how ADHD modulates brain activity. Multimodal spatiotemporal classification conducted for decoded fMRI and EEG data detected three attention-related brain activity patterns in a subsecond timescale (early: visual / dorsal attention, middle: ventral attention, late: default mode / somatomotor). Their findings suggest that task-dependent aberrant brain activity patterns in ADHD are observed in large-scale brain networks at multiple processing stages. In addition to paradigms focusing on one attention control mechanism at a time, they have developed naturalistic paradigms tapping multiple functions simultaneously. In a distracted multi-talker conversation condition, they manipulated a film by embedding it with various ambient noises (speech, music, white noise) to serve experimental purposes. Using the method of inter-subject correlation, they demonstrate that both higher-level attention networks as well as sensory cortices are desynchronized in participants with ADHD relative to healthy controls during viewing of a multi-talker condition. Specifically, desynchronization of the posterior parietal cortex occurred when irrelevant speech or music was presented in the background, but not when irrelevant white noise was presented, or when there were no distractors. Finally, Salmi and colleagues have developed a novel virtual reality approach to investigate ADHD-related alterations in behavioral and brain functions during active goal-directed behaviors. This work introduces several novel behavioral indices operationalized based on naturalistic symptoms-related behaviors and demonstrates how such task-performance and gaze data can be used in fMRI research.

The last presentation of the symposium will be given by Gaia Scerif and it is titled "Using developmental cognitive neuroscience tools to investigate mechanisms of typical and atypical attentional control". Attentional control plays a crucial role in biasing incoming information in favour of what is relevant to further processing, to encoding into memory and action selection. Gaia Scerif will describe how, from very early in development we are equipped with exquisite attentional skills, whose improvement is coupled with increased effectiveness of control networks. According to the work of Scerif and colleagues, both behavioural and neural indices suggest similarities, as well as differences, in how children and young adults deploy attentional control to optimize maintenance of information in memory. At the same time, attentional effects are not unidirectional: previously learnt information and attention during learning guide later attentional deployment, both in adulthood and in childhood. In the second part of the presentation, she will review data from atypically developing children and adolescents, with a focus on children's atypical inhibitory control and decision making. In conclusion, assessing attentional development and its dynamics point to the bidirectional influences between attention, memory, motivation, and perceptual processing, both over typical and atypical development. This presentation will draw from a combination of EEG and fMRI focused network analyses.

Arousal and cortical excitability shape adaptive perceptual decision making

Prof. Dr. Matthew McGinley[3,4,5], Dr. Elaine Corbett[6], Dr. Julian Kosciessa[1], Dr. Leonhard Waschke[1], Martin Dahl[1,2]

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Adaptive behavior relies on the accurate processing and integration of sensory information. Importantly, the acuity of sensory processing fluctuates across time-varying states of cortical excitability. States of heightened excitability, characterized by cortical desynchronization, allow for accurate sensory processing. By contrast, highly synchronized states largely shield the brain from external inputs. Studies in non-human animals suggest that arousal-related neuromodulatory drive sculpts patterns of cortical synchronization. However, much less is known about how the interplay of neuromodulation and cortical excitability shapes perceptual decisions in humans. Critically, neuromodulatory effects were difficult to study non-invasively in humans so far. Novel methodological approaches, however, enable researchers to investigate the influence of cortical desynchronization as well as arousal on human behavior using non-invasive proxies. This symposium bridges the gap between animal physiology and human cognitive neuroscience by directly interrelating findings and approaches from both fields. With an interdisciplinary set of speakers researching the neural predictors of perception, we foster the crucial transfer of ideas between different neuroscientific sub-disciplines.

In particular, we demonstrate that the effects of reward expectancy and arousal on perceptual decisions can be dissociated in mice. Switching to humans, we report findings indicating how electroencephalographic (EEG) signals related to perceptual decision making adapt to the demands of varying environments, and vary with brain state fluctuations. Next, we evaluate whether arousal and desynchronization jointly or distinctly shape perceptual performance. Finally, the relevance of these findings for age-related cognitive decline is discussed.

First, Matthew McGinley (Baylor College of Medicine) will present how reward expectancy and arousal affect perceptual decisions in mice. The expectation of reward can lead to heightened perceptual sensitivity and improved decision-making. This is sometimes referred to as 'the arousal effect.' However, it is not clear how reward expectancy relates to arousal in its underlying circuit mechanisms or precise behavioral impacts. In their study, Matt and colleagues developed a challenging auditory temporal-coherence detection paradigm in head-fixed mice, which they called the 'attentional effort' task. Mice responded to unpredictable emergence of temporal coherence in an otherwise incoherent tone cloud by licking for sugar-water reward, analogous to coherent motion in visual attention. Difficulty was parametrically varied by partially degrading the coherence. The paradigm alternated between large and small rewards across blocks, resulting in shifts in reward expectancy that manifested as shifts in effort. Arousal was monitored via pupil size.
They found that mice exhibited >5 effort shifts/session, tightly time-locked to transitions in reward block. In addition to affecting detection-theoretic decision criterion, expectation of large reward increased perceptual sensitivity (d'), particularly for weak coherence targets. They referred to this motivated improvement in d' as attentional effort. Contrary to the prediction that high reward expectancy increases arousal, baseline pupil size indicated mice slightly decreased their average arousal level in high reward blocks. Large moment-to-moment pupil fluctuations persisted across block types. Thus, slow, tonic shifts in global arousal did not account for the effects of reward expectation on attentional effort. Furthermore,

event-related phasic pupil dilation reported multiple other task-related signals, including: correctness, prediction errors, and indeed reward context. In ongoing experiments, Matt uses 2-photon calcium imaging to determine the roles of frontal-sensory and neuromodulatory signals in mediating sensory processing and behavior.

Next, Elaine Corbett (Trinity College Dublin) will talk about EEG signatures of adaptive perceptual decision formation in humans. The mechanisms underlying simple perceptual decisions have been the subject of decades of research across diverse disciplines. Much of this work has been anchored to the idea that decisions are made by accumulating evidence up to a criterion amount or “bound” that can trigger an appropriate action. Within this general framework, however, most studies have considered decisions with just two alternative outcomes. Much remains unknown regarding how continuous-outcome decision processes are adapted to the known temporal and perceptual demands of the environment, and how they are altered by varying brain states. In her talk Elaine will describe recent human neurophysiology experiments that exploit simple paradigm design principles to simultaneously trace continuous-outcome decision formation at the levels of evidence accumulation and sensory encoding. The sensory-level signal reflects trial-by trial variations in precision, while the evidence accumulation signal reflects additional decision process adaptations that lead to a complex pattern of response biases. She will demonstrate a joint neural and behavioural analysis, using a recently developed diffusion decision model for continuous-report tasks, to characterise continuous-outcome decision process adaptations due to biases, discriminability and speed pressure. She will also examine the influence of brain-state fluctuations on the neural signals of decision formation.

Afterwards, Julian Kosciessa (Max-Planck Institute for Human Development) will discuss the relevance of strategic excitability adjustments for perceptual decisions under environmental uncertainty. Perceptual decisions often require a systematic reduction of stimulus complexity. However, the extent to which relevant stimulus features are known during sensation varies between different environments. To ideally guide upcoming decisions, observers should thus flexibly adjust the fidelity of sensory information processing according to the current level of environmental uncertainty. Julian will present results from a multimodal EEG-pupillometry study in healthy human participants who performed a dynamic visual attention task, during which the amount of relevant visual features were parametrically varied to induce different levels of (expected) uncertainty. Increasing uncertainty decreased the rate of evidence accumulation for subsequent perceptual decisions, as jointly indicated by behavioral and electrophysiological modeling. During sensation, uncertainty increased pupil-based arousal and cognitive control as indicated by frontal theta power. Alongside, visual excitability increased, as indicated by stronger posterior alpha desynchronization and increased gamma power. Similarly, increases in sample entropy and shallowing of 1/f slopes jointly indicated an increase in the irregularity of neural dynamics during environmental uncertainty. Subjects with more pronounced excitability increases under uncertainty exhibited higher rates, and stronger modulation, of evidence accumulation. Jointly, these results suggest that humans dynamically adjust sensory excitability according to the processing fidelity required for an upcoming choice.

Next, Leonhard Waschke (Max-Planck Institute for Human Development) will present a study investigating the influence of arousal and cortical desynchronization on perceptual decisions. Perceptual decisions are not solely driven by the sensory information available. In addition, the momentary level of arousal and related neuromodulatory brain activity has been found to impact the processing of sensory information and the acuity of perceptual decisions. Furthermore, recordings in non-human animals suggest that periods of increased sensory cortical desynchronization foster sensory representations and perceptual performance. Despite a previously reported positive link between arousal and cortical desynchronization, it remains unclear to which degree both processes exert common and shared influences on sensory processing and behaviour. In his talk, Leo will present evidence from a series of experiments in healthy human participants that employed pupillometry and the entropy of electroencephalography as proxies of arousal and cortical desynchronization, respectively. Importantly, both processes did not only impact ongoing brain activity and early sensory processing in distinct ways but also differentially shaped perceptual performance. On the one hand, intermediate pupil-linked arousal was associated with highest sensitivity. On the other hand, intermediate levels of local cortical desynchronization coincided with minimal response bias and fastest responses. These results speak to a model in which arousal and cortical desynchronization exert at least partially distinct influences on sensory processing and perceptual performance but jointly shape brain states for optimal behaviour.

Finally, Martin Dahl (University of Southern California) is relating pupil-related arousal and cortical desynchronization to attentional performance in later life. On different levels of neural processing, pupil-indexed noradrenergic neuromodulation and cortical desynchronization have been linked to the selective processing of behaviorally-relevant information. Mechanistically, research in non-human animals suggests that norepinephrine release may dynamically sculpt patterns of cortical synchronization according to current demands. In later life, deficits in selective attention emerge. However, research linking noradrenergic neuromodulation and cortical synchronization with age-related changes in attention is scarce. In his talk, Martin will present data of a multimodal age-comparative study relating arousal-induced pupil dilation, a non-invasive proxy for noradrenergic activity, to EEG desynchronization. Relative to perceptually-matched control stimuli (CS–), fear-conditioned stimuli (CS+) induced a multimodal response, consisting of pupil dilation and EEG desynchronization. Crucially, greater pupil dilation in response to CS+ was associated with a stronger transient alpha–beta desynchronization (9–30 Hz), indicating a common dependence on phasic norepinephrine release. Using structural equation modeling, Martin and colleagues integrated over EEG desynchronization and pupil dilation markers to derive a single index reflecting the responsiveness of the noradrenergic system to arousing stimuli. Combining behavioral and physiological data, they observed that a more responsive noradrenergic system was associated with better performance across multiple attention tasks. Finally, they found that older age is associated with lower noradrenergic responsiveness, as reflected in pupil and EEG markers. In sum, their findings indicate that (1) noradrenergic neuromodulation dynamically sculpts oscillatory dynamics in posterior brain areas and (2) this interaction supports attention across the lifespan.

Taken together, the presented findings combine a variety of neuroimaging tools (2-photon imaging, EEG, pupil dilation) across non-human animals and humans to provide a more holistic picture of how arousal and cortical synchronization shape brain states for adaptive perceptual decisions.

Building bridges: Mapping the multifaceted architecture of the wandering mind

Josephine Maria Groot[1,2], Matthias Mittner[1], Julia Kam[3], Adrien Martel[4], Aaron Kucyi[5]
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Symposium summary:
Mind wandering involves the complex and dynamic cognitive processes that take place when attention disengages from events in the here and now. Mapping the heterogeneous aspects and underlying mechanisms of mind wandering has become an increasingly important research focus that poses fundamental methodological challenges. Using electrophysiological and neuroimaging techniques, researchers have discovered intriguing insights into how neural systems drive fluctuations in attention and orchestrate task-unrelated thought episodes. In addition, the application of sophisticated cognitive process models and machine-learning algorithms provide new and exciting ways to model and integrate information from multiple behavioral and neural sources. In this symposium, we bring together world-leading experts in the field of mind wandering and computational modeling, building bridges between the large variety of methodologies within the mind wandering field, including cognitive modeling, neuroimaging, and psychophysiology. The overarching goal is to highlight the different perspectives and advance the field toward an integrated approach that informs a comprehensive picture of the complex architecture of the wandering mind.
Symposium attendees are presented with a variety of state-of-the-art research methodologies that reveal novel insights into the underlying mechanisms of task-unrelated attentional states. Julia Kam will present an overview of the latest findings concerning electrophysiological correlates of mind wandering. Adrien Martel will present work on univariate and multivariate analyses to reveal distinct patterns in EEG dynamics mapping to distinct attentional states. Aaron Kucyi's work focuses on predicting mind wandering with dynamic functional connectivity between brain networks, and extending this to ADHD populations. Josephine Groot will present diverse direct and indirect markers of mind wandering based on fMRI, pupillometry, and behavioral measures from a finger-tapping task. Matthias Mittner will demonstrate the results of a customized Hidden Markov model to model the dynamics of mind wandering and reveal insights in the attentional switches between different attentional states. Together, the presentations focus on important and relevant questions in the mind wandering field, exploiting state-of-the-art research methodologies to advance the field toward a better understanding of the dynamic features of task-unrelated attentional states.

Speaker: Julia Kam
Title: General electrophysiological markers of mind wandering
Abstract: Recent years have witnessed a surge of interest in examining mind wandering using EEG. Some markers are more robust, whereas other markers appear to be context dependent. This talk will provide a comprehensive review that synthesizes evidence from EEG studies examining electrophysiological measures of mind wandering, with a focus on the most commonly studied ERP components and spectral measures. Conclusions drawn from this work will inform future endeavours in basic science to illuminate electrophysiological mechanisms underlying mind wandering and in translational science using machine learning to predict the occurrence of this phenomenon.

Speaker: Adrien Martel
Title: Distinct electrophysiological correlates for intentional and unintentional task-unrelated thoughts
Abstract: Mind-wandering, the universal experience of having one's attention shift from current external demands to self-generated, task-unrelated thoughts, has increasingly become the focus of EEG studies

aimed at uncovering its electrophysiological underpinnings. However, most of these studies have contrasted on- with off-task activity despite the consensus that mind-wandering is multifaceted and varies along several cognitive dimensions as a function of the variable contributions and interplay of distinct neurocognitive processes. The intentionality dimension of mind-wandering, i.e., the degree to which task-unrelated thoughts occur because of an intentional reallocation of attention, has recently emerged as a key explanatory variable for trait variations in psychopathologies and differences of cortical thickness in brain regions underlying executive control. Based on these findings we investigated the EEG markers of intentional and unintentional mind-wandering states of participants (N=26) performing a SART. Our results, drawn both from statistical and machine learning approaches, identified distinct constellations of EEG markers characteristic of on-task activity, intentional and unintentional task-unrelated thoughts. We believe our findings shed new light on the key role executive control plays in the onset and maintenance of mind-wandering, and reaffirm the importance of distinguishing between types of task-unrelated thoughts in particular with regard to robust predictive modelling based on EEG.

Speaker: Aaron Kucyi
Title: Prediction of mind wandering from time-varying functional connectivity in the healthy brain and in ADHD
Abstract: The brain exhibits multiscale dynamics regardless of external context. Time-varying functional connectivity (FC), especially as observed in fMRI data, has become a popular method to characterize these dynamics. Mind wandering, or self-generated experiences that unrelated to the present sensory environment, occurs frequently in daily life and in experimental settings, yet the relevance of this pervasive cognitive activity to time-varying FC remains poorly understood. I will present our novel findings from fMRI-based predictive modeling which reveal that episodes of mind wandering can be predicted from time-varying, whole-brain FC patterns. Combining task fMRI with online experience sampling in healthy adults, we defined a connectome-wide model of inter-regional coupling—dominated by default-frontoparietal control subnetwork interactions—that predicted trial-by-trial mind wandering ratings within novel individuals. Model predictions generalized in an independent sample of attention-deficit/hyperactivity disorder (ADHD) adults who reported increased mind wandering and also exhibited relatively elevated expression of our FC marker of mind wandering. In three additional resting-state fMRI studies, including healthy and ADHD adults, we demonstrated further prediction of mind wandering defined using multiple trait-level and in-scanner measures. Our findings suggest that mind wandering is represented within a common pattern of time-varying FC across task and resting states as well as across health and psychiatric illness.

Speaker: Matthias Mittner
Title: Dynamic modeling of the wandering mind
Abstract: Previous research has shown that large-scale brain networks such as the default mode network (DMN), the executive network and the dorsal-attention network (DAN) are involved in mind-wandering (MW). In particular, both their respective activity but also their (dynamic) functional connectivity seem to be highly predictive of MW. However, current state-of-the-art methods for predicting MW based on neural data are lacking an explicit model for the temporal evolution and dynamic switches between on-task and MW states. Based on a theoretical model of mind-wandering that postulates that attentional shifts are modulated by norepinephrinergic activity, we investigate attentional switches in a combined fMRI and pupillometry study (N=27). We are using a recently established task, the finger-tapping random-sequence generation task (FTRSGT) that was recently established as a useful paradigm for measuring the recruitment of executive control with high temporal resolution in a mind-wandering context. We report the results of a custom-tailored Hidden-Markov model (HMM) that we modified to allow for including all observed non-fMRI measures (including thought-probes) into the fitting process. This model features a specific representation of the dynamic process underlying attentional switches in a MW context and can be used to

extract brain-signatures of the different attentional states. We find that our novel HMM outperforms other models, providing important insights into the dynamics of mind wandering.

Speaker: Josephine Groot
Title: Catching wandering minds with tapping fingers: Neural and behavioral insights into task-unrelated thought
Abstract: When the human mind wanders, it engages in episodes during which attention is focused on self-generated thoughts rather than on external task demands. Although the sustained attention to response task is commonly used to examine relationships between mind wandering and executive functions, limited executive resources are required for optimal task performance. In the current study, we aimed to investigate the relationship between mind wandering and executive functions more closely by employing a recently developed finger-tapping task to monitor fluctuations in attention and executive control through task performance and periodical experience sampling during concurrent fMRI and pupillometry. Our results show that mind wandering was preceded by increases in finger-tapping variability, which was correlated with activity in dorsal and ventral attention networks. The entropy of random finger-tapping sequences was related to activity in frontoparietal regions associated with executive control, demonstrating the suitability of this paradigm for studying executive functioning. The neural correlates of behavioral performance, pupillary dynamics, and self-reported attentional state diverged, indicating a dissociation between direct and indirect markers of mind wandering. Together, the investigation of these relationships at both the behavioral and neural level provided novel insights in the identification of underlying mechanisms of mind wandering.

Frontal-midline theta brain dynamics - a core mechanism for cognitive control

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Which academic does not know these situations: concentrating on difficult tasks for long hours, switching between different assignments that have to get finished, blocking out distracting thoughts so that we can finally submit this one important manuscript or conference abstract. Such challenging work environments require highly efficient cognitive control. But is there an overarching neuronal mechanism that tunes cognitive processes towards an optimal level? In this symposium we argue that this core mechanism is frontal midline theta (FMT) activity – brain oscillations around 5 Hz that are found well-pronounced over (medial) prefrontal sites. We will show that FMT activity is related to a variety of processes requiring cognitive resource allocation. We will first discuss that temporal fluctuations in mental fatigue and cognitive effort are accompanied by dynamics in FMT amplitude. Next, trial-to-trial FMT fluctuations will be associated with switch costs in a task-switching paradigm. Particularly, preparing for an upcoming task-switch elicits strong FMT amplitude. We will then address the question how coordination of memory processes is reflected by FMT activity. It will be shown that via neurofeedback training FMT can be increased, leading to enhanced memory performance. Non-invasive brain stimulation approaches will be discussed by which FMT activity and fronto-parietal theta networks can be probed and entrained to study their causal involvement in the control of working memory processes. Finally, we will address the lifespan dynamics of FMT and distributed cortical theta activity during proactive interference. We will, therefore, be able to demonstrate that FMT activity is essential in cognitive control and coordination of distributed cortical processes; and its modulation leading to clear alterations in cognitive control.

Arnau: Frontal midline theta power reflects the distribution of cognitive resources over time

The prefrontal cortex serves as a hub to coordinate executive functioning. This orchestration of brain regions is implemented via phase coupling in the theta range. FMT oscillatory activity thus reflects the exertion of cognitive control. Interestingly, FMT does not only vary as a function of task demands, but also as a function of cognitive effort. This allows for the investigation of the distribution of cognitive resources over time by means of the EEG. We conducted a study on mental fatigue and found the participants' performance and motivation ratings to decrease continuously over time. In order to specifically investigate time on task effects on FMT power in response to the stimulus, we used generalized eigendecomposition to identify a spatial filter optimized for theta-band activity. A subsequent single-trial regression on the extracted signal with time on task as predictor showed a decline of FMT reactivity over time, indicating a decline in cognitive effort. In a follow-up study, we investigate adjustments of cognitive effort on a smaller timescale. To this end, participants perform in a task-switch paradigm, in which sequences of trials associated with a high reward and sequences associated with a low reward alternate. Our findings suggest that FMT is a reliable measure to investigate the distribution of cognitive resources over time.

Cooper: Midfrontal theta dynamics predict specific cognitive control processes beyond general reaction time slowing

FMT activity is typically reported to increase with the need for cognitive control. However, most studies that show this link do so by reporting associations between theta and RT slowing – a phenomenon that, while contemporaneous with control, does not reflect the specific use of control per se. To overcome this, we assessed FMT responses associated with the switch cost in task switching – a specific index of cognitive control that does not rely exclusively on RT slowing. We made use of a large N, longitudinal design, combined with single-trial, model-based analyses to assess 1) how cognitive control demands beyond simple RT slowing were linked to FMT and 2) whether FMT effects remained stable over time. We found that FMT was modulated by switch costs, with enhanced theta power when preparing to switch vs. repeating a task. These effects were reliable after a two-year interval. Additionally, we found that trial-by-trial modulations of midfrontal theta power predicted the size of the switch cost – so that switch trials with increased theta produced smaller switch costs. Together, these findings suggest FMT supports the need for control beyond simple RT slowing and reveal that FMT effects remain relatively stable over time.

Eschmann: The Role of Frontal-midline Theta Oscillations in Memory Enhancement

FMT activity is proposed to reflect a mechanism for cognitive and memory control, which is needed for working memory maintenance, episodic memory retrieval, or interference resolution. Neurofeedback training can be used to upregulate FMT activity, thereby enhancing cognitive and memory performance. A training group, who upregulated FMT activity over the course of seven neurofeedback sessions, exhibited a larger FMT increase compared to an active control group, who trained randomly chosen frequency bands. Interestingly, the neurofeedback training group showed enhanced working memory and source memory performance 13 days after the last training session that was additionally predicted by FMT neurofeedback training increases. Transfer to memory performance one day after training and to a Stroop task was not significant, suggesting that neurofeedback training might enhance primarily proactive and barely reactive cognitive control processes. Moreover, training-induced source memory enhancement was associated with a decrease of underlying FMT activity, indicating less demands on memory control as a function of neurofeedback training. Several accounts for these findings, such as differing theta topographies in proactive and reactive control and increased protection from proactive interference after training, will be discussed. Additionally, an outlook on the role of FMT oscillations in the coordination of motivationally-driven memory enhancement will be given. Together, these findings suggest that cognitive and memory performance can be enhanced and FMT oscillations play a crucial role in the coordination of cognitive control processes and memory representations.

Biel: Probing theta activity related working memory processes using non-invasive brain stimulation

Non-invasive brain stimulation to modulate working memory (WM) processes is widely used, e.g. by targeting theta activity over medial prefrontal cortex and fronto-parietal networks. Following fronto-medial anodal tDCS, increased FMT was observed, however, without behavioural effects. Thus, we selectively targeted FMT using tACS. WM performance increased from baseline for participants receiving real stimulation but not for sham-stimulation. Targeting fronto-parietal theta networks, it was found that in-phase tACS increased whereas anti-phase tACS decreased WM performance. While this was partly replicated, our results from two experiments showed no modulation of WM performance by in-phase, anti-phase and focal in-phase tACS compared to sham-stimulation. Only in more difficult task conditions, we observed a benefit from in-phase tACS. This could be because dynamic interaction of WM control networks might entail more complex mechanisms than theta coherence, specifically the nesting of high frequency activity into slower brainwaves. Recent EEG data showed that enabling dynamic (de-)coupling of control networks, posterior gamma activity nested into different phases of prefrontal slow brainwaves depending on cognitive demand. Highlighting the causal relevance of this, right temporo-parietal TMS only impaired WM performance when we delivered TMS while FMT was at the phase to which temporo-parietal gamma activity coupled. Testing whether this mechanism is under voluntary control, we found that when the left visual hemifield was prioritized during WM maintenance, task performance was only impaired by right posterior TMS during the phase of FMT to which posterior gamma activity coupled. This suggests that fronto-parietal interaction for WM control is either facilitated or disrupted depending on task demands and priority during short, periodic time windows.

Pinal: Age-related changes in the deployment of theta activity related compensatory mechanisms for proactive interference inhibition.

In an aging world, downturns in cognitive control still characterize advancing age. Difficulties in filtering out irrelevant information may underlie such declines. For instance, no longer relevant information creates a disruptive effect on current memory processes, the so-called proactive interference (PI), which is larger in

old than young adults. Greater sensitivity to PI is accompanied by reduced activation of prefrontal cortex and lower medial frontal negativity ERP component amplitude in old than young adults. Nevertheless, the oscillatory brain activity signatures of PI resolution are yet unknown. Consequently, we had young and old adults completing two PI tasks while simultaneously recording their EEG signals. Data analyses focused on Theta frequency range activity, since it has been consistently associated with cognitive control and inhibitory functions. Results showed old adults to be slower and less accurate than their younger counterparts. However, the relative costs of PI on reaction time (RT) were greater for the younger group. Theta synchronisation was modulated by PI conditions in both groups: young adults showed higher frontal and parietal theta activity on high compared to low interference trials, while the opposite holds true for older adults in fronto-temporal regions. Interestingly, for both groups the greater the theta synchronization, the shorter the RT in that condition. Taken together, this may indicate a general difficulty in PI tasks execution for older adults, who then display compensatory mechanisms associated with theta activity at lower levels of demand than younger adults, in accordance with the Scaffolding theory of aging predictions.

Feeling and being in control: Interactions between monitoring and controlling our thoughts and actions

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Symposium Title:
Feeling and being in control: Interactions between monitoring and controlling our thoughts and actions

Symposium overview:
Humans have a remarkable capacity to shape their environment through voluntary action. This depends on continuously monitoring our thoughts and actions, assessing their consequences, and flexibly adapting to unexpected challenges. Cognitive control enables us to successfully respond to the challenges at hand. Yet, exerting cognitive control is often perceived as effortful and aversive, which might change our subjective experience of being in control (ie., our sense of agency) and our willingness to expend cognitive effort. This symposium aims to bring together disparate fields (sense of agency, metacognition, effort-based decision-making) and methodologies (behavioural, physiological, fMRI, neuropharmacological and computational modelling approaches) to improve our understanding of the interactions between how we monitor and control our thoughts and actions, and how this in turn impacts our subjective appraisal of being in control.

Eva Van den Bussche will present behavioural experiments on how our subjective experience of agency can be affected by exerting cognitive control, discussing the conditions under which greater cognitive demands can lead to an increase in sense of agency. Gethin Hughes will present contrasting findings, showing that different types of cognitive demands can lead to a reduction in sense of agency, linking these effects to physiological indices of arousal. Nura Sidarus will further examine whether there is a common metacognitive system involved in monitoring different cognitive demands, which results in a similar reduction in sense of agency. Moreover, the similarities and differences in their underlying neural networks and their impact on behavioural adaptation will be discussed. After linking cognitive control and agency to metacognitive systems, Annika Boldt will continue with a discussion of the commonalities and differences in the neural networks supporting the metacognitive monitoring of our confidence in cognitive capacities, and how metacognitive control enables using this information to strategically adapt our behaviour and environment to reduce cognitive demands. Finally, in the context of effort-based decision-making, Andrew Westbrook will describe the role of dopamine in motivational aspects of exerting cognitive effort, namely cost-benefit calculations that inform our willingness to exert cognitive effort. He will also highlight how behavioural and neuropharmacological effects can depend on interindividual variability in baseline dopamine synthesis.

Across these talks, the interaction between subjective experience (i.e., sense of agency, metacognition, willingness to expend effort) and the exertion of control is highlighted. More broadly, we will see how monitoring can in turn guide adaptive control, of both our thoughts and our actions.

Speaker 1: Eva Van den Bussche (KU Leuven, Belgium)
The effect of cognitive control on the sense of agency
Eva Van den Bussche, Maryna Reges, Yannick P. J. Murray & Gethin Hughes

While we are exerting cognitive control during a demanding cognitive task, we are also subjectively aware that we are initiating, executing and controlling our thoughts and actions (i.e., sense of agency). Previous studies have shown that cognitive control demands can be both detrimental and facilitative for the experienced sense of agency. We hypothesized that the reason for these contradictory findings might lie in the use of differential time windows in which cognitive control operates. The current study therefore examined the effect of cognitive control exerted on the current trial, on the previous trial or across a block of trials on sense of agency, using implicit (Experiment 1) and explicit (Experiment 2) measures of sense of agency. We showed that the exertion of more cognitive control on current trials led to a higher explicit sense of agency. This surprising result will be contrasted to previous studies to establish potential reasons for this surprising finding and to formulate recommendations for future studies. Specifically, we argue that the length of the action-outcome interval and the precise way in which sense of agency is probed might be crucial factors determining the effect of cognitive control exertion on sense of agency.

Speaker 2: Gethin Hughes (University of Essex, UK)
The role of physiological arousal in feelings of control.
Gethin Hughes & Peter Gooding

Previous studies have shown that we feel less in control of our actions when action selection fluency is reduced by response conflict. Given that response conflict has been previously shown to generate an arousal response, and because arousal has been found to be involved in other aspects of metacognition, we reasoned that it may also play a key role in the reduction in sense of control in these studies. In a first study, we demonstrated that increased arousal (pupil dilation and heart rate deceleration), evoked via conflict in a flanker task, was associated with a reduced sense of control. In a second study, we extended this finding to show that anticipatory bodily arousal in an intuitive reasoning task was also associated with reduced feelings of control. Overall our findings point to a key role for arousal in the feeling of control.

Speaker 3: Nura Sidarus (Royal Holloway University of London, UK)
The impact of response conflict and dysfluent processing on cognitive control and sense of agency
Nura Sidarus, Frederike Beyer, Patrick Haggard & Valérian Chambon

Voluntary action is typically associated with a sense of agency, the experience of being in control of our actions and their consequences. Experiencing conflict during action selection has been shown to reduce our sense of agency, highlighting a role for metacognitive monitoring of action. Yet, it remains unclear whether there is a common metacognitive system involved in monitoring different types of disruptions of action selection, which might similarly influence the sense of agency. Therefore, we compared the impact of disrupting action selection through response conflict (incongruent flankers) and dysfluent visual processing (masked stimuli). Although the two disruptions require differential cognitive control recruitment, they were matched in their cost on action selection. Both manipulations also resulted in a similar reduction in agency ratings, suggesting some common monitoring of difficulty during action selection. In a second study, we replicated these behavioural effects, while also collecting fMRI data. I will discuss commonalities and differences in the neural networks involved in monitoring both disruptions, and implications for proactive cognitive control.

Speaker 4: Annika Boldt (University College London, UK)
Distinct and overlapping neural correlates of metacognitive monitoring and metacognitive control
Annika Boldt & Sam Gilbert

Metacognition is the act of reflecting on one's own mental states, often for the purpose of cognitive control. Previous research has shown that people can accurately report their confidence in their decisions and memories. Research has also investigated how these metacognitive signals are generated and which brain networks encode them. However, we are only just beginning to understand how metacognitive knowledge gets selected to optimise behaviour (metacognitive control). I will present data from a study in which I investigate how metacognition can guide people's decisions to cognitively offload, that is using external aids to reduce the demands of a task. In this context, I then show that metacognitive monitoring and metacognitive control share overlapping brain patterns using a multivariate analysis approach.

Speaker 5: Andrew Westbrook (Brown University, US)
Dopamine Promotes Cognitive Effort by Biasing the Benefits versus Costs of Cognitive Work
Westbrook, A., van den Bosch, R., Määttä, J.I., Hofmans, L., Papadopetraki, D., Frank, M.J.*, Cools, R.*

Stimulants like methylphenidate are increasingly used for cognitive enhancement, but precise mechanisms are unknown. We found that methylphenidate boosts willingness to expend cognitive effort by altering the benefit-to-cost ratio of cognitive work. Willingness to expend effort was greater for participants with higher striatal dopamine synthesis capacity, while methylphenidate and sulpiride – a selective D2 receptor antagonist – increased cognitive motivation more for participants with lower synthesis capacity. A sequential sampling model informed by momentary gaze revealed that decisions to expend effort are related to amplification of benefit-versus-cost information attended early in the decision process, while the effect of benefits is strengthened with higher synthesis capacity and by methylphenidate. These findings demonstrate that methylphenidate boosts the perceived benefits-versus-costs of cognitive effort by modulating striatal dopamine signaling with implications for promoting cognitive control.

The predictive brain: How expectations influence perception, attention and action

Dr. Peter Kok[1], Dr. Heleen Slagter[2], Dr. Uta Noppeney[3], Dr. Máté Lengyel[4]
[1]University College London, [2]Vrije Universiteit Amsterdam, [3]Donders Institute for Brain, Cognition and Behaviour, [4]Cambridge University, Engineering Department

Cognitive neuroscience is currently witnessing a paradigm shift: from the traditional view of the brain as an organ that processes information, to a view of the brain that continuously creates its own reality from within, a reality that is modeled based on past experience and continuously aligned with the outside world through perceptual and active inference. In this perspective, the brain continuously generates top-down predictions about incoming sensory input that are updated when precise prediction errors occur. Yet, how predictions are neurally implemented and modulate sensory processing and action, and how this may depend on the relevance of the sensory information, remains unclear. This symposium will address this outstanding question using a convergence of methods, combining psychophysical tests with high temporal (EEG) and spatial (fMRI) resolution neuroimaging, as well as computational modelling. It specifically highlights recent work showing that top-down predictions and prior knowledge are pervasive to many aspects of cognition, and can optimise perception and guide our attention and actions. First, Kok will discuss findings from ultra-high field fMRI that reveal the neural circuitry underlying effects of expectation on sensory processing, and that identify the hippocampus as a potential generator of these effects. Next, Slagter will present findings from recent EEG studies on how (contextual) expectations about target or distractor information modulate their sensory processing and representation using ERPs, multivariate decoding analyses, and inverted encoding models. This work suggests that expectations about goal-relevant and distracting information are implemented via different neural mechanisms. Then, Noppeney will discuss predictive processing and attention in multisensory contexts based on recent behavioural and neuroimaging work. This work collectively reveals how the brain integrates signals weighted by their relative precisions from common causes and segregates those from different causes. Finally, Lengyel will address the outstanding question how the brain represents and computes with uncertainty. In summary, this symposium will highlight recent research on the neural, cognitive and computational mechanisms underlying predictive processing in (multisensory) perception, attention and action.

TALK 1
The neural circuit underlying perceptual expectations
Peter Kok, University College London
The way we perceive the world is strongly influenced by our expectations about what we are likely to see at any given moment. However, the neural mechanisms by which the brain achieves this remarkable feat have yet to be established. In order to understand the neural mechanisms underlying the interplay between sensory inputs and prior expectations, we need to investigate the way these signals flow through the cortical layers. Until recently, it was not possible to do this in non-invasive studies of humans, because the typical voxel size in fMRI is bigger than the full thickness of the cortex (2-2.5mm). I will discuss recent work in which we met this challenge by using fMRI at ultra-high field (7T) to obtain BOLD signals at very high resolution, and using a novel spatial regression analysis to disambiguate signals from the different cortical layers. This approach has allowed us to reveal the neural circuitry underlying effects of expectation on sensory processing. I will also discuss the role of the hippocampus as a potential generator of top-down expectation effects in visual cortex. Together, this work demonstrates that expectations play a fundamental role in sensory processing, and ultimately in the way we perceive the world.

TALK 2
Learning to ignore: Expectation-dependent distractor suppression

Heleen Slagter, Vrije Universiteit Amsterdam
Much insight has been gained into how selective attention may filter information processing at the neural level, by directly boosting relevant information (target facilitation), and/or by suppressing irrelevant information (distractor inhibition). Yet, there is still debate as to whether target facilitation and distractor inhibition are simply two sides of the same coin or whether they are controlled by distinct neural mechanisms. Recent work indicates that distractor suppression only emerges when information about the distractor can be derived directly from experience, suggesting that suppression of distracting information is in particular expectation dependent. This raises the question as to how attention and expectation interact to bias information processing. I will discuss recent findings from behavioral and EEG studies that examined how expectations about upcoming target or distractor locations and/or features influence facilitatory and inhibitory effects of attention on visual information processing and representation using ERPs, multivariate decoding analyses, and inverted encoding models. Collectively, these confirm an important role for alpha oscillatory activity in town-down biasing of attention to, and sharpening of representations of target locations. Yet, they also show that target facilitation and distractor suppression are differentially influenced by expectations, and rely at least in part on different neural mechanisms, with expectation-dependent distractor suppression selectively occurring after stimulus presentation.

TALK 3
The predictive brain in a multisensory world
Uta Noppeney, Donders Institute for Brain, Cognition and Behaviour, Nijmegen, NL
In busy traffic, our senses are inundated with myriads of signals: motor noise, flashing lights, the smell of fumes and the sight of other pedestrians. To make sense of this cacophony the brain should integrate signals weighted by their relative precisions from common causes and segregate those from different causes. Priors that evolve across multiple timescales inform the interpretation of this sensory chaos. They can pertain to environmental properties (e.g. object's location), the world's causal structure (i.e. common or separate sources) or, as hyperpriors, to the precisions of the sensory signals. In this talk, I will discuss recent behavioural and neuroimaging research that shows how the brain dynamically adapts these different sorts of priors to a changing multisensory world.

TALK 4
Predictions with error bars in the brain — probabilistic neural computations in perception, action, and navigation
Máté Lengyel, Cambridge University, Engineering Department, Cambridge, UK
Being able to make predictions is important for the brain. In this talk, I will present behavioural and neural evidence that the brain achieves more than this: it even places error bars (or ellipsoids in the multivariate case) on these predictions, i.e. that it represents and computes with uncertainty. We used a combination of Bayesian inference-based theory and novel data analysis techniques to reveal how particular, behaviourally relevant forms of uncertainty account for a broad range of puzzling observations in a number of different cognitive domains. In visual perception, we show how aspects of neural responses in the primary visual cortex often regarded as epiphenomenal at best, or nuisance at worst (noise variability, oscillations, and transients), all emerge as a consequence of the efficient implementation of the same computational function — a fast sampling-based representation of uncertainty about elementary visual features. In motor learning, we develop a normative theory for how uncertainty about the ever-changing context of our movements (e.g. the object we are handling) should affect the creation, updating and expression of memories. We show that this theory accounts for key features of motor learning that had no unified explanation (e.g. spontaneous recovery, savings, anterograde interference), as well as novel phenomena (e.g. evoked recovery) which we confirmed experimentally. Finally, in navigation, we show how uncertainty about location in deformed environments unifies a diverse set of findings about idiosyncratic patterns of human homing behaviour as well as the distortions of tuning curves in rodent entorhinal grid cells.

Age differences in episodic memory: Lessons from neural pattern analyses

Dr Joshua Koen[1], Dr Christine Bastin[2], Dr Alexa Morcom[3]
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Age-related memory decline is a longstanding finding in cognitive aging research. While earlier research mostly used univariate analysis when focusing on age differences in memory processes, researchers have recently started to apply multivariate neural pattern analysis to understand how memory performance depends on the informational content of neural activity. Currently, evidence is accumulating that aging affects the quality of information representation in the brain ("neural dedifferentiation"). However, it remains to be clarified which level of information representation is impaired/altered in old age, and how neural dedifferentiation relates to declining cognitive abilities in older adults. The first talk in this symposium by Dr Koen will address these questions and reveal how different measures of distinctiveness at the category level and item level relate to interindividual and intraindividual differences in memory performance. Dr Bastin will show that age-related reductions in regional specificity of neural activation are also evident when the similarity of neural representations is examined across, rather than within, participants. Dr Morcom will present data using a Bayesian multivariate and multiregion analysis to investigate whether brain networks become less efficient with age. She will provide evidence for reduced levels of information in older people's prefrontal cortex despite elevated average activation in long- and short-term memory tasks. In sum, the talks in this symposium will paint a rich and coherent picture of age-related differences in information representation from item to category level, and from single brain regions to memory networks, and highlight the utility of neural pattern analysis for understanding age differences in episodic memory.

Talk 1: The relationship between category-level and item-level pattern similarity to episodic memory in young and older adults (J. Koen)

Many cognitive abilities, most notably episodic memory, decline in the course of healthy aging. Age-related neural dedifferentiation – reductions in the regional specificity and precision of neural representations – is proposed compromise the ability of older adults to form distinct neural representations that are sufficient to support episodic memory encoding. To evaluate this hypothesis, we examined trial-level neural responses elicited by scene and object images in the parahippocampal place area (PPA) and lateral occipital cortex (LOC). Category-level neural differentiation was quantified for broad image categories using a within participant pattern similarity analysis approach. Item-level differentiation was measured over both the PPA and LOC using a novel across-participant pattern similarity measure. Age differences in category-level neural dedifferentiation were more prominent in the PPA in comparison to the LOC. Importantly, the category-level differentiation in the PPA showed a positive, age-invariant relationship with subsequent memory performance. The item-level pattern similarity measure was reduced in older relative to younger adults. Moreover, the item level similarity measure showed robust subsequent memory effects in younger adults, but not in older adults. These results suggest that age-related neural dedifferentiation is present at the level of both categories and individual stimuli, and that these two differentiation measures are associated with different sources of variance in episodic memory (inter- versus intraindividual, respectively). Together, these data provide support for the idea that dedifferentiated neural representations contribute to age differences in episodic memory.

Talk 2: Age-related differences in across-participants similarity of neural representations in episodic memory (C. Bastin)

With increasing age, the ability to encode and retrieve specific details from past events decreases, with a concomitant reduction in the specificity of the associated neural representations. Recent advances in multivariate neuroimaging analyses have made possible the examination of the similarity of the neural patterns of activations measured across participants, but it has not been investigated yet whether such across-participants neural similarity is age-sensitive. Here, using fMRI, we examined across-participants similarity of neural patterns of activations measured during memory encoding and retrieval in young and older adults. During a scanned study phase, young and older participants viewed scene pictures associated with labels. At test, in the scanner, participants were presented with the labels and were asked to recollect the associated picture. To examine across-participants neural similarity, we used Pattern Similarity Analyses by which we compared patterns of neural activation during the encoding or the remembering of each picture of one participant with the averaged pattern of activation of the same trial across the remaining participants. Results revealed that across-participants neural similarity was significantly higher in young than in older adults in the occipital gyrus, the cuneus and the lingual gyrus during memory encoding. Moreover, patterns of brain activation associated with memory retrieval were more similar across young than older participants in distributed parietal (angular gyrus and precuneus) and occipital (cuneus and lingual gyrus) regions. Considered together, these findings extend prior evidence by demonstrating that an age-related reduction in regional specificity of neural activation is also evident when the similarity of neural representations is examined across, rather than within, participants.

Talk 3: Multivariate Bayesian tests of large-scale functional shifts in ageing (A. Morcom)

Theories of neurocognitive ageing have proposed that large-scale compensatory shifts in functional brain organisation contribute to maintenance of task performance. Functional imaging studies often show striking and apparently qualitative age-related differences in activity, with older people recruiting additional regions or showing elevated activity relative to young people. An alternative view is that brain activity becomes less specific or less efficient as a direct result of deleterious neural changes. It is difficult to distinguish these accounts using univariate activation measures within regions. Multivariate and multiregion analysis can provide direct tests of whether additional activity carries more information. In two studies, Multivariate Bayesian analysis of functional magnetic resonance imaging data from adult lifespan samples showed reduced information in older people despite elevated average activation in prefrontal cortex in memory tasks, and in contralateral motor cortex in motor tasks. This model-based approach also allows assessment of unique information that regions contribute to tasks, over and above other regions. In both studies, the regions showing elevated activity contributed unique information to the tasks across the lifespan. However, this contribution did not increase with age, arguing against compensatory increases in prefrontal processing (posterior-to-anterior shift) and contralateral motor processing (asymmetry reduction) that help to maintain performance.

Interactions between sensory representations as well as cognitive control in working memory

Corinna Haenschel[1], Prof Brad Postle[2], Prof Tina Forster[1], Dr Aytaç Karabay[3], Prof Elkan G. Akyürek[3]
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Working memory (WM) is the ability to encode, retain and manipulate information for a brief period. WM is a fundamental cognitive function and is widely researched across many fields of neuroscience. Visual WM consists of a distributed network including the occipital pole during visual perception, parietal and temporal regions for higher order visual processing and storage and prefrontal cortical regions for top-down guidance. Even though there has been significant progress in the understanding of the interactions between these processes contributing to WM, how these different operations are implemented and coordinated are not yet fully understood.
In this symposium, four speakers will discuss several recent EEG and fMRI studies with the first two talks emphasizing neural systems that support visual WM, whereas the last two talks emphasize principles of neural coding that support visual WM.
Haenschel will present ERP studies that indicate a close link between visual WM and visual perception and that a decoupling of these links may be evident in schizophrenia. Forster will present a study to show that visual WM is not "just" visual, because stimuli (i.e. body images) that afford representation with other sensory modalities (i.e. somatosensory) can also engage them. Karabay & Akyürek will then present data that show that in some conditions, retention in WM relies on patterns of functional connectivity, suggesting that sustained elevated activity is not always necessary. Finally, Postle will talk about priority-based remapping. His studies show that when an item needs to be retained in WM in a manner that will NOT interfere with current behavior, it undergoes a transformation of its representational geometry, such that the representation is "inside-out" when unprioritized, and then reverses itself when prioritized.

Title: Low-level visual signals facilitate perception-working memory interactions in typical participants, but not in schizophrenia
Corinna Haenschel
Working Memory (WM) deficits are a core feature of schizophrenia and may underlie many of the patient's day-to-day difficulties. Research has shown a relationship between neural measures of visual stimulus encoding and WM performance in schizophrenia. It remains unclear how the neural mechanisms of low-level visual processing contribute to the initial formation of WM representations in the typical population and to the abnormalities found in schizophrenia. Here we combined visual psychophysics and EEG to investigate the influence of low-level stimulus properties on visual WM performance and early visual ERP responses in two delayed discrimination tasks in both typical participants and people with schizophrenia. We used a delayed shape recognition task to probe how WM differ for stimuli that bias processing towards different visual pathways. To account for saliency differences between the different stimulus classes, we measured contrast thresholds individually for each participant. Patients with schizophrenia compared to controls showed increased thresholds and greater variability in functional contrast sensitivity. Luminance-defined shapes resulted in higher WM accuracy and faster reaction times. Early visual ERPs (P1 and N1) responded preferentially to luminance and chromatic stimuli, respectively. This was not the case in the patient group as both the visual performance and ERPs were reduced. However, group differences in task performance disappeared in the sample that used individually established contrast thresholds. This study confirms the link between deficits in the early encoding phase and WM performance. Such impairments can have an impact on everyday life of people with schizophrenia.

Title: Recruitment of somatosensory cortex during active maintenance of body images in working memory
Bettina Forster
Social interactions are supported by our perception of others' gestures and facial expressions and may require the maintenance of such multifaceted information over time. While working memory processes (WM) have been shown to be associated with persistent activity in the sensory cortex processing the information (e.g., visual stimuli activate visual cortex), we argue that more multifaceted stimuli (e.g. hand images) moderate this sensory-locked activity and recruit distinctive cortices. Specifically, perception of bodies recruits somatosensory cortex (SCx) beyond early visual areas (suggesting embodiment processes). Using visual and somatosensory evoked-potentials in a visual WM task, we isolated different levels of visual and somatosensory involvement during encoding of body and non-body-related images. Persistent activity increased in SCx only when maintaining body images in WM, whereas visual/posterior regions' activity increased significantly when maintaining non-body images. Our results bridge WM and embodiment frameworks, supporting a dynamic WM process where the nature of the information summons specific processing resources.

Title: A visual impulse reveals memoranda embedded in functional connectivity: Evidence for activity-silent WM states
Aytaç Karabay & Elkan G. Akyürek
A task-irrelevant, high-contrast stimulus can be used as a visual impulse signal to implement a functional non-invasive perturbation method that reveals working memory (WM) content. Stokes (2015) suggested that the impulse acts like a sonar signal used in echolocation, from which structural information (e.g., the surface of the ocean floor) can be derived. Similarly, in the brain the visual impulse reveals memoranda embedded in functional connectivity, which might by themselves be activity-silent. However, Barbosa et al. (2021) suggested that the impulse might only decrease non-WM-related EEG noise, thereby improving the ability to decode already-active memoranda. In this study, we sought to arbitrate between these two possibilities. We matched a task-irrelevant feature (spatial frequency) of a visual impulse with memory items (orientation gratings), while equalizing intensity and contrast. Better decoding of WM content in the match condition than in the no-match condition would suggest that the impulse interacts with the actual content within WM network, in line with activity-silent accounts. Conversely, if no differences between conditions are observed, this would fit with a noise reduction account, and suggest that WM might rely primarily on active storage. Results showed an advantage for matching impulses, supporting the former hypothesis that visual impulses work as a neural sonar. Further, although the visual impulse decreased average EEG variance, there was no difference between match and no-match conditions. We conclude that visual impulse perturbation reveals memoranda embedded in functional connectivity, in line with the idea that WM might rely on activity-silent states.

Title: Interpreting delay-period signals in visual working memory
Bradley R. Postle
Although it's clear that stimulus representations in working memory are supported by sensory cortex, to what extent are they "sensory"? To address the representational bases of visual working memory, this talk will consider two phenomena: the sensitivity of neural representations to priority; and the evidence for stimulus-level decoding in regions associated with the Dorsal Attention Network (i.e., intraparietal sulcus [IPS] and frontal eye field [FEF]). One classic operationalization of priority is the 2-back task, in which item n transitions in status from memory probe to unprioritized memory item (UMI) to prioritized memory item (PMI), before being dropped. Analyses of EEG data from the 2-back task, informed by recurrent neural network simulations, suggest that although the IMI is held in the same perceptual code into which it was encoded as a PMI, it is nonetheless transformed into a "decision-null" format that may minimize the likelihood that it will interfere with decisions about the current PMI. Studies with fMRI provide evidence for

simultaneous representation in multiple codes, as well as differences in delay-period activity between IPS and occipital cortex: IPS tracks stimulus context more closely than stimulus content; activity in IPS, but not occipital cortex, scales with context binding requirements; from a dynamical systems perspective, occipital cortex implements the drift of delay-period representations into attractor basins, whereas activity in IPS tracks the stimulus-nonspecific factor of diffusion. In general terms, these findings are consistent with a conceptualization of frontoparietal circuits as a source of the control of visual representations whose site is occipitotemporal.

Neural underpinnings of episodic memory: a focus on the formation and retrieval of contextual memories

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Contextual information seems to serve a special role in memory formation and retrieval. By providing spatial and temporal boundaries to events unfolding throughout a day, context shapes episodes by organizing experiences. By means of specification of defining features of the setting within which an episode occurs, context helps us to generalize across similar events in order to build knowledge about the world. At the same time, context has discriminatory power, by providing mnemonic details that help to distinguish between events and promote memory specificity.
While different lines of research have recently made exciting advances, integrated knowledge of the different facets involved in the formation and retrieval of episodically detailed memories would benefit the current state of the field. In this symposium, we are bringing together recent work providing novel insights on the implications of context reinstatement on memory retrieval and the neural underpinnings of the reactivation of mnemonic content, including contextual information, at the time of retrieval. In addition, these aspects will be integrated with research emphasizing the direction of attentional processes towards the associative link between an item and its context. Finally, age-comparative research will provide insights into the mechanisms underlying successful item–context binding.
While integrating these different lines of research, the contributors will highlight theoretical problems, current trends, and open questions towards a detailed understanding of processes involved in the shaping of episodic memories.

Electrophysiological signatures of human memory reactivation
The capacity to remember past events with rich contextual details and conscious access characterizes human episodic memory and enables us to mentally travel to the past. The reactivation of neural activity that was present during the encoding of an event is assumed to be essential for such episodic remembering. Focusing on human electrophysiology, we used pattern similarity analyses to characterize content-specific memory signatures associated with memory reactivation and reveal the effects of context reinstatement on memory retrieval. Besides its role for awake retrieval, memory reactivation is assumed to mediate the beneficial effects of sleep on memory performance. To elucidate the neural mechanisms carrying reactivation-related mnemonic information during both physiological states, we investigated whether electrophysiological memory signatures of awake memory reactivation reoccur during subsequent sleep. We show that oscillatory activity orchestrates the reactivation of memories during both wakefulness and sleep.

Electrophysiological signatures revealing the temporal dynamics of episodic retrieval
Episodic memory enables mental time travel, allowing us to relive specific, personally experienced events tied in time and place. This feat of human memory is considered to be dependent on the reinstatement of the cortical patterns that were active at the time of encoding. A growing body of recent literature has provided support for this idea by showing that retrieval success co-varies with the neural encoding patterns being reinstated at the time of retrieval. In this presentation, we will discuss findings from multivariate pattern analysis of electrophysiological data revealing the temporal dynamics of such reinstatement during retrieval and its consequences for episodic remembering. First, we will discuss both benefits and costs of cortical pattern reinstatement. Accumulating evidence has shown that memory typically benefits when the

neural patterns established during encoding are reinstated during retrieval. However, our data show that reinstatement can also have detrimental effects on later episodic remembering depending on which aspects of the event are called-for. Next, we will show that contextual background features of an encoding episode are reinstated during selective retrieval even when such information is task-irrelevant. These data elucidate that context reinstatement tracks retrieval competition between similar episodes and interference resolution. Combined, our data elucidate the temporal dynamics of episodic remembering and shed new light on encoding and retrieval interactions in episodic memory.

Brain oscillatory correlates of attention allocation to item and its context

The ability to remember the temporal relationship between an item and its context is essential for forming new episodic memories. In addition, such encoding is often initiated voluntarily and kept under conscious control to make sure that certain episodes are remembered. Here we present an episodic long-term memory (LTM) EEG experiment where we examined brain oscillatory activity associated with attention allocation towards the temporal link between an item and its context. Participants saw a background picture and a word in a central position on a computer screen and were instructed to memorise (a) the picture only, (b) the word only, (c) both individually (i.e. ignoring their co-occurrence) and (d) both as in (c) but also specifically that they were presented together.

We show that voluntary attention allocation towards memorizing the temporal contiguity between an item and its context (i.e. towards LTM encoding) is associated with upper alpha desynchronization in predominantly left posterior brain regions at a rather late stage of the 3s encoding time. This decreased alpha activity is likely an indicator of additional visual processes employed for consciously directed mnemonic processes and not so much item-context binding per se. In addition, we also found that picture encoding is associated with decreased power not in the alpha, but in the beta band over bilateral posterior brain areas.

In sum, these results suggest a complex role of cortical alpha oscillatory activity in memory encoding and attention allocation that goes beyond a simple inhibitory function.

Theta–gamma coupling support contextual binding in younger and older adults

Episodic memory is dependent on the integration of item and contextual information during encoding. In older age, memory is particularly impaired when items need to be associated with their contexts. Theories of neural communication posits that the precise coupling of gamma power to the phase of the theta rhythm supports item–context binding during memory formation. We investigated whether age differences in memory for items and their associated contexts are related to altered theta–gamma coupling in older age. We show that the coupling of gamma power to a specific phase of the theta rhythm supports successful formation of item–context associations in both age groups. Whereas subsequent successful memory for the item and its associated context was accompanied by coupling closer to the peak of the theta rhythm, item memory without the successful recovery of the associated context was characterized by a deviation in phase angle relative to pair memory. Additionally, a stable relationship between coupling phase angle and pair memory performance demonstrated that coupling to a specific theta phase is beneficial for the subsequent recovery of a bound memory trace. Crucially, older adults' reduced memory for item–context associations were accompanied by a shift in coupling phase relative to younger adults. Together, these findings highlight the necessity of precisely timed neural communication for the binding of items to their contexts during memory formation.

Midline structures in explicit memory: Is there a hippocampus-independent route to cortical engrams?

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The brain's midline structures, particularly the medial prefrontal cortex (mPFC), the posterior cingulate cortex (PCC), and the adjacent precuneus are best known for their relatively increased activation during conditions of relative rest and have therefore been termed the Default Mode Network (DMN). The DMN is commonly engaged during tasks like self-reference, Theory of Mind (ToM) and other social cognitive tasks. In a thus far largely independent line of research, it has become evident that certain structures of the DMN, especially midline structures, seem to be involved in a special type of long-term memory (LTM) formation that is hippocampus-independent. During this symposium, we will propose a role for DMN structures in the mnemonic representation of complex associative information. In a series of four talks, we will present converging evidence from research on prior knowledge-related and schema-dependent learning showing that the mPFC and posterior medial cortex (PMC) may be differentially involved in establishing schemas and incorporating novel information into prior semantic associations. In an outlook, we will discuss the implications of the proposed midline memory network for memory function in the elderly.
Svenja Brodt (University of Tübingen, Germany) will present data on "Engrams in the posterior medial cortex - conditions for rapid neocortical memory formation". Systems memory consolidation is generally considered to be a slow process of neuronal reorganization between brain systems. Fresh memories rely mostly on the hippocampus, which during retrieval reinstates the cortical ensembles that were active during encoding, whereas a stable neocortical memory trace develops only slowly (Frankland and Bontempi, 2005). Recent findings suggest that the PMC can acquire an online memory representation rapidly during learning (Brodt et al., 2016). Rapid microstructural plasticity in the PMC, assessed via whole-brain diffusion-weighted MRI (Sagi et al., 2012), confirms that these early contributions do not merely reflect a hippocampus-driven reinstatement of previous activity but rather a genuine neocortically stored engram (Brodt et al., 2018). Functional and microstructural changes in the PMC with repeated rehearsal and sleep suggest that the amount of reactivation, rather than time alone is the critical factor determining the speed of neocortical memory formation (Himmer et al., 2019).

Björn H. Schott (Leibniz Institute of Neurobiology, Magdeburg, Department of Psychiatry and Psychotherapy, University Medicine Göttingen, and German Center for Neurodegenerative Diseases, Göttingen, Germany) will make us reconsider the well-known role of the DMN in social and self-referential cognition from a memory perspective in his talk "Information integration in the brain's midline - an underappreciated memory network?". Following a brief review of the established role of the DMN in episodic retrieval and autobiographical memory, converging evidence will be presented for the engagement of certain DMN structures like the mPFC and the precuneus during both the encoding of personally relevant content (Schott et al., 2013) and the gradual acquisition complex spatial memory traces (Schott et al., 2018). Furthermore, mechanisms of information flow into the DMN will be discussed, based on Dynamic Causal Modeling (DCM) investigations (Soch et al., 2016). Finally, this talk will also tackle the observation that the elderly commonly show increased recruitment of DMN structures during episodic encoding.

Jasmin M. Kizilirmak (German Center for Neurodegenerative Diseases, Göttingen, Germany) will conclude the symposium with cumulating evidence on "Learning from insight: A hippocampus-independent form of long-term memory encoding - implications for memory in old age". In her talk, Kizilirmak will present converging evidence on a special type of learning that seems to facilitate LTM formation via prior knowledge-related and intrinsic reward-related processing. In fMRI studies employing a task using verbal riddles, the Compound Remote Associate (CRA) Task, Kizilirmak and colleagues could repeatedly show that a special kind of learning is hippocampus-independent, i.e., when a novel semantic association is suddenly comprehended in an insight-like manner (Kizilirmak et al., 2016, 2019). Encoding seems to rely more on midline structures such as the mPFC and precuneus. Importantly, the network they found involved in learning from insight highly overlaps with the DMN, which is more commonly used by the elderly for successful episodic encoding, even though in younger adults it is normally associated with later forgetting. The talk will conclude with first evidence from behavioral and fMRI studies, comparing learning from insight in young (18-35 yrs) and old adults (60-85 yrs). Preliminary results suggest older adults benefit more from sudden comprehension with respect to the correct recognition of old items, suggesting that facilitated encoding via sudden comprehension might provide a putative compensatory mechanism for age-related decline in MTL-dependent episodic memory.

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The effects of novelty on long-term memory

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Summary
Novelty can have beneficial effects on long-term memory (LTM) in both animal and human populations. The human and animal studies have differing research traditions, answering different research questions. This symposium aims to bring together the two fields. Recent animal work has provided exciting new insight into the underlying mechanisms by which novelty can promote memory: Hippocampal dopamine underlying novelty-associated memory enhancements can have two sources, coming from either the ventral tegmental area or locus coeruleus, depending on the type of novelty (Presentation 1; Dr. Tomonori Takeuchi). Studies in humans provide the opportunity to investigate new research questions: The role of volition, expectations and the novelty seeking trait on the effects of novelty on memory in virtual reality paradigms will be discussed in Presentation 2 (Dr. J. Schomaker). Interestingly, enhanced effects of exploring novel environments were found in children with ADHD, but not in typically developing children. Potential causes for these findings will be discussed in Presentation 3 (Prof. Dr. Kerstin Krauel). Despite age-related memory decline, anticipation of novelty versus familiarity recruits the same medial temporal lobe regions, is associated with neural beta oscillations, and drives recognition memory in elderly as well as in young adults (Presentation 4; Prof. Dr. Nico Bunzeck). Similarly, patients with mild cognitive impairment benefitted from novelty, just as healthy elderly (Presentation 5: Prof. Dr. Christine Bastin). Taken together, the work covered in Presentations 4 and 5 suggests that (anticipation of) novelty can promote memory processes, regardless of age- or disease-related memory deficits. Presentation 3 suggests that beneficial effects of novelty on memory may even be more pronounced in children with ADHD. As such, we offer a translational view on the effects of novelty on LTM with potential applications in health and disease.

Presentation 1: Dopamine, initial memory consolidation and two distinct novelty systems in rodents

Many people have vivid memories of the first dinner date with their partner, including details like the name of the restaurant and the food they had. In contrast, it is very difficult to remember what you had for dinner a few weeks ago. Most everyday memories may be formed automatically in the hippocampus. The key role of this memory system is to filter out unnecessary information, but keep the important memories by a mechanism that involves novelty-associated dopamine release in the hippocampus.

Recently, our studies (Takeuchi et al., Nature, 2016) revealed that projections from neurons in the locus coeruleus to the hippocampus can drive novelty-associated enhancement of memory retention through non-canonical release of dopamine in the hippocampus, in line with the synaptic tagging and capture theory of initial memory consolidation. These studies also raise a possibility that the impact of distinct novel experiences which, by their very nature, bear minimal relationship to past experiences ('distinct novelty') may differ from novel experiences that share some commonality with past experiences ('common novelty') (Yamasaki and Takeuchi, 2017; Duszkiewicz et al., 2019). We now propose that memory of events accompanied by novelty can be selectively retained through two distinct dopaminergic mechanisms, depending on the nature of the novel experience itself.

Presentation 2: Factors influencing the effects of novelty on long-term memory across the lifespan

When visiting a new place learning about where to expect danger and where to find rewards is crucial for survival. Animal studies have reliably shown that exploring a new environment enhances plasticity in the brain, specifically in the hippocampus, to promote such learning. One study using virtual reality investigated the effects of spatial novelty on learning in humans, showing that learning is enhanced after exploration of novel versus familiar environments in humans too. The specific aspects of exploring a novel environment that underlie such memory benefits, however, are not yet well understood. Exploring a new environment also taxes decision-making processes more than exploring a familiar one: In a new environment active navigational choice are made, whereas navigating through a familiar environment relies strongly on habits. In the first study, the role of volition was investigated by having participants either actively explore or be passively exposed to novel and familiar virtual environments. Findings suggested that active exploration may be required to induce beneficial effects of novelty. In the second study the level of processing of the to-be-learned material was experimentally manipulated. Irrespective of encoding depth exposure to a novel environment was shown to improve memory, with effects peaking in adolescents and younger adults, and no beneficial effects in older adults. These findings are in line with the rise and fall of the dopaminergic system.

Presentation 3: Novelty via beta oscillations and medial temporal lobe activity

Learning new declarative information is modulated by expectations (i.e., anticipation) and prediction errors (i.e., outcome) but the underlying mechanisms and possible changes across the life span remain unclear. To further investigate this issue, we used electroencephalography (EEG, study 1) and functional magnetic resonance imaging (fMRI, study 2) in combination with a modified version of a previously established paradigm in healthy young and older humans. Here, subjects viewed symbolic cues that predicted either novel or familiar scene images with 75% validity (encoding) and recognition memory was tested 24 h later. Behaviorally, (a) older subjects showed worse overall memory performance, (b) predicted novel images were subsequently better recognized than unpredicted novel images, and (c) this effect was not significantly modulated by age. At the neural level, no specific effects of novelty anticipation on subsequent memory formation could be observed in both studies. However, subsequent memory effects for expected novel images were associated with increases in beta power (13-25 Hz) and MTL activity during novelty processing at outcome. Together, despite age-related memory impairments, expected novelty appears to drive recognition memory across the life span via medial temporal lobe activity and neural beta oscillations.

Presentation 4: Novelty-related memory effect in amnestic Mild Cognitive Impairment

The detection and processing of novelty plays a critical role in memory function. Yet, relatively little is known about how novelty influences learning in memory-impaired populations, such as Alzheimer’s disease and its early stage, amnestic Mild Cognitive Impairment (MCI). In the current study, 20 patients with amnestic MCI and 20 age- and education-matched healthy older individuals performed a task using the Von Restorff paradigm. Participants studied 22 lists of 10 words. Among those lists, 18 contained an isolate word, which differed from the others in terms of font size. The isolate word could take one of 3 different font sizes, whereas other non-isolate words were shown in 60-point font size. Four control lists contained no isolate word. After studying each list, participants had to freely recall as many words as possible. When the isolate words were presented in larger font sizes, both amnestic MCI patients and healthy older adults recalled them more often than other words. Novelty-related memory benefit was computed as the difference between recall score for the isolate words and recall score for the other words. The findings suggested that amnesic MCI patients benefited from novelty similarly as healthy older adults. The preservation of the boosting effect of isolation-related novelty on subsequent recall despite impaired episodic memory in the patients is interesting to consider at the light of divergent theoretical viewpoints relative to the relationship between novelty and memory, as either parts of the same continuum or independent functions.

New Insights into the Contributions of Multiple Memory Systems to Learning

Professor Carol Seger[1,2], Research Associate G. Elliott Wimmer[3,4], Postdoctoral Scholar Lisa M. Wirz[5,6], Associate Professor Tyler H. Davis[7]
[1]Department of Psychology, Colorado State University, [2]School of Psychology, South China Normal University, [3] Max Planck UCL Centre for Computational Psychiatry and Ageing, [4]Wellcome Centre for Human NeuroImaging, University College London, [5]Cognitive and Affective Neuroscience laboratory, Donders Centre for Cognitive Neuroimaging, [6]Cognitive Psychology laboratory, Hamburg University , [7]Department of Psychological Sciences, Texas Tech University

Classic theories of learning postulated that learning depends on independent subcortical memory systems including the striatum and hippocampus that compete during acquisition and performance. Modern research has revealed a greater breadth of neural systems involved in learning and memory, and greater variety of interactions between these neural systems. This symposium will introduce attendees to some of the most interesting recent research in memory system contributions to learning. Carol Seger will begin the symposium with an historical introduction to multiple memory systems and an overview of modern approaches to identifying memory systems and their interactions. Then three leading researchers in the area will present new research. Elliott Wimmer will describe complex interactions between hippocampal, striatal, and orbitofrontal regions during acquisition of structural knowledge of novel mazes. Tyler Davis shows that learning and generalizing knowledge of complex conceptual structures relies on multiple areas of prefrontal and parietal cortex. Lisa Wirz examines how neuromodulators, in particular stress and stress-related hormones, affect recruitment of and interactions between memory systems.

Multiple Memory Systems in Learning: History and Current Trends
Carol A. Seger

Multiple memory system theories have a long history in cognitive neuroscience. Early research largely focused on using dissociation logic to identify contributions of hippocampal declarative memory systems in contrast to striatal habit learning systems. With the development of fMRI and other advanced cognitive neuroscience methods, researchers have been able to better characterize the complexity of multiple system contributions and patterns of interactivity between systems.   Current research focuses on questions such as how complex conceptual information is learned, how learning is affected by modulatory factors such as emotion and stress, and how reliance on neural systems changes across the time course of learning, from initial acquisition through to the development of automaticity.

The Role of Multiple Memory Systems in Structure Learning and Feedback Processing
G. Elliott Wimmer

Forming representations of the environment around us is essential for planning and decision making, and feedback often serves to update our knowledge. In my talk I will present results from an experiment that examined learning from delayed rewards. Participants learned to find rewards in multiple different temporally extended Y-maze environments. We found that hippocampal BOLD activity reflected encoding demands, with activity at the onset of mazes decreasing as performance increased. When feedback was presented more than 30 s later, both the striatum and the hippocampus exhibited increased activity for reward versus loss feedback. In the orbitofrontal cortex, we found that multivariate patterns came to represent predictive information about distant upcoming states, and the degree of this representation was related to increases in connectivity with the hippocampus. Our findings illuminate how memory systems in the human brain may learn to represent structure across long timescales and use this knowledge to make adaptive decisions.

How the Brain uses Structured Representations to Support Conceptual Generalization
Tyler H. Davis

Multiple memory systems research suggests that structured representations (rules, causal relations, etc.) are often used to guide new concept learning. However, rule use tends to quickly dissipate as automaticity develops, giving way to more automatic similarity-based processing. Nonetheless, people retain structured representations after automaticity has developed and can use them to support generalization. One question is how the brain determines whether to use such representations to guide generalization or inference after categories are well-learned. Here I'll present two functional neuroimaging studies examining how the brain uses structured representations to support inference and conceptual generalization in artificial and semantic categories (self-judgments). In the first study, participants learned a rule-based category learning task and later were asked to generalize this rule to novel items. Results showed that the rostrolateral prefrontal cortex tracked model-based measures of mismatch from previously learned examples. In the second study, participants made social comparison judgments for a number of trait words. Results from model-based analysis revealed that the medial prefrontal cortex and angular gyrus tracked the causal-topological relationships amongst words and were more active for traits with fewer dependencies. The combination of the two studies suggests that representational stability may be a factor in how the brain determines whether to use structured representations in generalization. However, the systems supporting such generalizations may vary depending on domain (artificial categorization vs semantic).

How Stress Modulates Multiple Memory Systems
Lisa M. Wirz

A long-standing debate exists about the effects of stress on the quality of learning and memory processes. Although several studies have shown that stress modulates the engagement of multiple memory systems in a manner that favors dorsal striatum-dependent habitual over hippocampus-dependent cognitive memory, not all individuals are equally susceptible to this stress-induced shift. Genetic differences in the two main stress mediator systems (noradrenaline and cortisol), may contribute to this existing variability. Therefore, in two independent neuroimaging studies, we investigated naturally occurring genetic variants of the noradrenergic and mineralocorticoid receptor systems and their modulation of stress effects on the relative contribution of multiple memory systems in a probabilistic classification learning task. Our results suggest that in response to stress, carriers of a noradrenergic receptor polymorphism associated with increased noradrenaline release rely more strongly on the cognitive, hippocampus-dependent system. In contrast, in carriers of a common functional mineralocorticoid receptor haplotype, we observed a stress-induced shift toward increased engagement of the habitual, dorsal striatum-dependent system. These individual differences in the relative engagement of cognitive and habitual learning processes after stress have highly relevant implications for our understanding and treatment of stress-related disorders.

Midline structures in explicit memory: Is there a hippocampus-independent route to cortical engrams?
Dr. Svenja Brodt3, Dr. Björn H. Schott1,2,4, Dr. Jasmin Kizilirmak1
1German Center for Neurodegenerative Diseases, 2Leibniz Institute for Neurobiology, 3Institute of Medical Psychology and Behavioral Neurobiology, University of Tübingen, 4Department of Psychiatry and Psychotherapy, University Medicine Göttingen
The brain's midline structures, particularly the medial prefrontal cortex (mPFC), the posterior cingulate cortex (PCC), and the adjacent precuneus are best known for their relatively increased activation during conditions of relative rest and have therefore been termed the Default Mode Network (DMN). The DMN is

commonly engaged during tasks like self-reference, Theory of Mind (ToM) and other social cognitive tasks. In a thus far largely independent line of research, it has become evident that certain structures of the DMN, especially midline structures, seem to be involved in a special type of long-term memory (LTM) formation that is hippocampus-independent. During this symposium, we will propose a role for DMN structures in the mnemonic representation of complex associative information. In a series of four talks, we will present converging evidence from research on prior knowledge-related and schema-dependent learning showing that the mPFC and posterior medial cortex (PMC) may be differentially involved in establishing schemas and incorporating novel information into prior semantic associations. In an outlook, we will discuss the implications of the proposed midline memory network for memory function in the elderly.
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Björn H. Schott (Leibniz Institute of Neurobiology, Magdeburg, Department of Psychiatry and Psychotherapy, University Medicine Göttingen, and German Center for Neurodegenerative Diseases, Göttingen, Germany) will make us reconsider the well-known role of the DMN in social and self-referential cognition from a memory perspective in his talk "Information integration in the brain's midline - an underappreciated memory network?". Following a brief review of the established role of the DMN in episodic retrieval and autobiographical memory, converging evidence will be presented for the engagement of certain DMN structures like the mPFC and the precuneus during both the encoding of personally relevant content (Schott et al., 2013) and the gradual acquisition complex spatial memory traces (Schott et al., 2018). Furthermore, mechanisms of information flow into the DMN will be discussed, based on Dynamic Causal Modeling (DCM) investigations (Soch et al., 2016). Finally, this talk will also tackle the observation that the elderly commonly show increased recruitment of DMN structures during episodic encoding.

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ConnectToBrain: Closed-loop multi-locus TMS for modification of cognitive processes

Prof. Risto Ilmoniemi[3], Prof. Vittorio Pizzella[2], Dr. Pedro Gordon[1], Prof. Gian Luca Romani[2], Prof. Ulf Ziemann[1]
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In transcranial magnetic stimulation (TMS), brief (~100 µs) pulses of strong (~1 tesla) magnetic fields are applied to the brain where they induce weak (~0.1 mA/mm2) electric currents that depolarize neurons and trigger action potentials. Repetitive TMS (rTMS) can be used as therapy, for example in treatment-refractory depression or pain, or to improve post-stroke recovery. Also, neurocognitive processes may be modified by rTMS. However, with current technology, rTMS is applied in predetermined, non-individualized manner, targeting a single site rather than distributed networks, and the effect sizes are rather limited.

ConnectToBrain is an ERC-funded synergy project that will create a radically novel multi-channel multi-locus TMS device (mTMS) with which one can change the location and pattern of the stimulating electric field (E-field) quickly (within ~1 ms) without moving the pulse-generating coils. In addition, using simultaneous electroencephalography (EEG) recordings will allow a bidirectional coupling of mTMS to the brain that can serve as the basis for closed-loop brain stimulation. This will facilitate targeting dysfunctional brain networks at the right instants of time (the right brain states) and at the right site(s) to maximize therapeutic benefit. One of the clinical use cases of this potentially paradigm-shifting therapeutic brain stimulation approach within the ConnectToBrain project will be amelioration of frontoparietal working memory network function in patients with Alzheimer's disease.

Four members of the ConnectToBrain consortium will present the scientific background and vision of this interdisciplinary and international project, and first data to improve working memory function in healthy adults, using the novel approach of brain-state-dependent rTMS based on real-time EEG analysis.

First speaker: Prof. Risto Ilmoniemi (Aalto University)
He will give an introduction into the ConnectToBrain project and how it may impact cognitive neuroscience. In particular, he will demonstrate first examples of the prototypes of the multi-channel multi-locus TMS devices and how they allow targeting highly precisely different sites of the cortex underneath the stimulating coils by superimposition of the induced E-fields of the single coils. He will also introduce the concomitant recording of EEG data that will allow targeting specific brain states (EEG-TMS) but also measuring directly from the brain the consequences of the TMS-induced perturbation (excitability and connectivity measures in EEG) for prediction of the perturbational effects in future trials, and possible adaptation of the stimulation protocol in a closed-loop manner. Finally, he will speculate on how this novel technology will allow highly specific and effective modification of brain networks, for instance to improve memory function.

Second speaker: Prof. Vittorio Pizzella (University of Chieti-Pescara)
He will demonstrate how network level brain states impact the effects of Transcranial Magnetic Stimulation and vice versa. The description of functional states of the brain is gaining more and more attention, while methods to disclose state patterns are moving from local to network dynamics. In fact, state-dependent non-invasive brain stimulation informed by electroencephalography (EEG) has concentrated on assessing brain states defined as local EEG characteristics before the stimulation, while it is acknowledged that the brain exhibits an intrinsic long-range dynamic organization in brain networks. Here, the author will test the hypothesis that network level brain states can influence the effects of TMS delivered at nodes of the motor network. He demonstrates that the connectivity state of the motor network predicts corticospinal

excitability as measured by the amplitude of the Motor Evoked Potential (MEP), paving the way for a connectomic-informed state-dependent stimulation. Additionally, TMS on specific key-nodes of selected resting state networks (dorsal attention, default mode network) can modify brain state dynamics as observed in specific resting EEG microstates' topography.

Third speaker: Dr. Pedro Gordon (Eberhard-Karls University Tübingen)
Prefrontal cortex oscillations in the theta band (4-7 Hz) are involved in several cognitive functions. Neuronal activity in the medial prefrontal cortex and other brain regions is connected through theta-band phase synchrony. The strength of this theta phase-dependent connectivity between brain regions significantly predicts working memory performance.

In this study, healthy adults were stimulated by brain-state-dependent rTMS of the left dorso-medial prefrontal cortex (DMPFC) in three different sessions. In each session the rTMS pulses were triggered during either the negative peak, positive peak or at random phases of the ongoing DMPFC theta oscillation. The real-time signal from the DMPFC was obtained using an individualized source-space-based EEG spatial filter.

RTMS triggered specifically during the negative peak of the theta oscillation resulted in an increase in TMS-induced theta power, while the otherwise identical rTMS protocol, but with pulses triggered during the positive peak resulted in a decrease. Moreover, no significant change in TMS-induced oscillations was observed after rTMS triggered at random phase. Importantly, the increase in TMS-induced theta power in the negative-peak condition was associated with an improvement in working memory performance, as measured by reduced reaction times in a Sternberg memory task, while this was not the case with the other two interventions.

These findings indicate, for the first time in humans, that function of the working memory network can be selectively enhanced by brain-state-dependent rTMS when selectively targeting the negative (most excitable) phase of the ongoing DMPFC theta rhythm. These findings may have implications for therapeutic applications of rTMS in patients with working memory disorders.

More speakers from the ConnectToBrain consortium could be added if requested by the conference organizers.

Rhythm processing and temporal predictions

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It is well established that the brain optimizes perception and action by generating temporal predictions about rhythmic aspects of its sensory environment (Arnal & Giraud, 2012). One influential hypothesis suggests that low-frequency neural oscillations can entrain to sensory rhythms, creating temporal windows of increased neural gain to incoming stimuli (Schroeder & Lakatos, 2009). However, the scope and implementation of temporal predictions in rhythmic sequence processing remains disputed (Haegens & Zion-Golumbic, 2018). It is controversial whether entrainment operates via alignment of neural activity to the exact frequencies in the stimulus stream, or through more discrete and frequency-general phase reset of ongoing oscillations, or perhaps reflects adjustment of non-oscillatory anticipatory ramping activity. It is also unclear whether neural activity can align to a broad range of sensory rhythms, or if entrainment is specific to certain preferred frequencies. The temporal dimension of neural entrainment is also poorly understood, and it is unknown whether the benefits of rhythmic expectation are accompanied by deficits in neural processing of stimuli presented at unexpected time points, creating temporal trade-offs. Finally, rhythmic expectations remain to be delineated from other kinds of temporal predictions in terms of the specific neural signatures and functional neuroanatomy.
Here we bring together recent evidence from invasive and non-invasive electrophysiology in human volunteers, behavioural studies, and computational modelling, to elucidate the determinants of neural entrainment to sensory rhythms. Using MEG, ECoG, and behavioural data, Saskia Haegens will demonstrate that periodic stimulus streams result in a general phase reset of neural activity, rather than frequency-specific entrainment of ongoing oscillations, suggesting that the current formulations of the neural entrainment hypotheses need to be revised. Ryszard Auksztulewicz will use M/EEG-based decoding and modelling to provide evidence that rhythmic expectations do indeed increase neural gain at expected time points, but that these modulations do not impair neural processing of irrelevant stimuli, further calling into question the content-selectivity of rhythmic predictions. Alessandro Tavano will question the generality of neural entrainment mechanisms, showing that neural and behavioural benefits of temporal prediction are not preserved within a sub-range of the delta band (1-4 Hz), previously hypothesised to be the optimal time scale for neural entrainment. Finally, Fleur Bouwer will present evidence for a dissociation between rhythmic and interval-based temporal predictions in EEG data, suggesting that nuanced analyses of EEG signals can help uncover the specific correlates of rhythmic temporal predictions.
Taken together, we provide convergent evidence that the current hypotheses of neural entrainment need to be revised with respect to both the specificity of neural and perceptual modulations induced by rhythmic stimulus structure, and the generality of neural entrainment mechanisms across brain signals and networks.

(1) Rhythmic facilitation of temporal prediction: testing the neural entrainment hypothesis

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The neural entrainment hypothesis proposes that rhythmic sensory streams produce phase-reset of ongoing neural oscillations, such that the high-excitability phase of intrinsic oscillations becomes aligned with the occurrence of task-relevant events, leading to amplified responses relative to events occurring out of phase with the entrained rhythm. Entrainment further represents a mechanism through which the brain may instantiate temporal predictions. We tested this hypothesis using MEG and ECoG recordings in subjects

performing an experimental task that specifically dissociates periodicity of sensory stimulation from temporal predictions.
Compared to aperiodic stimulus streams, periodic isochronous streams were followed by increased phase-alignment of low-frequency oscillations (though not limited to the stimulus rate) and faster reaction times. Our results suggest that periodic stimulus streams lead to a general phase reset, rather than frequency-specific neural entrainment of ongoing oscillations, calling into question the hypothesis of neural entrainment as it is currently formulated in the literature.

(2) Rhythmic temporal expectation boosts neural activity by non-specific gain increase
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Temporal orienting improves sensory processing, akin to other top-down biases. However, it is unknown to what extent these improvements reflect increased neural gain to any stimuli expected in time, or specific tuning to task-relevant stimuli. Here, across two magneto- and electroencephalography (M/EEG) studies, we examined the specificity of temporal orienting effects. In Experiment 1, volunteers (N=23) performed an auditory discrimination task while their brain activity was measured using M/EEG. Acoustic stimulation consisted of distractor sequences interspersed with targets, presented in a rhythmic or jittered way. Target rhythmicity not only improved behavioural discrimination accuracy and M/EEG-based decoding of targets, but also of irrelevant distractors preceding these targets. Based on estimated population tuning curves, we found that the effect of expectation on distractor decoding was linked to gain increase only, suggesting increased neural sensitivity to any stimuli presented at relevant time points. In Experiment 2, volunteers (N=22) listened to sequences of tones in which we orthogonally manipulated time-based and content-based predictability at two hierarchical levels: single elements and element pairs. We found that time-based predictability increased the effects of content-based predictions only at the respective hierarchical levels (i.e., fast/slow temporal predictions modulated responses to unexpected elements/pairs). However, the extent of these modulatory effects were similar across both hierarchical levels, and we did not find evidence for trade-offs between them. Taken together, these results suggest that temporal orienting has a high degree of time-based specificity, but operates largely on non-specific stimulus representations.

(3) A discontinuity in sensory processing within the delta band
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A general principle in sensory neuroscience is that regularity in stimulus delivery boosts neural processing and correlated behaviour, to the point that isochrony is assumed to always drive the best performance and the highest signal-to-noise ratio. We tested this principle by asking human participants to detect unpredictable pitch changes in pure tone sequences parametrically differing in stimulus onset asynchrony (SOA) across the delta band (250 ms = 4 Hz, 500 ms = 2 Hz, 1000 ms = 1 Hz), as well as in the amount of jitter at stimulus onset (isochrony, 10% jitter, 30% jitter). We expected the advantage of isochronous stimulation to be preserved across SOA levels, in terms of both sensory processes (deviancy detection, repetition suppression, phase reset effects) as well as accuracy and response speed. Surprisingly, we found a significant behavioral discontinuity in neurally resolving time in the middle of the delta band: at 2 Hz, a large temporal jitter benefits performance and sensory processing significantly more than isochrony. We conclude that the advantage of rhythmic regularity is not a universal principle of sensory processing.

(4) Beyond the beat: differentiating responses to a regular beat from responses to rhythmic patterns
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Being able to predict the timing of incoming information facilitates sensory processing. Temporal expectations are thought to result from entrainment of low-frequency cortical oscillations to rhythmic input. However, first, it is unclear whether entrainment can account for both expectations based on a regular beat and expectations based on predictable rhythmic patterns, and second, endogenous entrainment has to be differentiated from evoked responses to rhythmic patterns. Here, first, we aimed to differentiate between beat-based and pattern-based expectations. We examined behavioral (N = 32) and EEG (N = 27) responses to silent periods following rhythmic auditory sequences with a regular beat, a predictable pattern, or random timing. Behavioral responses to the rhythms were affected by beat-based expectations for multiple beat-cycles, while the effects of pattern-based expectations subsided immediately. Moreover, we found enhanced power at the beat frequency for beat-based sequences during listening, and, importantly, during silence. For pattern-based sequences, we observed such power enhancement only during listening, suggesting different underlying mechanisms. In a second study, we aimed to differentiate between entrainment and evoked responses to rhythmic patterns. Participants (N = 12) listened to non-isochronous rhythmic sequences played at five different rates. Behaviorally, participants shifted the perceived beat depending on the speed of the rhythm. We found a similar shift using EEG, with peaks in spectral power at the note rate for slow sequences, and at subharmonics of the note rate for fast sequences. We simulated these responses using an oscillator and an evoked response model. Our data was best captured by the oscillator model, while the evoked model could partly mimic the shifts in spectral power. Taken together, our findings suggest that neural responses to rhythm contain contributions from entrainment, as a mechanism for beat-based expectations, but also from expectations for and evoked responses to rhythmic patterns.

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Neural responses to auditory regularities as a function of attention and conscious awareness

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Summary
Our brains have the ability to extract patterns from the environment and form implicit predictions given past sensory experience. This fundamental ability represents a building block of many neural operations, one that is influenced by attentional resources, the degree of conscious access to incoming stimuli and the temporal scale of the regularity rule. Here we present a set of new intracranial and electroencephalographic experiments that uncover how the neural underpinnings of regularity extraction in humans are impacted by these cognitive and experimental factors. The first presentation provides evidence underscoring the influence of sustained attention on auditory regularity detection as indexed by high frequency broadband activity in the lateral prefrontal cortex. The second talk will present novel evidence of the involvement of the hippocampus and amygdala in the automatic auditory regularity processing, thus expanding the neural regions contributing to this phenomenon beyond the more established temporal and prefrontal cortices. The third and fourth talks will introduce new perspectives about the neural mechanisms underlying our sensitivity to auditory regularities, with a particular emphasis on the timing of the sensory regularity. The third talk delineates the distinct roles of the temporal and frontal cortices in regularity extraction on different time scales, while the last talk highlights a new mechanism for omission detection based on the synchronicity between sounds and heartbeat in conscious and unconscious states. Taken together, this series of experiments reveal the distinct contribution of brain regions and neural mechanisms of auditory regularity detection, as a function of the complexity of the auditory series and available cognitive resources, with sophisticated manipulations of stimulus presentation, task demands and advanced data processing methods.

Sustained attention modulates auditory deviance detection

A stimulus that deviates from the prevailing situational context unavoidably captures our attention. Our neural response to an infrequently occurring deviant sound embedded in a sequence of repetitive standard sounds is commonly considered as pre-attentive or subconscious. Past studies of attentional modulation of the deviance detection response have primarily adopted the passive listening approach in which a classic oddball paradigm is presented in the background of an ongoing task. Here, we directly compared sustained periods of external attention (commonly referred to as active listening) and internal attention (commonly referred to as passive listening) to characterize the effects of sustained attention on auditory deviance detection. We recorded intracranial electroencephalography (EEG) from epilepsy patients who were implanted with electrodes in the frontal and temporal cortices. Patients were presented with a series of tones in a classic two-tone oddball paradigm. For every 30 second block, they were instructed to direct their attention externally to the tones and respond to deviant tones, or internally to their own thoughts while ignoring the tones. Given the role of lateral prefrontal cortex in top down attentional control, we hypothesized this region to show stronger attentional effects compared to the temporal cortex. To test this, we computed the deviance detection effect, as indexed by the difference in high frequency broadband activity (70-150 Hz) between deviance and standard tones. Across attention states, the deviance detection effect was larger, peaked later and was more sustained in the frontal relative to temporal cortex. Importantly, only the frontal cortex showed larger deviance detection effects during externally relative to internally directed attention. Consistent with this finding, our subsequent analysis showed that frontal cortex showed a larger attention effect compared to the temporal cortex. These findings suggest that sustained attention does modulate our detection of auditory irregularity, an effect that is most pronounced in the lateral prefrontal cortex.

Detecting auditory regularities in the absence of consciousness or attention

The neural circuit processing environmental regularities is preserved even in the absence of conscious perception. In a series of studies we have shown that EEG responses of comatose patients are sensitive to violations of auditory regularities established over single sounds or sound sequences. Attempts to investigate the configuration of the neural circuit underlying implicit regularity detection have shown that multiple stages of sensory information processing are sensitive to regularities, through synchronised responses over widespread regions of the cortex. However, the extent to which subcortical structures and single unit activity therein support regularity detection and auditory predictions remains underexplored.
We performed intracranial EEG recordings in epileptic patients, and presented them with series of standard and deviant sounds while their attention was distracted. Deviant sounds occurred in a temporally predictable or unpredictable way. We analysed local field potentials and single unit activity from electrodes in the medial temporal lobe.
Mean firing rates peaked earlier for entorhinal and hippocampal compared to amygdala neurons, suggesting a subcortical hierarchy in processing of auditory events. Moreover, intracranial event related potentials showed deviance effects across all regions, with deviance responses in the temporal cortex peaking earlier and being stronger than in the hippocampus and amygdala. Among recorded regions, only the hippocampus was sensitive to predictability. When the occurrence of deviant sounds was fully predictable, hippocampal deviance effects occurred earlier, and low-frequency power (1-8 Hz) was higher. Interestingly, hippocampal low-frequency power was modulated by the number of standard sounds preceding a deviant, but only when the deviant sound occurrence was predictable.
In summary, our results expand the network of automatic regularity extraction by showing that subcortical regions of the temporal lobe play an important role in the detection of regularities and implicit formation of auditory predictions.

What does the frontal lobe tell (or hide from) the temporal lobe about the future?

According to the hierarchical predictive-coding framework, regularities in the environment are used by the nervous system for predicting the input, and deviations from this prediction are transmitted as ‘prediction errors’. However, regularities may be based on more than one dimension and may be based on different time windows. Multiple predictions, sometimes contradicting, may be formed simultaneously and it is not clear how the brain deals with this situation. I will present evidence from scalp and intracranial EEG showing that different parts of auditory cortex and frontal cortices are involved in predictions in multiple time scales. In a study involving intracranial EEG recordings, we recorded ERPs as well as high frequency broadband (HFB) power from multiple electrodes over temporal and prefrontal cortex, implanted for clinical purposes. Both temporal and prefrontal sites responded to deviations from regularity with an HFB increase. However, temporal sites responded to expected and unexpected deviations alike, whereas frontal sites responded exclusively to unexpected deviations. Furthermore, only prefrontal cortex showed anticipatory HFB power suppression prior to the onset of expected deviants, which correlated well with the post-stimulus response suppression to expected deviations. These results indicate a hierarchy of predictions: auditory cortex creates a mismatch response vis a vis short-range regularities, whereas the prefrontal cortex encodes high level and temporally long-range regularities. However, predictions from higher nodes or the putative network (frontal) did not ‘trickle down’ to lower nodes (temporal). Within auditory cortex, scalp EEG recordings revealed that the N1 and P2 responses rely on information accumulated over different time scales: the later P2 is sensitive to the immediate past while the earlier N1 is sensitive to long term history. We provide a computational model explaining this diversity based on adaptation dynamics. Altogether, the results indicate multiple representations of auditory regularity on multiple time scales, which do not obey a simple hierarchy.

Cardio-audio synchronization enables auditory omission detection in the absence of consciousness

After several repetition of identical sensory inputs, the human brain generates the expectation that the same signal will occur in the future. Numerous reports suggest that this phenomenon results from an active generation of an internal model predicting the most likely future events. One main evidence comes from the observation that our brain responds to the omission of a predictable sound within regular sequences with equally spaced sound onsets. In a recent study, we showed that an omission-evoked response can even occur within irregular sequences when sounds are synchronous to the ongoing heartbeats. Since healthy participants remained unaware of the heartbeat-sound synchronicity, we hypothesized that such omission response does not require awareness of stimulus regularity and we tested whether it can also be evoked in the absence of consciousness.
We recorded high-density EEG in seventeen comatose patients during the first day after cardiac arrest. We delivered sound sequences that were either occurring in synchrony with the ongoing heartbeat (synchronous condition) or at pseudorandom intervals (asynchronous condition), or at fixed and individually adjusted pace following mean heartbeat (isochronous condition). Sounds were randomly omitted within the auditory sequences 20% of the time. Statistical analyses revealed a significant higher global field power evoked in the synchronous vs the asynchronous conditions over the time-period 285-334ms post-omission onset, similar to previous observations in healthy subjects. In the same patients, we found no evidence of omission responses during the isochronous sequence indicating that auditory regularity per se did not suffice to induce accurate prediction of upcoming sound onset. As temporal regularity across heartbeats and sounds enabled omission detection, our results suggest that the unconscious brain preferentially process auditory regularities when coupled to an internal bodily signal as compared to equally spaced auditory sequences.

The Neuronal basis of predictive coding: Evidence from brain studies across species

Dr. Manuel S. Malmierca[1], Dr. Ryszard Auksztulewicz[2,7], Dr. Tobias Teichert[3], Dr. Alejandro Blenkmann[4], Dr. Lucia Melloni[5,6]

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Organizers:
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Description of theme and target audience:
There is growing evidence that a major function of the brain is to constantly predict the environment on multiple levels to allow for flexible behaviour. For example, one anticipates how a word of a friend will sound before it is uttered, and when and how a sentence will end before it finishes. Those predictions are critical for understanding specially under noisy conditions, such as a cocktail party. Yet, the mechanism by which generating and testing such predictions allow for flexible behaviour are only starting to be understood. In this symposium we will probe the assumption that the brain's neuronal circuitry is organized as a highly predictive machine, best exemplified by the predictive coding framework (for a recent review, see Heilbron & Chait, 2018, Neuroscience 389).
The auditory system is particularly important for predictive processing because it can detect signals coming from any direction within noisy backgrounds in a pre-attentive mode (e.g. during sleep). The auditory system can, thus, cope with the variability and redundancy in the auditory scene. This symposium will address the adaptive nature of the neural coding behind regularity extraction, novelty detection, and decision making in the auditory system of mammals under different degrees of stimulus predictability. These fundamental scientific questions will be addressed and discussed through five complementary talks that cover different aspects of 'predictive processing'.
Ryszard Auksztulewicz and Manuel S. Malmierca will discuss neural processes mediating the extraction of auditory statistics at the subcortical and cortical levels and the neurochemical and neuromodulatory mechanisms of deviance detection. Next, Tobias Teichert will further talk about the mechanisms of change detection and the behavioral evidence for the existence of two functionally distinct auditory short-term memory systems in the macaque, each having specific contributions to mismatch responses. Then, Alejandro Blenkmann will discuss his recent finding in humans on how areas other than auditory regions in the temporal cortex contribute to acoustic deviance. Finally, Lucia Melloni will present her recent studies on the effects of predictive processing in auditory event segmentation and episodic memory formation, showing evidence for multiple timescales of processing stimulus predictions at different hierarchical levels, from local transitional probability extraction to coding more complex statistical relationships and chunking. This symposium will provide a comprehensive overview of the mechanisms by which predictions and prediction errors are implemented in the brain; the conservation of those neural principles across the animal kingdom; and the implementation of concurrent predictions across the processing hierarchy.

Memorandum of understanding: Each speaker has been contacted and agreed to participate. The budget proposal is understood by all symposium participants.

Talk 1: Prediction error signalling across species and stimulus domains

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Neuronal message passing has a strong predictive component. Prediction error signalling, ensuing from comparisons between internal predictions and external sensations, has been identified in human studies and animal models. However, the extent to which animal models provide a useful operationalisation of predictive processing is largely unknown, since most animal studies use relatively simple stimuli and paradigms. In this talk I will present work in humans (using magnetoencephalography and electrocorticography) and rodents (using electrophysiology and calcium imaging), combining recordings of neural activity with computational modelling. First, mismatch responses to simple prediction violations across multiple acoustic features can be observed using ECoG in anaesthetised rodents. Second, neuronal mismatch responses in anaesthetised rats can occur after stimulus omissions, corresponding to violated temporal predictions. Third, mismatch responses can also be observed after violations of relatively complex predictions, such as element substitutions and order transpositions of stimulus sequences. Finally, I will outline the analogies between recordings in rodents and human studies, showing dissociations between prediction errors to violated expectations across stimulus features and complexity levels.

Talk 2: The neuromodulatory role of achetylcholine and dopamine in deviance detection

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Neuromodulatory inputs can not only gate plasticity (Martins and Froemke, 2015), but also change the balance of top-down versus bottom-up influence as it is well known that neuromodulation strongly impacts sensory processing, learning and memory.
According to the predictive coding theory (Friston, 2005), the brain constantly generates top-down predictions that are compared with sensory bottom-up signals. The ability of the brain to recognize which prediction errors carry reliable information is critical in the process of prediction error minimization. In addition, precision weights the driving power of prediction errors according to how reliable they are estimated to be (Friston, 2005).
Predictive coding models propose that neuromodulatory systems implement precision weighting through regulation of postsynaptic gain (Bastos et al., 2012), particularly theorizing about the involvement of acetylcholine (Moran et al., 2013) and dopamine (Friston et al., 2012). In this talk I will show our recent work that investigate which neuromodulators are involved in the encoding of the predictions and prediction errors and how neuromodulators regulate the precision of prediction errors in the rat brain

Talk 3: Two distinct auditory short-term memory systems may underlie the contribution of adaptation and deviance detection to mismatch negativity in the rhesus monkey

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By definition, mismatch negativity (MMN) – a macroscopic EEG deflection in response to a deviant sound – depends on auditory short-term memory. However, the memory-comparison account of MMN has been criticized and passive adaptation provides a simpler alternative. Here we present a framework that consolidates both accounts. First, we provide behavioural evidence for two functionally distinct auditory short-term memory systems in the macaque: a short-lived system with high discriminability (echoic memory), and a longer-lived system with lower discriminability (auditory recognition memory). Second, we present electrophysiological evidence that two functionally distinct mechanisms contribute to MMN in the macaque: (a) adaptation, which dominates MMN (i) if the time between tones is short and (ii) if the deviants are similar to the standards, as well as (b) deviance detection which (i) is largely independent of the time between tones, (ii) but emerges only if deviants can easily be discriminated from the standards. Integrating these behavioural and electrophysiological findings we suggest that adaptation and deviance detection are downstream of echoic and auditory recognition memory, respectively.

Talk 4: Auditory deviance detection in the human insula. Evidence from intracranial EEG recordings.

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Our brains can automatically detect changes in our environment by extracting regularities embedded in it. In the particular case of auditory processing in humans, most of the invasive electrophysiological evidence of this function comes from the temporal cortex. However, other areas are involved in this complex function, as pointed out by lesion and non-invasive neuroimaging studies. Notably, the human insula is known to be involved in auditory processing, but knowledge about its precise functional role and the underlying electrophysiology is limited.
To assess the role of the human insula in automatic deviance detection, we studied the High Frequency Activity (high gamma, 75-145 Hz) from 90 intracranial EEG channels across 16 patients undergoing pre-surgical monitoring for epilepsy treatment. The participants passively listened to a stream of standard and deviant tones differing in four physical dimensions: intensity, frequency, location or time. The results indicate that the insular cortex is engaged in auditory deviance detection, showing a greater amplitude and longer latency response to deviants relative to standards. Additionally, the responses were of longer latency compared to those of the temporal cortex, an indication that the insula is at a higher hierarchically level than the temporal cortex in the auditory processing network.
Expanding our focus to areas beyond the traditionally studied auditory areas will increase our understanding of the network of hierarchically organized brain areas that support deviance detection.

Talk 5: From continuous stream to segmented units: How units are created in perception and their role in memory.

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Our experience unravels in a continuous and forward manner, yet perception appears punctuated by objects and events. Our episodic memories are also snapshots of that continuous experience. The mechanism by which continuous input is segmented and its role in episodic memory formation are beginning to be understood. We have used tasks involving artificial sequences, visual narratives, and continuous visual presentation of images in conjunction with magnetoencephalography and electrocorticography to understand the mechanism supporting segmentation and encoding of sequences. We found evidence of multiple timescales of processing in different frequencies and for hierarchical representation of sequences from simpler features such as coding of transitional probability, to more complex coding of ordinal position and even chunks. Extracting those events has important consequences for memory of temporal order such that order is better preserved and remembered within an event than across an event. I will discuss a model linking event segmentation to episodic memory.

Communicative signals exploit complementary neural networks and acoustic attributes adapted to that purpose

Dr Luc Arnal[2], Dr Vani Rajendran[3], Benjamin Morillon[1], Pr Christian Kell[4]
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Symposium Title: Communicative signals exploit complementary neural networks and acoustic attributes adapted to that purpose
Chairperson: B. Morillon
Topics: 03 Sensory systems, perception
Authors (in order of appearance): L.H. Arnal, V. Rajendran, B. Morillon, C.A. Kell

Symposium Abstract: The aim of this symposium is to provide a state of the art of research investigating the neural processing streams supporting the perception and production of communicative signals in the brain. Communicative signals encompass speech, music and alarm signals. One key question we will address is the extent to which these different sound categories exploit complementary acoustic niches and different neural networks. Communicative signals are complex sounds that exploit a large variety of acoustic features to trigger specific emotional and behavioral responses in the listener. Although there exists a great diversity of languages and musical styles, the way we use some acoustic features to manipulate listeners' affective states and reactions is arguably conserved across cultures and even across species. Indeed, despite neuroanatomical variations, the core physiological principles underlying the transformation of sonic vibrations into exploitable neural signals are highly conserved across vertebrates. When we hear a sound, a complex sequence of perceptual and cognitive processes transforms auditory sensations into adapted behavioral responses. However, the auditory system is not equally sensitive to all frequencies and acoustic features, and ensuing reactions or emotions may differ across features. From reacting to the sudden crack of a wooden stick to interpreting the lyrics of our favorite song, this system can process and exploit a large variety of acoustic features inducing a multiplicity of percepts, affects and behaviors. All four speakers will present behavioral and neuroimaging data in humans and animal models to investigate how communicative signals exploit specific acoustic attributes and neural networks to elicit adapted behaviors. Luc Arnal will first describe the acoustic niche hypothesis and show that alarm signals exploit a specific acoustic feature, roughness, that selectively target brain networks involved in salience, anxiety and aversion processing. Vani Rajendran will then reveal how sensitivity to low-level spectrotemporal contrasts drive the coordination of sensory, motor and cognitive areas and accounts for the irresistible tendency to move in rhythm with a beat. Capitalizing on the spectrotemporal modulation framework, Benjamin Morillon will present a study which suggests that humans have developed complementary neural systems in each hemisphere for auditory stimuli, leading to specialization for speech and music. Finally, Christian Kell will identify two acoustic factors contributing to functional lateralization during production of speech or musical rhythms. Overall, this symposium highlights the fundamental relationship between acoustic properties and specific neural networks and reveal how it enables efficient communication.

#1 Title: The sound of salience: how rough sounds hijack exogenous attentional systems
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Abstract: Communication signals exploit a large variety of acoustic features to trigger specific emotional and behavioral responses in the listener. However, the way we use some of these features to manipulate listeners' affective states and reactions remains mysterious. The acoustic niche hypothesis suggests that acoustic attributes (e.g. roughness, pitch, etc.) are naturally selected to carry specific information (danger, gender, etc.) as a function of the fitness of the stimulus and inducible reactions to promote survival. Supporting this idea, I recently showed that alarm signals (e.g. screams, sirens, but not neutral sounds like speech) exploit a restricted acoustic regime, known as roughness. This feature is devoted to communicate danger, enhance negative affective responses and elicit faster reactions. Although they are scarcely present in the natural environment, rough sounds have considerable effects on perceptual, emotional and behavioral responses. Fast repetitive inputs such as strobe lights, phone vibrators or rough alarm signals induce temporally salient, annoying percepts that efficiently capture attention, even at low signal-to-noise ratio. These sounds are almost impossible to ignore or suppress perceptually, and long-term exposure to rough sounds like screams causes tremendous stress in the listener's brain, sometimes leading to maladaptive reactions (e.g. shaken baby syndrome). Here, I will describe the neural underpinning of roughness in the human brain to illuminate how these sounds take over the control of our salience system by forcing exogenous attention in time. Measuring neural responses to click trains of varying rates during intracranial recordings in eleven epileptic patients, I show that sounds in the roughness [30–80 Hz] range are maximally aversive by synchronizing a widespread network of subcortical and cortico-limbic regions belonging to the salience system. In a subsequent EEG experiment, I show that the acoustic responsivity of this system predicts inter-individual anxiety and sound aversion. Finally, I will argue that these results are compatible with the notion that rough sounds target the salience system via a primitive, non-classical subcortical system involved in sensory salience and arousal.

#2 Title: Sensitivity to spectrotemporal contrast in the auditory cortex may predispose musical beat perception

Vani Rajendran (vani.g.rajendran@gmail.com)
City University of Hong Kong

Abstract: The perception of musical beat requires widespread neural coordination across higher-order sensory, motor, and cognitive areas. However, the question of how music, or any rhythmic auditory stimulus, drives the coordination of these processes is not well understood. Here, we present evidence that the sensitivity to spectrotemporal contrast in the auditory cortex creates points of neural emphasis that may predispose the location and clarity of the perceived musical beat. Extracellular firing rates in the anaesthetised rat auditory cortex were recorded in response to twenty musical excerpts diverse in tempo and genre, for which musical beat perception had been characterised by the tapping behaviour of 40 human listeners. Firing rates in the rat auditory cortex, even in the absence of motor or top-down activations, were on average higher on the beat than off the beat. This neural emphasis distinguished the beat that was perceived from other possible interpretations of beat, was predictive of the degree of tapping consensus across human listeners, and was accounted for by a spectrotemporal receptive field model. These findings strongly suggest that low-level spectrotemporal contrast sensitivity in the auditory system may be key in shaping higher level perception of music and speech.

#3 Title: Differential sensitivity to spectrotemporal modulation supports brain asymmetry for speech and music

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Abstract: A major debate in cognitive neuroscience concerns whether brain asymmetry for speech and music emerges from differential sensitivity to acoustical cues or from domain-specific neural networks. Here, we took advantage of the spectro-temporal modulation framework applied on a unique corpus of sung speech stimuli in which melodic and verbal content was crossed and balanced. We show that perception of speech content decreases selectively with degradation of temporal information, whereas perception of melodic content decreases only with spectral degradation. fMRI data show that the neural decoding of speech and music depends on activity patterns in left and right auditory regions, respectively. This asymmetry is supported by specific sensitivity of decoding accuracy to spectro-temporal modulation rates within each region. Finally, the effects of degradation on perception were paralleled by their effects on neural classification. Our results suggest a match between acoustical properties of human communicative signals and neural specializations adapted to that purpose.

#4 Title: Differential auditory-motor processing in the two cerebral hemispheres during rhythm and speech production

Christian A. Kell (c.kell@em.uni-frankfurt.de)
Goethe University, Department of Neurology and Brain Imaging Center, Frankfurt, Germany

Abstract: I will extend the notion of a spectro-temporal hemispheric asymmetry to speech production, one of the most strongly lateralized human brain functions. Using online manipulations of spectral or temporal speech features in the auditory speech feedback presentation we show that the left cerebral hemisphere compensates temporal feedback manipulations better while the right hemisphere adapts more strongly to spectral speech perturbations. While our results indicate hemispheric specialization along a spectro-temporal axis, this gradient does not constitute the only factor that determines functional lateralization. Ivry proposed a framework in which functional lateralization could pertain to a differential sensitivity of temporal modulations, with a representation of relative slow rhythms in the right hemisphere and of relative fast rhythms in the left hemisphere. We measured fMRI and MEG during bimanual finger tapping, in which fast tapping was defined at 2.5 Hz and slow tapping corresponded to tapping to every fourth auditory beat. We demonstrate that the left auditory cortex preferentially represents the relative fast rhythm in the amplitude modulation of low beta oscillations, while the right auditory cortex represents the internally generated slower rhythm. Moreover, the coupling of auditory-motor beta oscillations supports the building of a metric structure in the left hemisphere. Our findings reveal a strong contribution of sensory cortices to hemispheric specialization in action control and explain how the brain represents syncopated and non-syncopated polyrhythms to control rhythmic output.

Perceiving into the future - how internal states shape perception

Iria SanMiguel[1,2,3], Ashley Lewis[4], Roy Mukamel[5,6], Cristina Becchio[7,8]
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Sensory processing is highly sensitive to context, and depends on multiple variables including attention, movement, intention, expectation, and experience, to name a few. These variables are encoded as internal neural states. What shapes such internal states? and what drives their modulations? Current behavioral and neural evidence are inconsistent, with some studies reporting dampening effects and others sharpening effects of internal state modulation on perception. To date, there is no comprehensive model that can explain and reconcile existing data. By bringing together different perspectives and methods, we wish to converge on a potential overarching physiological mechanism underlying the processes that govern sensory perception. Together, the symposium will provide critical insights into the mechanism of how intentions and expectations of future sensory outcome, shape sensory processing and perception.

Lewis
The cortex is a massively recurrent network, characterized by feedforward and feedback connections between brain areas, as well as lateral connections within an area. Feedforward signals convey 'bottom-up' sensory information, whereas feedback signals can modulate this input based on our internal states. One of the more abstract forms that these internal states can take is the situation model one constructs while comprehending language. Lewis will describe recent MEG work using frequency-specific power and connectivity analyses to probe neural state changes under conditions of varying availability of feedforward and feedback information during reading.

Mukamel
Predictive coding models suggest that during execution of voluntary movement, signals from motor pathways are sent to relevant sensory regions in anticipation of the associated sensory outcome. Given the highly lateralized and somatotopic nature of the motor system, it is plausible that such predictive signals carry limb-specific information. During my talk I will provide empirical evidence in support of this notion and discuss possible implications for motor control.

SanMiguel
Internal states are shaped by our own motor behavior. The simple act of moving correlates with fluctuations in a variety of neurophysiological parameters, including the modulation of sensory responses. This modulation seems to be in part driven by expectations stemming from learnt associations between specific actions and sensory stimuli, however, expectations and movement per se may constitute independent parameters that interactively modulate perception. I will discuss the role of movement in shaping internal states in sensory regions and how such states modulate perceptual processing and memory encoding of stimuli that co-occur with voluntary actions.

Becchio
A convergence of modeling, behavioral and neural data indicate that the way individuals move reflects internal states. This raises the intriguing possibility that information about internal states can act as a social signal to others. But do human observers access this information? I introduce a novel formalism and experimental design to investigate how information encoded in naturalistic actions is read by human

observers with single-trial resolution. I present experiments applying this approach to action prediction and elaborate on how this approach may be used to generate and test new hypotheses.

New views on the genesis and modulation of gamma activity and coherence

Alina Peter[1], Andreas Canales Johnson[2,3], Prof Martin Vinck[4,5], Irene Onorato[4]
[1]MIT, [2]Department of Psychology, University of Cambridge, [3]Vicerrectoría de Investigación y Posgrado, Universidad Católica del Maule, [4]Ernst Struengmann Institute for Neuroscience in Cooperation with Max Planck Society, [5]Department of Neuroinformatics, Donders Centre for Neuroscience

Chair: Martin Vinck (replacing Brett Foster)
Professor, Ernst Struengmann Institute for Neuroscience in Cooperation with Max Planck Society, Frankfurt, Germany / Department of Neuroinformatics, Donders Centre for Neuroscience, Nijmegen, Netherlands

Title: New views on the genesis and modulation of gamma activity and coherence.

Summary:
High frequency 'gamma' activity (>30 Hz) has long been proposed as a critical signature of neural information processing and communication. Historically, evidence supporting a functional role for gamma were first obtained in studies of the visual system, which promoted more broader implications for cognition. Subsequently, an enormous literature has emerged focused on experimentally and computationally linking gamma dynamics to brain function. However, despite this progress, many facets of how gamma is generated and impacts neural processing remain unknown. Indeed, recent experimental findings promote a more nuanced view of how neural and behavioral factors impact the genesis and modulation of gamma activity. We will present a host of studies performed at multiple levels of investigation (cellular->population), and across species (mice->monkeys->humans), that convey new views on the physiology and function of gamma activity. These studies will highlight how specific cellular and population states impact gamma oscillation genesis, and how the definition and interpretation of 'gamma' activity and coherence requires careful examination. Speakers will highlight how gamma oscillations are generated by specific cellular mechanisms and stimulus configurations, in addition to considering how these responses are related to neural firing. Together, these new observations from the sensory systems will once again have a considerable impact on understanding the functional role of gamma in cognition, inter-areal communication and predictive coding more broadly.
Regarding diversity, this symposium is balanced for gender (2F/2M), reflects multiple levels of career stage (graduate student, postdocs, professor) and represents speakers of varied nationalities working across Europe and the United States. In summary, this symposium will present new and important work, from a diverse set of speakers, focused on an important topic of broad interest to many domains of cognitive neuroscience.

Speakers/Talks.

1. Alina Peter
MIT, Cambridge, USA

Title: Context matters: Spatial stimulus predictability determines V1 firing and gamma oscillations.
Abstract: Sensory responses result from integration of bottom-up sensory inputs with contextual predictions, conveyed by horizontal and feedback connections. In area V1, neurons may reduce their firing rates when their receptive field input can be predicted by spatial context. Gamma-synchronized (30–80 Hz) firing may provide a complementary signal to rates, reflecting stronger synchronization between neuronal populations receiving mutually predictable inputs. We show that large uniform surfaces, which have high spatial predictability, strongly suppressed firing yet induced prominent gamma synchronization in macaque

V1, particularly when they were colored. Yet, chromatic mismatches between center and surround, breaking predictability, strongly reduced gamma synchronization while increasing firing rates. Next, we formalized a measure of stimulus predictability and extended our findings to natural images. Synchrony signaled whether RF inputs were predicted from spatial context, while firing rates increased when stimuli were unpredicted from context, with distinct contributions of high- and low-level predictability. We will furthermore show how these processes are modulated by stimulus adaptation and repetition.

2. Andres Canales Johnson

Department of Psychology, University of Cambridge, United Kingdom.
Vicerrectoría de Investigación y Posgrado, Universidad Católica del Maule, Chile.

Title: Broadband Dynamics Rather than Frequency-Specific Rhythms Underlie Prediction Error in the Primate Auditory Cortex

Abstract: This talk will examine the contribution of the asynchronous and oscillatory ECoG components in the generation of auditory prediction error in the monkey brain. First, by decoupling the ECoG signal into arrhythmic and rhythmic components, we will show that the mismatch negativity (MMN) —an auditory prediction error response—is driven by the arrhythmic, broadband component and not by any of the rhythmic components. Second, by characterising cortical interactions across the temporal cortex using information theory metrics, we will show that the broadband component conveys mainly redundant information (i.e. copies of the MMN information are found across auditory areas), and spatially localised information about the prediction error response. We will conclude by highlighting the importance of information theory metrics for unraveling asynchronous cortical dynamics of predictive processing.

3. Prof. Martin Vinck
Symposium Chair.

Title: Cellular mechanisms and functional implications of inter-areal gamma coherence and signal propagation

Abstract: Despite its prevalence in the visual and hippocampal system and its association with attention and memory processes, much remains unknown about the physiological basis and functional interpretation of inter-areal gamma coherence. Our lab investigated this question using inter-areal high-density electrophysiology combined with mathematical modelling and optogenetic perturbation techniques. This talk will show key mechanisms through which inter-areal gamma coherence is established, in a cell- and layer-type specific manner, and following basic mathematical rules. This will shine new (and perhaps surprising) light on the function of inter-areal gamma coherence and its excitatory/inhibitory nature. I will furthermore provide evidence that gamma oscillations in a local circuit may not derive from a local, oscillatory E/I circuit, but can simply result from afferent, linear signal propagation.

4. Irene Onorato
Graduate Student (Martin Vinck lab); Ernst Strungmann Institute, Germany.

Title: Good timing, good communication: A new class of neurons plays a role in sensory processing and gamma synchronization in the visual system.
Abstract: Cortical computation depends on interactions between excitatory and inhibitory neurons. The contributions of distinct neuron types to sensory processing and network synchronization in primate visual cortex remain largely undetermined. We show that in awake monkey V1, there exists a distinct cell type (~30% of neurons) that shows high spontaneous discharge rates and fires in high-frequency bursts. These

neurons are more stimulus selective and phase locked to 30- to 80-Hz gamma oscillations than other neuron types. Unlike other neuron types, their gamma-phase locking is highly predictive of orientation tuning. We find evidence for strong rhythmic inhibition in these neurons, suggesting that they interact with interneurons to act as excitatory pacemakers for the V1 gamma rhythm. We did not find a similar class of narrow-wave (NW) bursting neurons in L2-L4 of mouse V1. Given its properties, this class of NW bursting neurons should be pivotal for the encoding and transmission of stimulus information.

On the Ups and Downs of Visual Perception

Biyu Jade He[2], Ying Joey Zhou[1], Lucia Melloni[2,8], Ayelet Landau[4], Laura Dugué[5,6,7], Saskia Haegens[1,3], Floris de Lange[1]

[1]Donders Institute for Brain, Cognition, and Behaviour, [2]New York University School of Medicine, [3]Columbia University, [4]The Hebrew University of Jerusalem, [5]CNRS (Integrative Neuroscience and Cognition Center, UMR 8002), [6]Université de Paris, [7]Institut Universitaire de France (IUF), [8]Max Planck Institute for Empirical Aesthetics

On the Ups and Downs of Visual Perception
Ying Joey Zhou (chair) and Saskia Haegens (co-chair)

Despite the fact that our perceptual experience is continuous, a large body of research has shown that the perceptual system operates discretely, resulting in optimal and non-optimal moments for sensory processing. Indeed, fluctuations of spontaneous neural activity (both oscillatory and non-oscillatory) contribute to the ups and downs of perception, with a low state of excitability in the sensory circuits more likely to lead to perceptual errors. However, it is unclear whether fluctuations in excitability simply reflect the overall arousal of the sensory system, or whether they carry content-specific perceptual knowledge about the incoming input. Furthermore, it is a matter of ongoing debate whether these spontaneous fluctuations are governed by brain oscillations—the idea being that sensory input is processed more optimally when it arrives at the excitatory phase of an oscillatory cycle. Despite reported correlations between spontaneous oscillations with trial-to-trial perceptual variability (e.g., spontaneous alpha oscillations predict whether a stimulus is perceived or not), the underlying neural mechanism via which these spontaneous oscillations promote (or dampen) sensory processing remains unclear. Moreover, if the internal neural rhythm determines how the external sensory input is processed, the immediate question is whether top-down control processes can use these rhythms for goal-directed behavior. For example, can the perceptual system actively "align" its excitatory phase to prioritize processing of the relevant input?

In this symposium, we will present new work using both behavioral and neural measures to address the above-mentioned questions. Dr. Biyu He will kick off the symposium with recent work from her lab on distinct mechanisms through which spontaneous neural activity influences object perception. Joey Zhou will discuss her project on neural mechanisms via which spontaneous oscillatory activity modulates predictive perception. Building up on this, Dr. Lucia Melloni will then discuss the role of perceptual predictions in stabilizing and shifting perception. Dr. Ayelet Landau will extend the focus and present work by her lab on the brain's top-down use of its neural rhythms in perception. Finally, Dr. Laura Dugué will further the discussion on top-down control of these neural rhythms and present a series of studies from her lab on attentional exploration and selection.

A dual role of pre-stimulus spontaneous neural activity in visual object recognition
Biyu Jade He
New York University School of Medicine, New York, USA
Preexisting brain states have enormous influences on conscious perception. Depending on the preexisting brain state at the time of stimulus arrival, a physically identical stimulus may be consciously perceived or not, a visual object may be consciously recognized or not, and we may perceive something that is not out there. In this talk, I will describe our recent work that combines magnetoencephalography (MEG) and 7 Tesla fMRI to investigate the role of prestimulus spontaneous activity (Baria et al., PLoS Comput Biol. 2017; He, TiCS 2018; Podvalny et al. Nat Commun 2019) in shaping conscious visual perception. Using multivariate analysis applied to sensor-level activity patterns recorded before stimulus presentation, we identified two separate spontaneous neural processes that influence visual recognition in distinct manners: a non-content-specific (NCS) process, which disregards stimulus category and correlates with pupil-linked arousal, and a

content-specific (CS) process, which facilitates recognition in a category-specific manner and does not correlate with pupil size fluctuations. The two processes have doubly-dissociable influences on perceptual processing: the NCS process shifts detection criterion whereas the CS process enhances perceptual sensitivity. Our findings point to a unifying framework for conceptualizing the functional role of spontaneous activity in perception.

The role of pre-stimulus oscillatory activity in predictive perception

Ying Joey Zhou1, Floris de Lange1, Saskia Haegens1,2
1 Donders Institute for Brain, Cognition, and Behaviour, Nijmegen, the Netherlands
2 Columbia University, New York, USA

Several studies have shown that the state of our brains before we receive external sensory input influences how neurons in the brain encode this input and, consequently, whether or not we perceive them. Ongoing brain oscillations in the alpha band (8–14 Hz) are proposed to play a key role in setting these brain states. In my talk, I will present our recent human MEG study on perceptual detection of ambiguous stimuli. Using a novel paradigm, subjects' decision criterion was qualitatively manipulated (i.e., we were able to shift subject's criterion to either a more conservative or more liberal state). We show that such criterion shifts do not require shifts of alpha states. Rather, ongoing alpha-band activity in early visual regions predicts the quality of visual information decodable in neural activity patterns, and subsequently human subject's detection sensitivity. Our results provide comprehensive evidence that visual representation is modulated by ongoing alpha-band activity, and advance our understanding on how, when faced with unchanging external stimuli, internal neural fluctuations influence perception and behavior.

The role of prior knowledge in perception and cognition

Lucia Melloni1,2
1 Max Planck Institute for Empirical Aesthetics, Frankfurt, Germany
2 New York University School of Medicine, New York, USA

Despite the fact that sensory input is continuous, we perceive it as punctuated. For instance, when hearing a continuous acoustic stream, we hear breaks and pauses between words and sentences in places when there is none. A similar phenomenon occurs during event perception, where we break the continuous input based on expectations or situational models. Intriguingly, we fail to perceive breaks in the continuous stream as in the case of blinks and eye movements. We are pursuing the hypothesis that expectations either based on prior experience and abstract knowledge and/or motor-predictions provide the mechanism for segmentation or failure thereof. In this talk I will present a series of studies in which we have exploited perceptual illusion to investigate the role of priors in stabilizing or changing perception using a combination of psychophysics and functional magnetic resonance imaging, and invasive electrophysiology.

Rhythmic sampling — the structure of our perceptions

Ayelet Landau
The Hebrew University of Jerusalem, Jerusalem, Israel

Neural signatures can entail rhythmic temporal structure. Such patterns have been known and measured, invasively, as well as noninvasively, for almost a century. What is the functional relevance of brain rhythms? What type of mechanisms can brain rhythms
support? In my talk I will present human psychophysics and MEG studies that support the notion of rhythmic sampling — a temporal structure we find in perceptual performance. In the lab, we find a characteristic temporal structure that governs attention. Examples from selection processes at different levels of the visual hierarchy will be discussed. Those range from spatial selection, feature-based selection as well as occular channel selection. Finally I will also present work on rhythmic sampling in audition in

individuals with and without visual experience. I will assess whether rhythmic sampling might be a domain-general property of perceptual selection across different
systems and discuss the possible generative underlying mechanisms for consideration.

Theta and alpha: the rhythms of attentional exploration and selection

Laura Dugué1,2,3
1 CNRS (Integrative Neuroscience and Cognition Center, UMR 8002), Paris, France
2 Université de Paris, Paris Descartes, Paris, France
3 Institut Universitaire de France (IUF), Paris, France

Covert attention can explore the visual environment in the absence of eye or head movement and select information to facilitate its processing. Mounting evidence suggests that the phenomenological, continuous stream of our attentional experience relies on a series of discrete moments, similar to the snapshots of a video clip. I will present a series of experiments, using multimodal functional neuroimaging combined with psychophysical measurements in healthy humans, suggesting that attentional exploration and selection are rhythmic processes, and are supported by rhythmic brain signals, i.e. oscillations, in distinct frequency bands. I will argue that theta oscillations (4–7 Hz) support rhythmic, attentional exploration, involving both visual and higher-level brain regions. Alpha oscillations (8–13 Hz), however, support rhythmic attentional sampling when attention is sustained at a particular visual location. Finally, I will present the latest work of our lab investigating the spatio-temporal organization of such rhythms. Using psychophysics combined with electro-encephalography, our new results provide a systematic characterization of the effect of the spatial distribution within occipital cortex of theta and alpha brain oscillations on rhythmic visual performance across retinotopic space.

What can deafness and blindness tell us about cognition?

Velia Cardin[1], Davide Bottari[2], Josefine Andin[3], Stefania Benetti[4], Amir Amedi[5]
[1]University College London, [2]IMT School for Advanced Studies Lucca, [3]Linkoping University, [4]CIMeC – University of Trento, [5]The Baruch Ivcher Institute For Brain, Mind & Technology, Interdisciplinary Center Herzliya

The extraordinary capacity of the brain for functional and structural reorganisation is known as neural plasticity. Understanding this phenomenon not only provides insights into brain function, but also into its potential for change and enhancement, with implications for sensorimotor substitution, artificial intelligence, policy and education.

Focusing on congenital deafness and blindness, this symposium will discuss the influence of sensory absence on the organisation of cognitive processing in the human brain. The study of higher-order cognitive functions has been focused strongly on neurotypical individuals or those with neurological disorders. Less research has tried to understand the effects of sensory deprivation on such functions, when indeed sensory systems feed and interact with all aspects of cognition. Congenital deafness and blindness constitute some of the most striking cases of neural plasticity. Studying perceptual and cognitive processes in congenitally deaf and blind individuals unravels the impact that sensory developmental experience has on the organisation of cognitive networks in the brain, and how these processes are differentially affected by nature and nurture.

This symposium brings together world leaders in the study of deafness and blindness, at all stages of their careers, to discuss the mechanisms that result in activity in the same cortical region supporting different perceptual and cognitive experiences in deaf, blind, hearing and sighted individuals. This multidisciplinary group of speakers will discuss psychophysical, neuroimaging, electrophysiological and sensory-substitution studies revealing the functional and anatomical reorganisation caused by deafness and blindness, and their consequences on perceptual and cognitive processes such as executive functions, language, social and spatial cognition.

Benetti will present recent work on functional specialization and reorganization within the face-voice processing systems of individuals who recovered from early blindness due to bilateral eye cataracts or experienced profound and prolonged deafness since early in life. She will then illustrate the potential implications for our understanding of how innate programs and sensory experience interact and guide the functional specialisation of this brain network.

Andin will show that the secondary auditory cortex of deaf early signers reorganises to process sign-based working memory. Activation of this region does not, however, increase with either increasing working memory load or poor stimulus resolution. Instead, frontal regions are sensitive to working memory load, and occipital regions are sensitive to resolution, suggesting that mechanisms underlying visual and auditory language processing under adverse conditions are at least partially separate.

Cardin will discuss the impact of deafness and language on the organisation of executive functions in the brain. She will show that the absence of early sensory stimulation results in different profiles of activations in cognitive networks in deaf and hearing individuals. Specifically, the absence of auditory stimulation during early development modulated the functional reorganisation of temporal and frontoparietal regions differentially for executive functions such as working memory, planning, inhibition and interference.

Amedi will discuss nature vs. nurture factors in shaping up category selectivity and topographic maps in the human brain. He will discuss the technology, behavior and neural correlates of novel Visual-to-Auditory and Speech-to-Touch Sensory-Substitution-Devices. His findings support a paradigm shift in the conceptualisation of the brain by suggesting that sensory experience during critical periods is not necessary to develop anatomically consistent specialisations in higher-order ‘visual’ or ‘auditory’ regions.

Bottari will provide evidence demonstrating the experience-dependence of the cortical organisation of the face processing and social identity systems. By using EEG frequency-tagging, he will provide evidence that in congenitally deaf individuals different experience-dependent neural changes occur as a function of the aspect of face processing. These changes are revealed by intramodal effects comprising alterations of the lateralisation of the visual cortex response and by crossmodal effects as suggested by a greater activation of the auditory cortex.

Overall, this symposium will show that deafness and blindness provide not only an opportunity to learn about sensory processing and crossmodal plasticity, but more generally about the capabilities of the brain, communicating insights that can be applied across all areas of neuroscience.

Dynamic Metacognition

Dr Kobe Desender[1,2], Dr Annika Boldt[3], Dr Lucie Charles[3], Dr Shannon Locke[4], Dr Romy Frömer[5]
[1]University Medical Center Hamburg-Eppendorf, [2]Ghent University, [3]Institute of Cognitive Neuroscience, UCL, [4]Laboratoire des Systèmes Perceptifs, Département d'Etudes Cognitives, ENS, [5]Brown University

Symposium abstract
Monitoring our actions and decisions is a key function of the brain, as it allows to dynamically and strategically optimize behavior. Despite the wide relevance of metacognition in various fields of research, the study of metacognition is often approached from a highly static point of view. For example, the reigning model of confidence assumes that a single bout of evidence determines both the choice and our evaluation of that choice. This stands in contrast with current knowledge about the dynamic process by which the brain interacts with its environment and makes decisions by dynamically sampling evidence from that environment. In the current symposium, we will broaden the scope of metacognition, and target its dynamic aspects from various perspectives. To achieve this, we will bring together a group of experts with a strong background in cognitive neuroscience and computational modeling, who will showcase recent work on how metacognition and confidence arise from the dynamic sampling of evidence.

Speaker I: *Shannon M Locke*, Michael S. Landy, & Pascal Mamassian
Laboratoire des Systèmes Perceptifs, Département d'Etudes Cognitives, ENS, PSL, CNRS, France
Performance Monitoring for Sensorimotor Confidence
Interactions with external world typically involve a complex interplay between action and perception, with the perceived outcome of previous movements influencing subsequent movements. When there is no external feedback concerning sensorimotor performance, the actor must make subjective evaluations of performance from a continuous stream of sensory and motor evidence (i.e., metacognition). Yet, very little is known about how humans sample this evidence to form such judgements of sensorimotor confidence. Can they dynamically monitor their performance? Or do they rely on cues to sensorimotor uncertainty to infer how likely it is they performed well? We investigated sensorimotor metacognition in two visuomotor tracking experiments, where participants followed an unpredictably moving dot cloud with a mouse cursor as it followed a random trajectory. Their goal was to infer the underlying target generating the dots, track it for several seconds, and then report their confidence in their tracking as better or worse than their average. In Experiment 1, we manipulated task difficulty with two methods: varying the size of the dot cloud and varying the stability of the target's velocity. In Experiment 2, the stimulus statistics were fixed and duration of the stimulus presentation was varied. We found similar levels of metacognitive sensitivity in all experiments, with the temporal analysis revealing a recency effect in the dynamics of metacognition, where error later in the trial had a greater influence on the sensorimotor confidence. In sum, these results indicate humans predominantly monitor their tracking performance, albeit inefficiently, to judge sensorimotor confidence.

Speaker II: *Lucie Charles*
Institute of Cognitive Neuroscience, UCL, United-Kingdom
Introspecting influence in choice: accuracy of metacognitive reports in detecting choice bias
What do we know about the factors that influence our decisions? Are we aware of the true reasons of our choices? The ability to introspect and evaluate the origin of our actions constitutes a key metacognitive function. However, little is known of the cognitive processes that underlie our subjective sense of being able to detect and resist unwanted influence. In this talk I will present new studies investigating participants' ability to make decisions free of influence and introspect how much their decisions can be biased by irrelevant information. In a series of novel behavioural and neuroimaging experiments, we measured participants' ability to voluntarily ignore information and detach their choice from potential bias by irrelevant or unreliable perceptual information. By asking participants to evaluate after each decision how

much they were influenced by a given piece of information, and comparing these ratings to how much they were actually biased on each trial, we were able to reveal novel findings on the dynamics of choice introspection. First, sensory input influenced action selection between alternative actions even when participants were trying to ignore it. Second, the direction of such biasing effect could be manipulated experimentally. Third, participants remained largely unaware of being influenced in their choices. And fourth, participants often mistook acting in opposition with incoming perceptual information for not being influenced by it.

Speaker III: *Romy Frömer*[1 2], Matthew R. Nassar[2], Rasmus Brucker[3], Birgit Stürmer[4], Werner Sommer[1], & Nick Yeung[5].
1. Humboldt-Universität zu Berlin, 2. Brown University, 3. Freie University Berlin, 4. International Psychoanalytic University, 5. University of Oxford
I knew that! Error Magnitude Predictions and Confidence therein Regulate Feedback Processing and Learning.
Influential theories emphasize the importance of predictions in learning: We learn from feedback to the extent that it is surprising, and thus conveys new information. This surprise should be reduced if individuals detect execution failures prior to feedback. Here we propose that individuals detect such execution failures by predicting outcomes of their actions and assessing their confidence in those predictions to control learning from feedback. Based on this proposal it follows that outcome predictions and confidence judgments made prior to feedback should modulate how feedback is processed. In line with predictions from a computational model implementing this proposal we find that people who are better at calibrating their confidence to the precision of their predictions learn better. Using EEG we demonstrate that predictions and confidence modify how feedback is processed. Thus, predictions and confidence modulate the efficiency of learning from feedback, likely via adaptive feedback use based on credit assignment.

Speaker IV: *Annika Boldt*[1], Kobe Desender[2 3], & Nick Yeung[4]
1. Institute of Cognitive Neuroscience, UCL, United-Kingdom. 2. University Medical Center, Hamburg, Germany. 3. Ghent University, Ghent, Belgium. 4. Oxford University, Oxford, United-Kingdom.
Suboptimal reliance on incongruent evidence for the computation of confidence
Evaluating one’s own decisions is a key feature of cognition, as it allows to dynamically adapt behavior. Normative models argue that the brain makes optimal use of the available evidence in order to make such evaluations. Thus, when judging the accuracy of a decision across several samples of evidence, the normative strategy would be to equally weight each sample. Here, we present data from nine experiments in which human participants judged the average color of eight shapes and then additionally rated their confidence in this decision. Contrary to predictions of the normative model, in all datasets participants excessively relied on evidence that was incongruent with the choice made. This suggests that, rather than using an optimal strategy, participants use heuristics when evaluating their own performance. Importantly, our results also go against recent, opposite findings which have suggested that decision-incongruent evidence tends to be ignored when reporting confidence. We explore possible explanations for why the brain might have developed this mechanism, such as a simple heuristic which assumes that highly incongruous evidence is associated with high variability.

Speaker V: *Kobe Desender*[1 2], Tobias H Donner[1], & Tom Verguts[2]
1. University Medical Center, Hamburg, Germany. 2. Ghent University, Ghent, Belgium
Dynamic expressions of confidence within an evidence accumulation framework
Human observers can reliably report their confidence in the choices they make. An influential framework conceptualizes decision confidence as the probability of a decision being correct, given the choice made and the evidence on which it was based. This framework accounts for a diagnostic signature of human confidence reports: an opposite dependence of confidence on evidence strength for correct and error trials. However, the framework does not account for the temporal evolution of the above signature because it

only describes the transformation of a static representation of evidence into choice and the associated confidence. Here, we combine this framework with another influential framework: dynamic accumulation of evidence over time. We propose that confidence reflects the probability of being correct, given the choice and accumulated evidence up until that point. This model predicts an increase of the above interaction between evidence strength and choice correctness as a function of time. We tested, and confirmed, this prediction in human behavior during random dot motion discrimination, in which confidence judgments were queried at different points in time. We conclude that human confidence reports reflect the dynamics of the probability of being correct given the accumulated evidence and choice.

An exploration of the multi-scale and multi-dimensional dynamics of consciousness and cognitive processes

Dr. Jacobo Sitt[1], Dr. Tristan Bekinschtein[2], Dr. Damian Cruse[3], Dr. Victoria Leong[2,4]
[1]ICM Institute - INSERM, [2]Department of Psychology, University of Cambridge, [3]Birmingham University, [4]Division of Psychology, Nanyang Technological University

Recent results demonstrate that consciousness and cognitive processes have specific characteristics that are based on the temporal dynamics of ongoing brain activity, the complexity of these dynamics, and its coordination over distant cortical regions and across individuals. In this symposium, we will explore some of these results in four presentations spanning from changes in decision making within alertness fluctuations, states of consciousness across species, language processing, and synchronized activity in hyperscanning.

Presentation 1
Title: What do you lose first? Behavioral and neural dynamics of decision-making when challenged by alertness fluctuations.

Speaker: Dr. Tristan Bekinschtein (in collaboration with Daniel Bor, Andres Canales-Johnson, Anat Arzi, Valdas Noreika, Alejandro Ezquerro-Nassar, Barbara Jachs)
Affiliation: Department of Psychology, University of Cambridge

How resilient of vulnerable are cognitive processes when challenged by internal and external modulators? In these series of experiments, we show how changes in alertness via normal arousal fluctuations or pharmacological challenges modulate the behavioral and neural dynamics of decision-making.
The complexity of neural networks can be used as a characteristic of the cognitive system to predict performance, and this capacity is enhanced when the participant is changing conscious state (getting sedated or getting drowsy). How resilient are the brain networks to the alertness challenge? When in the course of perception, decision, and action is the system hit first? Using EEG neural dynamics (microstates, complexity, connectivity, graph theory) during resting state and decision making tasks, we characterize the fragmentation of cognition and the neural and behavioral reconfiguration that humans undergo to maintain performance in the face of arousal challenges.
We see that non-linear neural measures partially predict performance when drowsy or sedated. We show that even executive functions can resist the challenge, but they display a neural reconfiguration to attain similar performance. We see that this is mostly reflected in change in the connectivity networks. We further show how adaptative the brain can be to these changes and how much these small fluctuations can affect most cognitive neuroscience experiments. We characterize conscious access, metacognitive perceptual decisions, spatial awareness, and central interference effects to show the commonalities and differences of how consciousness fluctuations fragment and reconfigure cognitive processes.

Presentation 2
Title: Brain patterns dynamics and states of consciousness
Speaker: Dr. Jacobo Diego Sitt
Affiliation: ICM Institute – INSERM. Paris, France

Every day when we fall asleep and wake up again, we naturally lose and recovers consciousness. Loss of consciousness is also associated with abnormal conditions, such as coma, vegetative state, complex epileptic seizures, or general anesthesia. However, the precise neuronal mechanisms responsible for the loss of consciousness in these conditions are poorly understood. Recent work in the field of consciousness has focused on finding associations between behaviourally defined states-of- consciousness and patterns of brain activity observed during those states.

In this presentation, I will show the relevance of dynamical patterns of brain activity observed across different types of states-of-consciousness. I will show results in humans and non-human primates, demonstrating that conscious states are associated with brain patterns of recurrent coordinated activity. In contrast, unconscious states are related to low inter-areal coordinated brain patterns.

A dynamic pattern of coordinated and anticoordinated functional magnetic resonance imaging signals characterize conscious human healthy participants, patients, and non-human primates. On the other hand, the brains of unresponsive patients and anesthetized non-human primates primarily show a pattern of low interareal phase coherence mainly mediated by structural connectivity and had smaller chances to transition between patterns.

In conclusion, these results establish that consciousness rests on the brain's ability to sustain rich brain dynamics and pave the way for determining specific and generalizable fingerprints of conscious and unconscious states.

Presentation 3

Title: Speech comprehension across levels of consciousness
Speaker: Dr. Damian Cruse
Affiliation: University of Birmingham, England

The conscious experience of understanding spoken language, arising from a complex hierarchy of unconscious and controlled processes over multiple time-scales, provides a fruitful experimental paradigm for unraveling the neural basis of consciousness. Speech comprehension is also arguably the residual cognitive capacity that is most important for clinical decision-making in disorders of consciousness. To be diagnosed as aware and to benefit from rehabilitation, a patient must produce purposeful movement in response to verbal commands – i.e. they must understand what is being said to them, and respond appropriately. However, we know that motor responsiveness is diminished or inconsistent in many patients, and that concomitant motor impairments have occluded high levels of residual cognition – even the ability to communicate via brain-computer interface. While examinations of brain responses to speech have offered some insight into the residual capacity for speech processing in disorders of consciousness, it is a considerable challenge to infer from these responses that the patient is having a conscious experience of comprehension. In this talk, I will present some putative electrophysiological markers of conscious processing and comprehension of speech in healthy individuals, and examine how they manifest in individuals with disorders of consciousness. Together this data helps to delineate the neural correlates of the conscious experience of meaning from the array of processing that occurs without reportability.

Presentation 4

Title: Exploring the neural basis of early shared emotional experiences using parent-infant EEG hyperscanning
Speaker: Dr. Victoria Leong1
Affiliation: Department of Psychology, University of Cambridge, UK and Division of Psychology, Nanyang Technological University, Singapore

During early life, parent and infant function as a mutually co-ordinated unit whose emotion, behaviour and neurophysiology are intimately connected and synchronised in a "dyadic dance”. Close emotional co-ordination and communication between parents and their offspring engenders healthy development of affective cognition and emotional regulation skills. To explore how the interpersonal dynamics of early conscious emotional experiences unfold across interacting brains, here we employ a “two-person neuroscience” (i.e. hyperscanning) approach using dyadic-electroencephalography (EEG).

Fifteen mothers modeled positive and negative emotions during object-based social interaction with their infants, whilst their EEG activity was concurrently acquired. Mothers’ and infants’ intra-brain and inter-brain connectivity during maternal expression of positive and negative emotions were computed using directed (partial directed coherence, PDC) and non-directed (phase-locking value, PLV) metrics. Graph theory-based indices were then used to examine how maternal emotion modulates complex hierarchical features of the parent-infant alpha neural network.

We found that mothers and infants showed significantly stronger integration of their neural processes during positive than negative emotional states (i.e. higher interbrain Density and Strength, lower Divisibility). Furthermore, directed inter-brain connectivity metrics (based on PDC) revealed that mothers had a stronger directional influence on the dyadic network during positive emotional states. In contrast, infants had a more substantial influence during negative emotional states (see Figure 1). These results indicate that the parent-infant inter-brain network is exquisitely sensitive to the emotional tone of social interactions, and may help to mediate our conscious experience of shared emotions with early social partners.

Neurophysiological mechanisms that support novel-word learning in typical and atypical language learners

Monica Wagner[1], Tiina Parviainen[2], Jarmo Hämäläinen[2], Lilli Kimppa[3], Yury Shtyrov[4]
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(Introduction)
Individuals with Developmental Language Disorder and Dyslexia have difficulty learning novel-word forms. These deficits restrict vocabulary growth, particularly as atypical learners approach adolescence, and affect daily life, as well as academic and career opportunities. Over the past two decades, research has begun to explore neural mechanisms that support novel-word learning. The aim of this symposium is to present a body of this research, which assesses various levels of cortical processing that contribute to novel-word learning. We begin by presenting electrophysiology (EEG) studies that explore cortical-level enhancement of acoustic structures associated with native-language phonotactic patterns, which should support streamlined processing of pre-lexical forms. This is followed by studies using magnetoencephalography (MEG) to examine hemispheric processing of pre-lexical and lexical forms and inter-hemispheric relationships at varied stages of language development in both typical and atypical-language learners. Subsequent presentations address neural mechanisms that sub-serve learning of pre-lexical and lexical-word forms. These include studies using EEG and MEG to investigate processes that support learning sound-letter associations and EEG studies that investigate novel word-form learning and the effect of having learned multiple languages on learning unfamiliar phonological patterns within word forms. We conclude with a series of studies that explores the formation of memory circuits for novel words and their semantic associations. These processes are examined using multiple neurophysiological methods, including EEG, MEG, transcranial magnetic stimulation (TMS), transcranial direct current stimulation (tDCS) and magnetic resonance imaging (MRI).
(Presentation 1)
Evidence suggests that acoustic structures associated with native-language phonotactic patterns are enhanced within auditory pathways for perception. This process is envisioned to streamline sensory processing, supporting novel-word learning. Our EEG studies have compared encoding of native and non-native phonological sequences within non-words. Native-English and native-Polish adults listened to same and different non-word pairs within attend and passive conditions. Non-words within the pairs contained the onsets /pt/, /pət/, /st/ and /sət/ that occur in both the English and Polish languages with the exception of /pt/, which never occurs in English without a preceding vowel. Examination of the auditory evoked potentials (AEP) to the first words in the pairs identified signature waveforms (P1-P1-P2, T-complex) that were specific for each onset sequence and consistent across listening conditions. These waveforms were highly-similar for the language groups, suggesting acoustic-phonetic levels of processing, with the T-complex also modulated by language experience. Time-frequency analyses of the EEGs to the first words from two bilateral source-level channels in auditory cortex revealed language-specific processing in low gamma and theta at early cortical stages. Increased power to the /pt/ onsets was found in low gamma (31-40 Hz, 0-400 ms) from a right auditory source-level channel for the English compared to the Polish listeners. Also, differences in inter-trial phase locking to the /pt/ compared to /pət/ onsets reached significance only for the Polish group. This suggests increased variability in phase synchrony to the unfamiliar contrast for the English listeners. We consider these results in light of atypical patterns of language learning.
(Presentation 2)
Disorders of language development are associated with impairments at different levels of the language processing pathway in the brain. Crucially, intact processing of auditory language is dependent on the recruitment of needed cortical processes in a correctly timed manner. MEG offers the unique ability to

follow the progression of activation representing the pre-lexical and lexical level processing of the incoming linguistic signal, with precise temporal and spatial resolution. Our MEG studies have characterized the time-course of auditory (and visual) language perception and comprehension in children. Specifically, we have explored the cortical sequence of language processing in children with typical language development, as well as the cortical indicators of compromised language learning abilities in adults and children with dyslexia and specific language impairment (developmental language disorder). Spatially-specific measures of activation strength and timing were correlated with relevant cognitive measures including phonological skills, verbal short-term memory, vocabulary and linguistic reasoning. Our results indicate distinct anomalies in the auditory language processing pathway in specific language impairment and dyslexia. Comparing the cortical resources utilized in auditory language processing in typically developed vs. compromised learners highlights especially the role of left hemisphere auditory areas and/or age-appropriate inter-hemispheric balance for competent language development. Our findings also suggest that understanding of the neuro-cognitive determinants of impaired language learning requires integration of neural and behavioral measures at different levels of development and in children with varied skill level.

(Presentation 3)

Learning of letter-speech sound associations is a crucial step towards reading words. Previous studies have found changes in brain activity after learning novel grapheme-phoneme associations near posterior superior temporal sulcus and inferior temporal areas. Learning of grapheme-phoneme associations was examined while training took place. In the first experiment, automatic extraction of systematic AV associations was examined using EEG. After 5 min of exposure the auditory P2 was enhanced to systematic AV pairings and after 10 min of exposure a later time window around 400 ms exhibited larger amplitudes. In the second experiment, participants were actively learning to associate syllables with novel characters during MEG recording. After 10 min of training MEG responses from frontal and inferior temporal cortex were enhanced at ca. 350 ms and 500 ms, respectively. In the third experiment, participants were memorizing phoneme-letter pairs and then tested for recognition of the correct pairs in consecutive blocks. Enhanced brain activity was observed after learning at 400 ms in the superior temporal regions in response to the AV pairs. Interestingly, learning cues during memorization blocks exhibited large activity before learning at 300 ms in the inferior temporal regions. Auditory P2 seems to quickly show sensitivity to regularities in AV stimuli even without active effort to learn AV associations. Time window around 400 ms was shown to be sensitive to AV associations after learning had occurred, in line with earlier studies. The learning process is supported by attentional mechanisms and by successful integration of learning cues to the AV associations.

(Presentation 4)

The development of large lexicons is enabled by the brain's ability to rapidly acquire new words. Some of the learning happens effortlessly, yet in some developmental disorders, language acquisition is particularly arduous. I will present electrophysiological evidence for a neural mechanism supporting novel spoken word-form learning via repetitive exposure. In typically developed (TD) adults, we showed that 15-30 minutes of passive exposure to novel spoken word-forms enhanced the lexical ERP response, which we suggest reflects neural memory-trace formation for new words. This was corroborated by a positive correlation with recognition performance. The enhancement originated in the left perisylvian cortex, and was established regardless of the locus of attention, indicating automaticity of this learning mechanism. In contrast, repetition-related suppression of existing memory-trace activation occurred for familiar words. Furthermore, individual background in non-native language learning had a marked effect on how efficiently the memory trace formation for novel word-forms with familiar and unfamiliar phonology took place. Previous experience with non-native languages seems to improve the acquisition of new, phonologically unfamiliar, spoken input. Studies with TD children demonstrated even faster automatic memory-trace build-up of novel word-forms and manifested flexible exposure-related change in the memory circuits of already established complex words. Children with atypical language development (dyslexia and developmental language disorder) lacked such neural dynamics, even after extended exposure period, showing no changes in the relevant neural responses. This refers to underlying deficits in the neural mechanism that facilitates the acquisition of lexical representations in language disorders.

(Presentation 5)

We review our recent studies addressing the brain mechanisms of online formation of representations for novel words. To register functional dynamics during the learning process, we used electro- and magnetoencephalography (EEG, MEG) to track memory circuit activation. Furthermore, to tackle the causal role of the neurophysiological processes at hand, we used brain stimulation methods – transcranial magnetic and direct current stimulation techniques (TMS, tDCS) – to interfere with the cortical function during learning. Finally, we used novel structural MRI methods (diffusion kurtosis imaging, DKI) to query possible microstructural changes underpinning word acquisition. We find that frontotemporal neocortical circuits exhibit complex activation pattern changes in the process of acquiring novel representations, which chiefly become exhibited as a gradual increase in activation for novel representations. By using neurostimulation, we could show the role of modality-specific systems in the acquisition of semantics: e.g., stimulation of motor cortex using TMS affects learning of action-relation words. Modulating activity in the language network using tDCS has a non-specific facilitatory effect on learning, and may also specifically change the balance between the acquisition of concrete and abstract language. Finally, our microimaging experiments using DKI suggest rapid plastic changes taking place in the microstructure of a range of cortical areas within even a short (40 minutes) language learning session. We conclude that our brain is capable of a rapid formation of new cortical memory circuits online, as it gets exposed to novel linguistic patterns in the input. This becomes evident in functional and structural neural dynamics, and through causal relationships.

The brain in complex social contexts

Yoni Levy[1,2], Prof. Abraham Goldstein[3], Ville Harjunen[4], Niloufar Zebarjadi[1]
[1]Aalto university, [2]Reichman University, [3]Bar-Ilan University, [4]University of Helsinki

Symposium title:
The brain in complex social contexts
Chair: Jonathan Levy (Aalto University; Reichman University)
Presenters: Abraham Goldstein (Bar-Ilan University), Ville Harjunen (University of Helsinki), Niloufar Zebarjadi (Aalto University), Jonathan Levy (Aalto University; Reichman University)

Symposium summary:
The past decade has seen a growing interest in the neural mechanisms underlying social cognition. Yet, very little research has monitored these mechanisms in complex societal contexts. In this symposium, four talks will present novel neuroimaging findings on various social phenomena, and will discuss the added value of this approach. The first talk will present findings of speaker charisma on neural similarity among listeners. Then, in the second talk, two virtual-reality combined with EEG studies will present the influence of ethnicity and bodily resemblance on sensorimotor processing of vicarious pain and skin contact. The third talk will demonstrate the relation between political Ideology and the empathy neural response to vicarious suffering. Finally, a decade-long study will report on the neuro-development of empathy and social behaviour. Altogether, this symposium will showcase insights from the study of the brain in various complex situations, projecting innovative current approaches into the near future.

1. Inter-brain synchrony in mediated communication: factors beyond the message
Authors:
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2 DeGroote School of Business, McMaster University

Abstract
In communicating a message, the content (narrative or facts) is encapsulated in physical characteristics (acoustic attributes, voice rhythm, prosody) and is accompanied by other non-verbal cues (hand and body gestures, facial expressions, posture, gaze), as well as rhetoric and emotion evoking means, and is presented within a situational context (social, non-social) to an audience with prior beliefs and attitudes. Peripheral aspects of the message that enhance listeners' alignment to the speaker may be manifested as inter-subject brain synchrony. In a series of studies measuring inter-subject correlations (ISC) with MEG we focused on four aspects: a) non-verbal aspects of delivery, b) emotion and motivation induced by message, c) situational context (social/non-social) and d) audience prior attitude towards the communicator. Speeches induced ISC in sensory areas overall. The effects of speaker charisma, non-verbal aspects of delivery, as well as motivation and emotion, manifested as greater ISC in higher-order areas mainly in the beta and gamma bands. We believe that our findings can help to optimize mass mediated messages and to elucidate the cognitive and affective processes underlying message reception and audience engagement.

2. Influence of ethnicity and bodily resemblance on sensorimotor processing of vicarious pain and skin contact
Ville Harjunen, University of Helsinki
Abstract
People are shown to exhibit greater vicarious responses to ethnic ingroup members' than outgroup members´ pain. It has remained unclear, however, whether this ingroup bias is malleable and whether it extends also to the processing of interpersonal skin contact. The presentation will give an overview of two

VR-EEG studies where sensorimotor processing of vicarious pain and interpersonal touch were studied by manipulating the perceiver's bodily appearance using VR technology. In the first study, the perceivers were put in a different color body and were shown virtual humans with similar or different skin color being touched by pain-inducing (e.g. needle) or non-noxious objects (e.g. feather). The results showed that transfer to a different color body modulates ingroup bias in sensorimotor beta oscillations. The second study examined sensorimotor processing of interpersonal proximity and touch in intergroup encounters. The participants saw a set of immersive 360◦ videos from a first person's perspective of another person approaching and touching the participant's arm. The videos depicted persons from various different ethnic backgrounds. Induced cortical oscillatory responses were examined at different stages of the physical contact to examine responses to different groups. In the presentation, hypothesized effects and preliminary findings will be discussed.

3. Ideological values parametrically modulate empathy neural response to vicarious suffering.

Niloufar Zebarjadi, Aalto University

Abstract

Magnetoencephalography (MEG) has not been applied thus far to investigate political psychology. In the current study, we exploited MEG spatiotemporal resolution to test whether empathy neural response to vicarious suffering is stronger among political leftists (i.e., liberals) as compared to political rightists (i.e., conservatives). The literature in political psychology tends to point to this ideological asymmetry, however, it leans on self-reports, which is often limited by subjective bias and conformity to social norms. Here, we aimed to test this asymmetry by investigating the neural empathy response and by exploring insights from the neural findings. We recorded oscillatory neural activity in fifty-five participants while they completed a well-validated neuroimaging paradigm for empathy to vicarious suffering. The findings revealed a typical rhythmic empathy response (i.e., in the alpha-band) in a typical neural substrate for cognitive empathy (i.e., the temporal-parietal junction). This empathy neural response was significantly stronger in the leftist than in the rightist group. In addition to this dichotomous division, the neural response was parametrically modulated by political inclination and driven by right-wing ideological values. This is the first study to reveal an asymmetry in the neural empathy response as a function of political ideology. The findings reported in this study further consolidate the self-reported literature in this research area of political psychology, and further suggest that ideological values can parametrically modulate empathy neural response to vicarious suffering. This study opens new vistas for addressing questions in political psychology by using MEG.

4. Social interaction and Chronic Adversity Shape the Neuro-Development of Empathy

Authors:
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Abstract

Exposure to chronic adversity impairs cognitive and affective processing. Yet, it remains unclear how adversity may affect the neuro-development of social-emotional behaviour; does it impair our ability to understand others and to feel for them (i.e., empathy), and our ability to socially interact with each other? In this prospective longitudinal study, we followed eighty-four children and their mothers (N = 168), while half of the sample was exposed to chronic war-related adversity (in Israel) for more than a decade. By using magnetoencephalography (MEG), we assessed the neural response to distressing stimuli (i.e., thereby probing empathy) and to vignettes depicting mother-child interaction (i.e., thereby probing social interaction). We found that chronic adversity affects higher-order representations of empathy in the brains

of both children and mothers, and that positive social interaction between mother and child separately predicted their ability to empathize. Furthermore, we found that the brains of mothers and their children synchronized during the perception of social interaction cues. Findings demonstrate the important roles of social interaction and chronic adversity, throughout life, in shaping the development of the social brain.

Neurocinematics: Investigation of intersubjectively shared experiences

Dr. Clare Grall[1], Prof. Uri Hasson[2], Dr. Heini Saarimäki[4], Dr. Pia Tikka[6]
[1]FINN Lab, Department of Psychological and Brain Sciences, Dartmouth College, [2]Hasson Lab, Psychology department and Neuroscience Institute, Princeton University, [3]Brain and Mind Laboratory, Department of Neuroscience and Biomedical Engineering, Aalto University, [4]Human Information Processing Laboratory, Faculty of Social Sciences, Tampere University, [5]Enactive Virtuality Lab, Baltic FIlm, Media, and Arts School, Tallinn University

The use of films and narratives as stimuli that mediate intersubjectively shared experiences has allowed expanding the scope of neuroscientific studies to socio-emotional and politico-cultural contexts. In this multidisciplinary area of research spanning neuroimaging, cognitive science, psychology, and film studies, it is one of the most topical questions how the temporally unfolding contextual situatedness of each subject relates to observed brain activity. The talks in this symposium address this challenge from different viewpoints.

Abstract 1

Leveraging the power of media to drive cognition: A media-informed approach to naturalistic neuroscience

Clare Grall

Over the last 15 years, neuroscientists have increasingly adopted media as stimuli in human neuroimaging research where they are commonly referred to as “naturalistic tasks.” The adoption of media stimuli, especially audio and audiovisual narratives, for neuroscience has led to a wealth of new insights into memory, language, emotion, and social cognition. However, to date, the process of choosing a specific piece of media has been largely ad hoc: researchers choose movies that they intuitively believe will evoke certain processes of interest, but typically do not consider formal features as defined by filmmakers, writers, and other media creators. At present, there is no guide outlining what to consider from a media perspective when selecting a preexisting media stimulus for a given experimental goal.
In this talk, I will address this gap by providing a practical, media-informed approach to guide psychologists and neuroscientists on their approach to media for neuroscience. I argue that rather than being “naturalistic” in the sense of spontaneous and unstructured, works of media offer complex and hierarchically-nested information that is deliberately crafted to elicit a particular audience experience. Therefore, if a neuroscientist wishes to study a particular cognitive process using a movie stimulus, having a basic knowledge of cinematic features, editing techniques, and genre conventions will allow them to more effectively realize the many advantages that media offer because they are artificial. With data from my team, I will discuss the importance of specific narrative features when using media stimuli to study brain function.

Abstract 2:

Using deep neural networks as cognitive models for how brains act in the natural world

Uri Hasson

Naturalistic experimental paradigms in neuroimaging arose from a pressure to test the validity of models we derive from highly controlled experiments in real-world contexts. In many cases, however, such efforts led to the realization that models developed under particular experimental manipulations failed to capture much variance outside the context of that manipulation. The critique of non-naturalistic experiments is not a recent development; it echoes a persistent and subversive thread in the history of modern psychology.

The brain has evolved to guide behavior in a multidimensional world with many interacting variables. The assumption that artificially decoupling and manipulating these variables will lead to a good understanding of the brain may be untenable.
Recent advances in artificial neural networks provide an alternative computational framework to model cognition in natural contexts. In contrast to the simplified and interpretable hypotheses we test in the lab, these models do not learn simple, human-interpretable rules or representations of the world. Instead, they use local computations to interpolate over task-relevant manifolds in high-dimensional parameter space. Counterintuitively, over-parameterized deep neural models are parsimonious and straightforward, as they provide a versatile, robust solution for learning a diverse set of functions in natural contexts. Naturalistic paradigms should not be deployed as an afterthought if we hope to build models of brain and behavior that extend beyond the laboratory into the real world.
In my talk I will discuss the relevance of deep neural models to cognition in the context of natural language and deep language models.

Abstract 3:

Naturalistic stimuli in affective neuroscience: the neural basis of perceived and experienced emotions

Heini Saarimäki

Naturalistic, dynamic stimuli such as movies and stories are increasingly used in affective neuroscience to study the neural basis of human emotions. Compared to traditional paradigms eliciting emotional processing with simple stimuli such as pictures or sounds, movies elicit strong emotions and allow brain imaging of emotions in more naturalistic settings. However, emotions as multimodal, highly distributed, and individually varied phenomena pose specific methodological challenges for naturalistic neuroimaging. Especially emotions are related to automatic changes in multiple functional components, including perception, physiology, behavior, and conscious experiences. During movie viewing, we automatically both perceive emotions portrayed by the characters and experience our own emotions elicited by the movie. Brain activity during movies thus reflects all these processes, suggesting that investigating emotions with movies depends on reliable modeling of dynamic, emotion-related features both in the environment and within the individual. In this talk, I will highlight how emotion-related features can be extracted from movies and combined with neuroimaging data. Drawing on our recent research, I demonstrate how we apply functional magnetic resonance imaging and movies to distinguish the neural basis of perceived and experienced emotions. I show that humans perceive and experience a wide array of distinct emotions during movie viewing, and different emotion categories recruit the brain to a different extent. While the emotions portrayed in the movies and the emotions experienced by the observers often align, I highlight how these two types of emotional processing are also sometimes decoupled.

Abstract 4:

Multidisciplinary viewpoints to the sense-making brain in context

Pia Tikka

Naturalistic neurosciences and its subfield neurocinematics (Hasson et al. Projections 2008) call for inquiry into the contextually situated nature of human experience and its bodily manifestation. In several studies, the correlation of neuro-physiological activity between subjects engaged with the same attentive task has been shown to relate specifically to narrative content rather than the medium. In Tikka et al. (2018) intersubjectively cognitive processes of narrative sense-making were found independent of whether the story was mediated via audiovisual film or text, in line with reading text against listening to the same text

(Deniz et al. 2019) or listening to the same text in different languages (Honey et al. 2021). In another study using the puzzle film Memento (dir. C. Nolan) we identified shared context-dependent neural fingerprints that could be related to cognitive reconstruction of the plot at moments when new context information was revealed (Kauttonen et al 2018). I suggest putting these findings into a bigger picture of triadic epistemology of narrative sense-making (Tikka & Kaipainen 2019; Tikka 2022). It implies analysing data in three perspectives: (1) psycho-physiological and neuroscientific experiments that unravel narrative-related unconscious bodily activity, (2) subjective reports of idiosyncratic narrative experience in terms of contextual reasoning, and (3) descriptions that map narrative content in shared terms. Interrelating these perspectives allows the following explanatory interrelations: Bodily activity analysed in reference to both (2) and (3), subjective reports mapped against (1) and (3), and finally projections of narrative content against (1) and (2). Though this amounts to an yet unseen multi-disciplinary effort, I believe it is both compelling and possible.

On the role of gamma activity and synchrony in information processing in the human brain: research and clinical evidence

Gabriele Arnulfo[1,2], Eshter Florin[4], Daniel Pacheco[3], Felix Siebenhuehner[2], Sheng Wang[2]
[1]University of Genoa, [2]University of Helsinki, [3]Heinrich Heine University Düsseldorf, [4]Universität Düsseldorf

Neuronal oscillations are ubiquitous phenomena in the human brain and have been linked to different aspects of everyday cognitive tasks such as memory consolidation, and sensory information processing. In particular, high-frequency (i.e. gamma and high-gamma) activity as measured by extracellular field potentials is gaining increasing interest for its highly local origin and its role in coding sensory information. Several lines of evidence show that gamma plays a central role in information routing (Palmigliano, 2017), memory (Griffiths, 2019) and processing of sensory input (Avanzini, 2017). Moreover, high-gamma activity such as ripples (130-200Hz) and fast-ripples (>200Hz) has been investigated with great interest because of its potential interpretation as proxy of underlying multi-unit activity (Buszaki, 2012) and as pathological biomarkers (Frauscher, 2018).
By presenting four different applications, in this symposium we will discuss the importance of gamma and high-gamma rhythms in perceptual and cognitive neuroscience. First, we will present a set of novel evidence that timely co-activations measured by phase synchronization of high-gamma activity are a robust and wide-spread phenomena of the human cortex during spontaneous and visual-motor tasks. Then we will concentrate on the interactions between gamma and slower rhythms and how cross-frequency interactions promotes information processing and coding. In particular we first will discuss how spontaneous brain activity shapes gamma responses and predict task performances during somatosensory and visual tasks. Then we will discuss the relevance of theta-gamma phase-amplitude coupling in the coding of episodic memories. Finally,
we will further discuss how gamma and high-gamma oscillations interact with theta and alpha rhythms via cross-frequency coupling in spontaneous and visual working memory tasks.

Long-range phase synchronization of high-gamma activity in human cortex - Gabriele Arnulfo
Inter-areal synchronization of neuronal oscillations below 100 Hz is ubiquitous in cortical circuitry and thought to regulate neuronal communication. In contrast, faster activities are generally considered to be exclusively local-circuit phenomena. We show with human intracerebral recordings that 100–300 Hz high-gamma activity (HGA) may be synchronized between widely distributed regions. HGA synchronization was not attributable to artefacts or to epileptic pathophysiology. Instead, HGA synchronization exhibited a reliable cortical connectivity and community structures, and a laminar profile opposite to that of lower frequencies. Importantly, HGA synchronization among functional brain systems during non-REM sleep was distinct from that in resting state. Moreover, HGA synchronization was transiently enhanced for correctly inhibited responses in a Go/NoGo task. These findings show that HGA synchronization constitutes a new, functionally significant form of neuronal spike-timing relationships in brain activity. We suggest that HGA synchronization reflects the temporal microstructure of spiking-based neuronal communication per se in cortical circuits.

Predicting task performance based on electrophysiological resting state networks – Esther Florin
Human performance differs not only between individuals, but also within individuals between repetitions of the same task. To understand these differences, we identify intrinsic dynamic brain features from spontaneous MEG recordings and the interaction between brain regions using Hidden Markov Models. The talk will focus on the relationship between spontaneous network activity and somatosensory behavioral and visual brain responses. Within the visual domain, gamma responses to visual stimuli vary substantially within and across participants. By applying Hidden Markov modelling to MEG data, we reveal that the trial-averaged gamma response depends on the individual network dynamics, inferred from slower brain activity

in the absence of stimulation (resting-state and task baseline). In addition, modulation of network activity in the task baseline influences the gamma response at the trial level. By leveraging a data-driven pipeline we provide novel insights into the spatial, spectral, and temporal dynamics of whole-brain networks and their relationship to behavioural variability.

Phase-coding of semantic memory representations during episodic retrieval – Daniel Pacheco
It has been proposed that neural phase coding supports a range of cognitive processes, including multi-item working memory, episodic memory, and mental time travel. In humans, this proposal has received empirical support from phase-amplitude coupling studies looking at the relationship between the amplitude of high-frequency activity and the phase of activity at a lower frequency, in particular theta. However, these analyses are agnostic to the specific content that is coupled to the theta phase and thus do not reflect “phase coding” in the narrower sense. We recently applied multivariate analysis techniques to identify stimulus-specific representational signals at the high temporal resolution provided by human intracranial electroencephalography (iEEG) data. The use of time-resolved representational signals allowed us to evaluate phase coding without having to assume that high-frequency activity is a proxy for the representation of specific content. Our analyses demonstrated the relevance of theta oscillations for hippocampal reinstatement of item-context associations and revealed the key signatures of volitional learning in the human brain by showing a phase-based segregation of semantically similar items during episodic memory retrieval.

Cross-frequency coupling of gamma and theta/alpha oscillations - Felix Siebenhuehner
One important question in our understanding of neuronal oscillations is how oscillatory processes of different frequencies are coordinated and integrated for cognitive function. While gamma oscillations are associated with bottom-up processing of sensory data and neuronal representations, low-frequency oscillations in the theta and bands are thought to underlie shifting of attention and cognitive control. Both gamma and low-frequency oscillations have been associated with performance in various tasks, such as working memory and visual attention.
Several forms of cross-frequency coupling have been proposed as possible mechanisms for the integration of oscillations of different frequencies. In my talk, I will discuss the two most promising mechanisms, phase-amplitude coupling and cross-frequency phase synchrony, which have been observed to couple low-frequency and gamma oscillations in animals and humans during resting-state and task performance.

Alterations in oscillation dynamics in understanding pathophysiology of brain diseases

Jaana Simola[1], Marina Diachenko[2], Dr Ehtasham Javed[1], David López-Sanz[3], Hanna Renvall[4]
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Alterations in oscillation dynamics in understanding pathophysiology of brain diseases

Neuronal oscillations and their inter-areal synchronization play a fundamental role in coordinating neuronal computations in neuronal circuits. Alterations in neural oscillation dynamics have been proposed to underlie pathophysiological mechanism in brain disorders. In recent years, novel approaches have begun to highlight the possible role of deficits in temporal dynamics in neuropathologies.

In this symposium, we will discuss the oscillation pathophysiology leading to neurodegenerative brain diseases as well as their link with underlying changes in genetics and neuronal excitation-inhibition balance/imbalance. These data highlight the potential role of changes in temporal coordination as a pathophysiological mechanism in brain disorders.

Genetic polymorphisms in COMT and BDNF influence synchronization dynamics of human neuronal oscillations

Jaana Simola, Felix Siebenhühner, Vladislav Myrov, Katri Kantojärvi, Tiina Paunio,
J. Matias Palva, Elvira Brattico, and Satu Palva

Neuronal oscillations, their inter-areal synchronization, and scale-free dynamics constitute fundamental mechanisms for cognition by regulating communication in neuronal networks. These oscillatory dynamics have large inter-individual variability that is partly heritable. However, the genetic underpinnings of oscillatory dynamics have remained poorly understood. We recorded resting-state magnetoencephalography (MEG) from 82 healthy participants and investigated whether oscillation dynamics were influenced by genetic polymorphisms in Catechol-O-methyltransferase (COMT) Val158Met and brain-derived neurotrophic factor (BDNF) Val66Met. Polymorphisms in these genes have been found to influence dopaminergic and serotonergic neuromodulation, respectively. We show that both COMT and BDNF polymorphisms influenced local oscillation amplitudes and their long-range temporal correlations (LRTCs), while only BDNF polymorphism affected the strength of large-scale synchronization. Our findings thus demonstrate that COMT and BDNF genetic polymorphisms contribute to inter-individual variability in local and large-scale synchronization dynamics of neuronal oscillations. We also compared these results to computational modelling of near-critical synchronization dynamics, which further suggested that COMT and BDNF polymorphisms affected local oscillations by influencing the excitation-inhibition balance according to the brain criticality framework. Differences in these dynamics caused by genetic polymorphisms are likely to influence individuals' cognitive and mental development and may predispose them to specific brain diseases.

Excitation/inhibition imbalance as a multi-scale mechanism of pathophysiological brain dynamics

Marina Diachenko, Additya Sharma, Arthur Avramiea, Huibert D. Mansvelder, Hilgo Bruining and Klaus Linkenkaer-Hansen

The opposing forces of excitatory (E) and inhibitory (I) signaling fundamentally shape activity at many levels of neuronal organization. Heuristic arguments have favored a certain "E/I balance" to be important for normal brain function, and "E/I imbalance" is thought to characterize many neurological and psychiatric disorders. The concept of E/I balance, however, is not uniquely defined at the mechanistic level because of many contributing factors, such as the size, number and cellular distribution of synapses, the decay time of synaptic currents and network topology. Here, we explain a definition of E/I balance that is inspired by computational modeling of critical brain dynamics. In this framework, E/I balance is an emergent network property—a functional state characterized by high spatio-temporal complexity emerging in neuronal networks balancing between order and disorder. The definition enables measuring an "E/I ratio", and in this talk we show its utility for understanding basic principles of information processing in neuronal networks and for studying brain disorders in animal models and humans.

Progressive attenuation of long-range temporal correlations and elevated excitability during preclinical and prodromal stages of Alzheimer's disease

Ehtasham Javed, Isabel Suárez-Méndez, Gianluca Susi, Fernando Maestú, J. Matias Palva, and Satu Palva

In a time scales from second to minutes, neuronal oscillations are characterized by power-law long-range-temporal correlations (LRTCs). Our previous findings suggest that individual variability in the LRTCs of oscillation amplitude fluctuations correlate with the variability of LRTCs in behavioral dynamics suggesting that LRTCs reflect a trait-like phenomena. Power-law LRTCs are characteristic to systems in the critical state and suggest that brain operates near a critical point with moderate levels of synchronization between chaos (inadequate synchronization) and order (hyper-synchronization). Taken that, the main control parameter of critical brain dynamics is thought be excitation-inhibition (E/I) balance, and that persistent E/I imbalance has been proposed to be a leading cause to many brain disorders, we posited that aberrant LRTCs would be characteristic to preclinical stages of AD. I will talk about our findings where LRTCs in oscillation amplitude fluctuations robustly captured variability SCD and MCI compared to neurotypical control participants. Importantly, changes in LRTCs were a robust marker in Alzheimer's disease continuum and predicted the disease trajectory. In addition, I will show how changes in the brain excitation-inhibition (E/I) balance were associated with the results in agreement with the hyper-excitability found with animal models. In conclusion, I will discuss the confluence of our findings highlighting not only functional significance of the results but their potential as neuronal biomarkers for individuating patients in disease continuum for targeted interventions.

Electromagnetic brain alterations as a consequence of E/I imbalance in the early stages of Alzheimer´s Disease: The X-Model

David López-Sanz, Fernando Maestú, Pablo Cuesta, María Eugenia López, Alejandrea García-Colomo, Alberto Nebreda, Isabel Suárez-Méndez, Federico Ramírez-Toraño, and Jaisalmer de Frutos-Lucas

Alzheimer´s Disease is a major concern in modern societies, accounting for around 60% of the total amount of dementia cases. Even though relevant progresses have been recently made in the field of pharmacology and treatment, the electrophysiological and oscillatory alterations underpinning this pathology are still largely unknown and poorly understood.

The talk will give an overview of the most recent findings of our group, devoted to the identification of early AD biomarkers. Specifically, the electrophysiological brain signals were recorded using magnetoencephalography in participants in different stages of the AD preclinical continuum ranging from Mild Cognitive Impairment patients to healthy adults first-degree relatives of AD patients.

Most of the work carried out by our group is consistent with the so-called 'X model', that will be explained through the different results published by our groups in the last few years. These results are compatible with an initial increase in the excitability of the brain functional networks, which lead to an inceptive hypersynchrony that eventually collapses functional communication driving to the well-known disconnection syndrome, a hallmark of AD pathophysiology. Different approaches and techniques such as resting-state and task data during a delayed match-to-sample experiment will be presented to review the current state of the art in this field.

Brain spatiospectral fingerprints: Exploring heritable and individual characteristics in MEG data

Hanna Renvall, Eemeli Leppäaho, Samuel Kaski, Riitta Salmelin

Modern neuroimaging can provide reliable non-invasive measures of human brain functions at the group level. However, human cognitive functions as well as their decay in disease are highly individual. Cortical summary measures of different genetic and environmental effects could provide tools to capture the underlying individual neurophysiology, and determine how neural signaling changes, e.g., after brain insult. We have recently discovered that the cortical power spectra measured by MEG from > 100 healthy sibling pairs can be computationally deduced to individual component structures, or "cortical fingerprints" [1], using Bayesian reduced rank regression (BRRR). The method extracts a low-dimensional representation of the most differentiating features in the subjects' multidimensional brain data. The cortex-wide power spectral distribution at 1-90 Hz related the siblings to each other, and was associated with several genes with known functions in brain development. Interestingly, the method allowed us to identify each individual subject from multiple measurements with very high consistency, irrespective of the subjects' exact experimental state (during rest or task). In our preliminary analysis on neurological patients, the spectrotemporal fingerprint measure can distinguish, e.g., mild traumatic brain injury patients from controls with high sensitivity and specificity. Importantly, BRRR provides a feasible means to combine functional neuroimaging data with genetic, clinical, and behavioral measures, providing potential for simplified biomarkers also for clinical settings.

[1] Leppäaho E, Renvall H, Salmela E, Kere J, Salmelin R, Kaski S. Discovering heritable modes of MEG spectral power. Human Brain Mapping 40, 1391-1402, 2019.

Rhythms in Cognition: Revisiting the Evidence

Manuela Ruzzoli[1], Christian Keitel[2], Andrea Alamia[3], Rufin VanRullen[3], Sophie Herbst[4], Jonas Obleser[9], Virginie van Wassenhove[4], Mireia Torralba[5], Irene Vigué-Guix[5], Luis-Morís Fernández[5,10], Salvador Soto-Faraco[5,11], Christopher SY Benwell[6], Chiara F Tagliabue[12], Domenica Veniero[13], Roberto Cecere[13], Andra Coldea[13], Silvia Savazzi[14], Gregor Thut[13], Laura Dugué[7,15], Niko Busch[8]
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Chair(s): Manuela Ruzzoli, Christian Keitel, Niko Busch, Chris Benwell, Laura Dugué

Everyday experience may arise from a fundamentally discrete sampling of our sensory environment, just like a movie consists of still frames shown in rapid succession. Although it contrasts starkly with our intuition of a continuous perceptual flow, the idea of periodic sampling can be dated back to the 1930s when rhythmic activity in the alpha band (8-13 Hz) was suggested as a neural shutter mechanism: Waxing and waning alpha cycles affect cortical excitability and therefore impinge on the momentary processing of sensory input. Time and again, seminal experimental findings, concerning the alpha- and other frequency bands, fell in line with this notion. In an interesting twist however, more recent negative findings suggest that support for inherently rhythmic perception and cognition remains equivocal.
Our symposium brings together experts in the field, who will present their current electrophysiological and modelling research and discuss whether, how and when human perception and cognition underly cyclic patterns with close links to rhythmic brain activity.

ABSTRACTS

Part 1 -- Periodic sampling: a historical perspective

Manuela Ruzzoli, Christian Keitel

A perennial hypothesis in cognitive neuroscience is whether sensory areas can favour or block input through the phase of ongoing oscillations. Already Bishop (1932) suggested a discrete nature of perception based on the phase of the alpha waves. The prediction from this hypothesis is straightforward: perception should cycle along with cortical oscillations. Through the years, this idea changed names (e.g., excitability cycles, perceptual cycles, scanning hypothesis, discrete perception) but not its essence. While supporting evidence seems unequivocal at the level of single-neuron recordings, already in the fifties, controversial findings emerged using non-invasive recordings, such as EEG. Here, we will review the primary evidence in favour of and against the rhythmic sampling hypothesis, taking a historical perspective. By identifying some of the commonalities and discrepancies through almost a century of research, we will lay the ground for a stimulating discussion on an open debate.

Part 2 -- Can Predictive Coding generate Alpha oscillations and Travelling Waves?

Andrea Alamia, Rufin VanRullen

In recent years predictive coding emerged as a key paradigm to investigate the computational mechanisms involved in brain functioning. In a nutshell, given a hierarchical system, higher levels predict the activity of lower levels, and the difference between the prediction and the actual activity (i.e. the prediction error) is used to update and correct the next prediction. In this talk I will first show how a simple 2-level predictive coding model gives rise to alpha-band rhythms, when we considered physiological communication delays between levels in the system. Next, I will show how a multi-level version of the same model generates oscillatory travelling waves, propagating both feedforward (during visual stimulation) and backward (during rest). Remarkably, all predictions of the model are matched by the analysis of different EEG datasets. In the last part of the talk I will present ongoing studies investigating how cortical travelling waves play a crucial role in different cognitive functions (i.e. selective attention and visual awareness).

Part 3 -- Delta oscillations: endogenous timing for audition?

Sophie K. Herbst, Jonas Obleser, Virginie van Wassenhove

The influential theory of Dynamic Attending in Time (DAT) holds that endogenous rhythms implement a temporal structure in the cognitive architecture on which external events can be mapped. Such architecture would indeed be helpful for extracting temporal statistics in audition: acoustic signals contain essential periodicities which could be mapped on endogenous rhythms to efficiently generate temporal predictions within and across senses.
Seminal animal work has revealed that endogenous delta oscillations (0.5–3 Hz) can emulate the temporal statistics of sensory inputs through phase shifts and frequency entrainment. Magneto- and electro-encephalography (M/EEG) based investigations in humans have further strengthened the relevance of delta oscillatory phase for auditory processing. However, the existing evidence does not clearly separate the contribution of endogenous oscillations from exogenous stimulus dynamics for the delta phase effects.
In a recent study, to avoid local temporal structures to which brain rhythms can entrain, we induced temporal predictability using a foreperiod paradigm, and showed that even implicit and non-rhythmic temporal predictions are extracted by human listeners (Herbst & Obleser, 2019). The EEG results suggest that temporal predictions can be initiated by an optimized delta phase reset, and are encoded in delta oscillatory phase during the foreperiod interval. These findings provide the basis for future work to disentangle endogenously rhythmic brain dynamics from the brain's response to exogenous rhythms, when studying the role of slow neural oscillations for dynamic perception.

Part 4 -- Alpha cycles and visual perception

Mireia Torralba, Manuela Ruzzoli, Irene Vigué-Guix, Luis-Morís Fernández and Salvador Soto-Faraco

Neural oscillations in the low frequencies, roughly in the alpha band (~5-15 Hz), have been suggested to act as a gateway from sensation to perception. The hypothesis is that these oscillations reflect rhythmic fluctuations in neural excitability, rendering cyclical alternation between high and low sensitivity states in sensory cortex. If these cyclic alternations can be captured with EEG, then one should be able to find evidence for correlations between visual perception and the phase of pre-stimulus alpha oscillations, and even capitalise on this relationship to anticipate the outcome of perception via closed-loop Brain Computer Interfaces (BCI). However, despite the substantial amount of supporting evidence in the literature, the disparity between the various methodological and analytical approaches is remarkable. We aimed at developing and validating working protocols based on alpha phase in two EEG studies adopting hypothesis-driven approaches. In one experiment, we pre-registered the method and analytical pipeline of a cross-validation study to test the correlation between behaviour and pre-stimulus alpha-phase at individual and group level. In a second experiment, we aimed at obtaining proof-of-concept for BCI application by measuring speeded responses to visual targets presented at selected phases of the alpha cycle in real-time. None of these two studies produced evidence that behaviour in visual tasks is correlated with the phase of alpha oscillations measured from EEG sensors. Several reality checks and exploratory analyses allowed us to rule out some trivial explanations of these unexpected null effects. We will discuss the questions that remain open and the lessons learned from these two attempts at validating the theory. We conclude that, currently, alpha theories are not yet sufficiently mature to generate precise a priori hypothesis to be confirmed with human EEG, or to ground reliable BCI application.

Part 5 -- Prestimulus EEG power, but not phase, predicts the clarity of visual perception

Benwell, C.S.Y., Tagliabue, C.F., Veniero, D. , Cecere, R., Coldea, A., Savazzi, S., and Thut, G.

Prestimulus oscillatory neural activity has been linked to perceptual outcomes during performance of psychophysical detection and discrimination tasks. Specifically, the power and phase of low frequency oscillations have been found to predict whether an upcoming weak visual target will be detected or not. The mechanisms by which baseline oscillatory activity influence perception remain unclear. Recent studies suggest that the negative relationship between alpha power and stimulus detection may be explained by changes in detection criterion (i.e. increased target present responses regardless of whether the target was present/absent) driven by the state of neural excitability rather than changes in visual sensitivity (i.e. more veridical percepts). We hypothesised that prestimulus power may primarily influence perceived stimulus visibility, which in turn manifests in an effect on the detection criterion. Across two experiments, we recorded EEG whilst participants performed either a luminance discrimination task (exp 1) or a letter identification task (exp 2) with perithreshold stimuli in combination with single-trial ratings of perceptual awareness. We investigated whether the power and/or phase of pre-stimulus oscillatory activity predicted decision accuracy and/or perceptual awareness on a trial-by-trial basis. Pre-stimulus EEG power was inversely related to perceptual awareness ratings (i.e. higher ratings in states of low pre-stimulus alpha/high excitability) in both experiments but did not predict discrimination accuracy. In contrast, pre-stimulus oscillatory phase did not predict awareness ratings or accuracy in either experiment. These results provide robust evidence that pre-stimulus alpha power influences the level of subjective awareness of a threshold visual stimuli but does not influence visual sensitivity when a decision has to be made regarding stimulus features. Hence, we find a clear dissociation between the influence of ongoing neural activity on conscious awareness and objective performance. Furthermore, the results suggest that prestimulus oscillatory phase does not influence visual perception.

Part 6 -- Discussion

Chaired by Laura Dugué, Niko Busch

Joint discussion regarding the effect of oscillatory phase for perception and cognition. Specifically, we plan to re-evaluate the evidence for such effects in light of the findings presented at this symposium and of recent reports in the literature. Do certain findings, paradigms, techniques, or theoretical approaches appear more promising than others? What are the implications for the replicability of our research and for how the replicability can be improved? What are the most urgent open questions that we should address to move the field forward? After an initial discussion with the symposium speakers, we will open the debate to include all symposium attendees.

Eye movements during natural reading and visual exploration

Dr. Yali Pan[1], Dr. Tzvetaa Popov[2], Dr. Ashley Lewis[3], Dr. Anthony Harris[4], Dr. Joshua Snell[5]
[1]University of Birmingham, [2]University of Zurich, [3]Donders Institute for Brain, Cognition and Behaviour, [4]The University of Queensland, [5]Vrije Universiteit Amsterdam

Abstract Summary
Humans typically make 3-5 saccades per second to shift attention and structure the in-flow of information in the visual system. However, given that eye movements are not made at random, some degree of information must be extracted from the parafovea. For example, readers can obtain orthographic, phonological, and even lexico-semantic information about upcoming words. Similarly, during vision exploration, saccades tend to land on the informative parts of the visual scene. The pre-processed parafoveal information can direct eye movements and visual attention. However, how the brain coordinates the ocular and visual system during natural vision remains an open question, especially the underlying electrophysiological mechanism. In this symposium, the speakers will discuss their perspectives of active visual sensing through eye movements in reading and free exploration. We will bring together vision and language researchers to explore shared underlying processes in both fields. Our target audience is researchers who are interested in understanding how the brain process visual information in a natural scenario.

Individual Abstracts
Title: Saccades are locked to the phase of alpha activity during natural reading
Speaker: Yali Pan
Affiliation: University of Birmingham
Abstract: We saccade three to five times per second when reading natural text. However, little is known about how we coordinate the ocular and visual system during such rapid processing. Here, eye tracker and MEG were used to simultaneously collect eye movements and brain activity during a free reading task. Every sentence was embedded with target words of either high or low lexical frequency. During natural reading, the alpha activity was strong in the power spectra. Our key finding was that the alpha phase concentrated more over trials prior to saccade towards low compared to high lexical frequency target. This phase consistency indicates that saccade onsets are locked to the phase of the alpha oscillations in particular low-frequency words. Finally, source modelling localized the saccade related alpha phase alignment to the right visual-motor area (BA7). Our findings suggest that the alpha phase acts to coordinate the ocular and visual system during natural reading; this coordination becomes more pronounced for demanding words.

Title: How do alpha oscillations move your eyes about?
Speaker: Tzvetan Popov
Affiliation: University of Zurich
Abstract: Solutions to core survival requirements such as attention are scaled, preserved, and present in nearly all creatures equipped with the ability to move. In this talk, a fundamental principle of neuronal rhythms (alpha oscillations) in monitoring sensory action across phyla is discussed (honey bee, non-human primates, and humans). The brain's active sensing of the surrounding environment entails clustering of ocular/antenna movements towards an object or location. This active sensing behavior is monitored by the phase and amplitude of spontaneous (alpha) rhythm. Independent of testing conditions (e.g. light or full darkness) and cognitive load (e.g. rest, spatial attention, working memory), space is inferred by the movement direction of the brain's sensors manifesting in location-specific place topographies. These observations are discussed in light of the conjecture that the dominant rhythm of the brain facilitates and monitors sensorimotor output as a prerequisite for a proactive processing chain in cognition beginning with action.

Title: Alpha oscillations facilitate gaze direction during natural reading

Speaker: Ashley Lewis
Affiliation: Donders Institute for Brain, Cognition and Behaviour
Abstract: An important component of natural reading is periodic eye movements, followed by brief periods where gaze position (fixation) is maintained. Recent work has suggested a close relationship between eye movement control and alpha oscillations. Alpha oscillations (8-14Hz) are proposed to regulate the amount of time gaze is maintained, and the timing of execution of the next saccade, with alpha lateralization reflecting saccade direction. Many electrophysiological studies examining neural correlates of reading have documented reliable left-hemispheric modulation of alpha power. In this talk, I will present recent observations that left-hemispheric lateralization of alpha power and a rightward bias in gaze position maintenance during reading are closely related. Magnetoencephalographic and eye movement evidence from 31 human volunteers during natural reading of sentence fragments is presented. Relationships going beyond simple oculomotor control of alpha activity associated with semantic contextual constraint are discussed.

Title: Alpha and theta phase predict the timing of pro- and anti-saccades

Speaker: Anthony Harris
Affiliation: The University of Queensland
Abstract: Neural oscillations are thought to organise neural signal processing, and to be adjusted to respond to different task demands. The phase of activity in the 3-8 Hz theta range and the 8-14 Hz alpha range have been associated with different goal-directed behaviours in the past, but no prior work has assessed their relative import, or compared their contributions under differing levels of cognitive demand. We addressed this question by having human participants perform a combined pro- and anti-saccade task while measuring their gaze with a video-based eye-tracker, and their brain activity with electroencephalography (EEG). We used trigonometric multiple regression to assess the proportion of variance in pro- and anti-saccade reaction times accounted for by the phase of posterior alpha and frontal-midline theta oscillations. We found that alpha and theta oscillations predicted saccadic reaction times to a similar extent in both tasks. The tasks were differentiated, however, by their pre-trial phase relationships; anti-saccades were predicted by the direct effects of the two frequencies, whereas pro-saccades were predicted only by their interaction. Furthermore, optimal timing of pro- and anti-saccades were associated with theta oscillations of roughly opposite phase angles. Rather than being recruited by different tasks, these results suggest that both posterior alpha and frontal-midline theta oscillations constitute integral components of a network that controls the movement of the eyes based on a combination of external inputs and internal task demands. Furthermore, they suggest that one way in which this network adjusts to different task requirements is through realignment of phase in accordance with the cognitive demands of the task.

Title: Parallel word reading revealed by fixation-related potentials

Speaker: Joshua Snell
Affiliation: Vrije Universiteit Amsterdam
Abstract: During reading, the brain is confronted with many relevant objects at once. But does lexical processing occur for multiple words simultaneously? Cognitive science has yet to answer this prominent question. Recently it has been argued that the issue warrants supplementing the field's traditional toolbox (response times, eye-tracking) with neuroscientific techniques (EEG, fMRI). Indeed, according to the OB1-reader model, upcoming words need not impact oculomotor behavior per se, but parallel processing of these words must nonetheless be reflected in neural activity. Here we combined eye-tracking with EEG, time-locking the neural window of interest to the fixation on target words in sentence reading. During these

fixations, we manipulated the identity of the subsequent word so that it posed either a syntactically legal or illegal continuation of the sentence. In line with previous research, oculomotor measures were unaffected. Yet, syntax impacted brain potentials as early as 350 ms after the target fixation onset. Given the EEG literature on syntax processing, the presently observed timings suggest parallel word reading. We reckon that parallel word processing typifies reading, and that OB1-reader offers a good platform for theorizing about the reading brain.

Vistas on alpha-rhythms revisited

Gregor Thut[1], Ole Jensen[2], Mila Halgren[3], Laura Marzetti[4], J. Matias Palva[5]
[1]University of Glasgow, [2]University of Birmingham, [3]Massachusetts Institute of Technology, [4]University of Chieti-Pescara, [5]Aalto University

Chairs: Gregor Thut and Matias Palva

Summary
Brain oscillations in the alpha frequency band is a prime measure of oscillatory activity in the awake brain. It is associated with a clear frequency-peak against background activity and its excellent signal-to-noise ratio allows its reliable measurement even from extra-cerebral (scalp) sensors. Whilst EEG-pioneers have already linked alpha-oscillations with visual and attentional states, it is only over the last decade and a half where studies into this oscillation have taken off. Various roles have been assigned to alpha oscillations including in coordinating areas of large-scale brain networks, gating of information across these networks and local sampling of information by sensory areas. In line with these views, alpha oscillations are modulated by attention, predict perception of upcoming sensory stimuli and have been reported to co-fluctuate in power and phase with sensory experience. There is evidence that this oscillation can also be entrained by extrinsic periodic forces, and by this means be subject to frequency-modulation to some extent, leading to specific changes in sensory task performance, that support its causal role in sensory gating/sampling. Yet, recent findings reveal that alpha fluctuations do not co-vary with other attention-modulated signals (such as steady-state evoked potentials), or predict subjective but not objective performance in perceptual tasks. Others report on independent drifts of alpha-power and alpha-frequency over time in the same signal, suggesting alpha source mixing in recordings. And recent evidence speaks against a thalamic pacemaker. Collectively, these and other data challenge some of the prevailing models of alpha oscillations. In this symposium, we will provide an overview of new findings and concepts in the alpha literature. We will outline recently appearing cracks in common assumption that indicate the need for revisiting our models, and present new pointers towards an integrated view of alpha oscillations.

Contribution speaker 1:
Cracks in alpha prediction of perception
Gregor Thut, Jelena Trajkovic and Vincenzo Romei; School of Psychology and Neuroscience, University of Glasgow, UK and Centro studi e ricerche in Neuroscienze Cognitive, Dipartimento di Psicologia, Università di Bologna, Italia.

Over the last 15 years, numerous studies on EEG predictors of task performance have identified alpha oscillations over posterior sites to predict forthcoming perception. However, while the link between alpha oscillations (in particular its amplitude) prior to stimulus onset and perception is a common finding, recent evidence points to cracks in the common assumption that pre-stimulus alpha oscillations are gain-modulating incoming sensory signals and thereby influence visual sensitivity, in analogy to the effects of attention. My talk will outline some of the recent findings calling into question this assumption and our recent attempts to pinpoint alternative functional loci of the pre-stimulus alpha-perception interaction. This will include new correlative evidence from EEG and causative evidence from rhythmic TMS-EEG studies. Collectively, our findings suggest an interaction between ongoing alpha-amplitude and visual processing at late processing stages, in agreement with alpha-amplitude modulating visual bias rather than sensitivity (i.e. subjective, rather than objective aspects of visual perception). On the other hand, our results indicate a causal link between pre-stimulus alpha-frequency and visual sensitivity (i.e. objective aspects of visual perception) but not with the subjective representation of the visual stimulus. This is in line with alpha-amplitude gating read-out from sensory areas, rather than the input into them, while alpha pace influences information processing capacities likely at early input stages.

Contribution speaker 2:
Gating by alpha inhibition updated
Ole Jensen, Alexander Zhigalov and Tjerk Gutteling; Centre for Human Brain Health, School of Psychology, University of Birmingham, UK

We and others have in the past suggested that alpha oscillations serve to gate the information flow in the visual system and beyond by actively suppressing task-irrelevant regions. From this notion followed that alpha activity would increase in regions processing anticipated distractors. Furthermore, the framework implicitly predicted that the feed-forward gain in e.g. sensory regions would increase with a decrease in alpha power. Recent work has challenged some of these notions and calls for an update of the framework. For instance, spatial attention tasks in which respectively the load of the target and the interference of the distractor are manipulated, demonstrate that target load control the magnitude of the alpha power (ipsi-lateral to the target) rather than the degree of anticipated distractor interference. We have also used 'rapid frequency tagging' (target and distractors flickered at different frequencies above 60 Hz) to access excitability, i.e. feed-forward gain, in early visual cortex. The core finding was that alpha power did not modulate the magnitude of the frequency tagged signal. These findings have promoted a reformulation of the gating by alpha inhibition notion. The new framework is consistent with perceptual load theory in which distractor inhibition – and thus alpha power increase – is reflected by the perceptual load of the target. Furthermore, gating by alpha oscillations does not seem to be operating by gain regulation in early sensory regions; rather, the gating seems to operate in down-stream regions, i.e. parietal and extra-striate regions in the case of the visual system.

Contribution speaker 3:
Insights on alpha's generation and propagation from human intracranial recordings
Mila Halgren, Brain and Cognitive Science, MIT, Boston, USA

The alpha rhythm is the longest-studied brain oscillation and has been theorized to play a key role in cognition. Still, its physiology is poorly understood. We therefore used microelectrodes and macroelectrodes in surgical epilepsy patients to measure the intracortical and thalamic generators of the alpha rhythm during quiet wakefulness. We first found that alpha in both visual and somatosensory cortex propagates from higher-order to lower-order areas. In posterior cortex, alpha propagates from higher-order anterosuperior areas toward the occipital pole, whereas alpha in somatosensory cortex propagates from associative regions toward primary cortex. Several analyses suggest that this cortical alpha leads pulvinar alpha, complicating prevailing theories of a thalamic pacemaker. Finally, alpha is dominated by currents and firing in supragranular cortical layers. Together, these results suggest that the alpha rhythm likely reflects short-range supragranular feedback, which propagates from higher- to lower-order cortex and cortex to thalamus. These physiological insights suggest how alpha could mediate feedback throughout the thalamocortical system.

Contribution speaker 4:
Alpha coordination of large-scale brain networks
Laura Marzetti, Department of Neuroscience, Imaging and Clinical Sciences, University of Chieti-Pescara, Italy

Whilst it is acknowledged that the brain is organized as an ensemble of highly specialized networks, the role of brain rhythms in the coordinating mechanism supporting brain inter-areal functional cooperation is yet not clearly understood, due to different findings leading to possibly different underlying models. This is especially true for alpha oscillations. Recently, theoretical and computational work has suggested a unified framework according to which the role of coherent alpha oscillations is that of routing non-novel information along pathways that have already been reinforced by synaptic plasticity. This routing is achieved by adjusting the phase of alpha between sender and receiver areas of the network.
In this talk, I will frame our alpha-band connectivity results for visuo-spatial attention and resting state magnetoencephalographic data in this context. Specifically, I will firstly show that, in visuo-spatial attention, phase-coherence can be observed in the alpha band between parietal (sender) and visual (receiver) regions, in a lateralized manner consistent with the direction of attention and related to task performance. To reconcile these findings with the idea that phase-coherence of alpha oscillation routes information along already established pathways, I will provide evidence from resting state connectivity results between the visual-system and the whole brain. The latter show that feed-back pathways between parietal and visual areas can be observed with phase-coherence based metrics in the resting brain in the alpha-band, consistently with those observed in visuo-spatial attention.

Contribution speaker 5:
Meso- and macro-scale network coupling of alpha oscillations
J. Matias Palva, Department of Neuroscience and Biomedical Engineering, Aalto University, Finland

Despite decades of research, alpha oscillations have remained enigmatic in terms of both their synaptic and micro-circuit mechanisms and functional significance in cognitive operations. We have used magnetoencephalography (MEG) and stereo-encephalography (SEEG) to obtain macro- and meso-scale, respectively, insight into the structure and functions of alpha oscillations in human large-scale networks. We have earlier proposed that long-range phase synchronization of alpha oscillations could mediate neuronal communication of top-down information and beget, e.g., attentional functions, even though local, large-amplitude alpha oscillations appear to play a role in suppressing information processing. Several lines of recent studies have supported and expanded this framework. Our SEEG data show that the alpha band is predominant in expressing narrow-band oscillations and that their phase synchronization is observed predominantly among supragranular cortical layers. Alpha phase synchronization was found both with significant systematic phase lags as well as with true zero-lag coupling. MEG studies have shown that large-scale phase synchronization of alpha oscillations between the visual cortex and the fronto-parietal attentional networks characterizes both visuo-spatial attention and visual working memory. Our new data show comprehensively that both alpha- and gamma-band phase synchrony, and their cross-frequency coupling, among sensory and attentional brain systems are highly reliable characteristics of visual working memory and visual multi-object tracking tasks, and predictive of individual cognitive capacity. Long-range alpha-band phase interactions are thus likely to be central in the mechanisms of attentional and executive control in human cognitive functions.

Representational dynamics of image processing during perception, conscious access and mental reconstruction

Dr Maria Wimber[1], Dr Daniel Lindh[5,6], Dr Tim Kietzmann[2,3], Dr Peter Kok[4]
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Summary of the symposium
Organizers: Maria Wimber, Ian Charest

Object recognition has traditionally been conceptualized as a feed-forward process. While travelling up the visual hierarchy, the neural representation of a sensory stimulus presumably undergoes a gradual transformation along a detailed-perceptual to abstract-conceptual gradient. Much less is known about when, where and how these representations are then read out and used for various cognitive processes. Over the past years, it has become increasingly clear that even simple object recognition is neither purely feed-forward, nor does it happen on a “blank neural slate”. Rather, information at all stages of the processing hierarchy is integrated with stored knowledge and previous experiences, in alignment with the specific task goals. This symposium is an attempt to integrate what we have learned from recent work about top-down influences on the object processing hierarchy. The four talks will cover a variety of domains beyond feed-forward visual processing, ranging from recurrence during simple object recognition, to attentional selection, mental imagery and mnemonic reconstruction of visual objects. All of the work presented in this symposium is based on methods that allow us to make inferences about neural representational architectures from dynamic patterns of brain activity, including time-sensitive decoding of electrophysiological signals, fMRI patterns, and deep neural network layers. Tim Kietzmann’s talk will emphasize the importance of recurrence for visual inference in humans and AI systems. Based on multivariate analyses of source-reconstructed MEG data and deep neural network modelling, he will argue that top-down and lateral connections are essential ingredients for efficient object recognition, as well as for understanding human ventral stream dynamics and behaviour. Ian Charest will talk about the representational features that determine conscious access in an attentional blink task. Similarity between target stimuli measured from late layers of a deep neural network, temporal patterns in EEG, or from fMRI patterns in the human inferior temporal cortex, has a massive influence on conscious target detection. Nadine Dijkstra will present her work on the representational dynamics of imagery and perception, demonstrating a reversal in the perceptual feed-forward hierarchy during mental imagery as well as alternating forward and reversed sweeps during perception. Maria Wimber will then present evidence for a flip in the representational hierarchy between perception and memory, showing that when images are reconstructed from memory, the processing hierarchy tends to follow a reversed, abstract-conceptual to detailed-perceptual gradient. Together, these talks will give insights into new emerging fields at the border of object recognition and high-level cognitive functions. We hope this symposium will stimulate a discussion between researchers in these different disciplines regarding the interaction of feed-forward and feed-back processing in the human (visual) brain.

Symposium Talks

1. Recurrence is required to capture the representational dynamics of the human visual system

Speaker: Tim Kietzmann:

Co-authors: Courtney J. Spoerer, Nikolaus Kriegeskorte

This talk will describe our recent methodological advances in understanding information processing in the human brain and artificial vision systems. A central theme of our work is the combination of neuroimaging and deep learning, a powerful computational framework for obtaining models of cortical information processing and task-performing vision systems. Operating in this interdisciplinary research area, I will cover our recent work in which we demonstrated that neural network architectures with recurrent connectivity provide better models of human visual processing (estimated via representational dynamics and behavioural measurements). This insight was made possible by a novel mechanism to directly infuse brain data into large-scale recurrent neural networks. In addition, we have shown that recurrent connectivity in artificial vision systems leads to computational benefits. Recurrence enables systems to flexibly trade-off speed for accuracy while exhibiting overall higher object recognition performance. Together, these findings suggest that recurrence is required to capture the representational dynamics of the human visual system.

2. Representational interactions dynamically influence conscious access in object recognition.

Speaker: Daniel Lindh
Co-authors: Ian Charest, Kimron L. Shapiro, Ilja G. Sligte

The ability to consciously recognise objects is crucial for adaptive behaviour and survival. Yet, it is still largely unknown how, when and where in the brain, the representations necessary for conscious access are established. Here, we used a novel approach which combines the strengths of electroencephalography (EEG), functional magnetic resonance imaging (fMRI), and Deep Convolutional Neuronal Networks (CNNs), to investigate the representational interactions between targets in an attentional blink (AB) task. Participants each completed 3840 trials of an AB paradigm, in four separate sessions, while we measured EEG data. In each trial, two targets were embedded in a rapid serial visual presentation of distractor masks. Two fMRI sessions were additionally collected in the same participants to characterise template brain representations for these natural object targets. Using representational similarity analyses (RSA), we show that target-target similarity in high-level visual cortex activity patterns, and late time-points of the EEG, explains large amounts of AB variance across trials and objects. This effect is also observed in late CNN layers. Critically, the target-target similarity based modulation of conscious access changes along the visual pathways in the brain where a dynamic gradient from low-level to high-level regions is associated with changes in awareness behaviour. These target-target similarity effects reveal that conscious access is modulated by interacting feed-forward and recurrent neuronal dynamics. Together our results highlight the significance of representational dynamics in models of consciousness, and inform the neurocognitive mechanisms behind conscious access in object recognition.

3. Representational dynamics during memory recall

Speaker: Maria Wimber
Co-authors: Juan Linde-Domingo, Casper Kerrén, Marije Ter Wal, Simon Hanslmayr

When recalling a memory, the human brain reinstates brain activity patterns that were active when an event was originally encoded, including sensory information about the event. How are the various features of a stored memory reactivated, step by step, during recall? We used a combination of time-sensitive, EEG-based decoding and behavioural measures to shed light onto the representational dynamics when visual objects are reconstructed from long-term memory. Two principles govern this mnemonic reconstruction process. First, the processing hierarchy is reversed between the initial perception and the later recall of an object. When objects are visually presented to participants, detailed-perceptual features come online more rapidly than abstract-conceptual features, as expected if perception follows a predominantly feed-forward trajectory along the ventral visual stream. When objects are reconstructed from memory, however, abstract-conceptual features are detected more rapidly than detailed-perceptual features. Across multiple experiments, this reversal between perception and memory was evident in neural decoding traces as well as overt reaction times. Second, we find robust evidence that the neural indices of memory reactivation rhythmically fluctuate, waxing and waning along a 7-8Hz theta oscillation. Critically, mnemonic information is maximally decodable at a phase of this oscillation where decoding of perceptual inputs is minimal, and vice versa, suggesting that the brain uses a phase code to avoid interference between feed-forward sensory and feed-back mnemonic processing. Together, the perception-to-memory reversal and the anti-phasic rhythmicity are two important principles that may help us understand the computations supporting memory recall.

4. Representation dynamics during imagery and expectation

Speaker: Peter Kok
Co-authors: N/A

Various top-down processes, such as working memory, imagery, and expectation, have been shown to activate sensory representations that resemble those activated by external stimuli. Yet surely there must be a difference between internally and externally generated signals, after all, we don't walk around hallucinating all the time. Here I discuss recent results on the temporal dynamics and layer specificity of internally generated sensory representations that partly address this issue. I also briefly hint at the possible role of reality monitoring mechanisms in distinguishing internally from externally generated sensory signals.

Effects of auditory exposure and intervention on early language development

Sari Ylinen[1], Teija Kujala[2], Minna Huotilainen[2], Paula Virtala[2], Eino Partanen[2]
[1]*Tampere University,* [2]*University of Helsinki*

Organizers: Sari Ylinen (Tampere University) & Teija Kujala (University of Helsinki)

The first years of life are critical for language development. Infants' language skills develop from discrimination to representing native language speech sounds and word forms. This development takes place via partly overlapping but cascading sensitive periods. Therefore, language-related deficits should be remediated with effective interventions as early as possible. For this purpose, we should find early markers of language-related deficits and most effective remedial interventions for them. Studying language skills by measuring behavior is, however, challenging in infants and young children that do not follow instructions. Research methods used in cognitive neuroscience, such as event-related potentials (ERP) measured with electroencephalography (EEG), are, therefore, valuable tools for investigating language development. Infants' ERPs patterns may reveal a risk for language deficits before the emergence of their behavioral indices. ERPs may also be used to show remedial effects as a result of intervention. Importantly, to develop effective remedial interventions, we need better understanding of neurocognitive mechanisms and processes underlying both typical and atypical language development. To this end, this symposium focuses on ERP studies addressing the effects of auditory exposure and intervention on early language development. The topic will be introduced by Minna Huotilainen. Then Paula Virtala will tell how musical activities affect speech sound processing in the brain and language development in 0-2-year-old children at risk for dyslexia. Eino Partanen will present results showing how parental singing activities in standard kangaroo care intervention affect auditory ERPs in prematurely born infants, who are at risk for abnormal auditory processing. Finally, Sari Ylinen will tell how predictive inference may facilitate the speech processing in newborn infants and whether these skills predict further language abilities. Together, the presentations of this symposium shed light on both typical and atypical language development as well as their neurocognitive mechanisms in infants and children.

Introduction

Minna Huotilainen
University of Helsinki

Effects of musical activities on neural speech processing and language development in 0-2-year-old children at risk for dyslexia

Paula Virtala1, Vesa Putkinen1,2,3, Anastasia Gallen1, Anja Thiede1, Laurel J. Trainor4,5,6, and Teija Kujala1

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Familial risk for developmental dyslexia can compromise auditory and speech processing and subsequent language and literacy development. In line with the phonological deficit theory, supporting phonological development during infancy could prevent or ameliorate prodromal dyslexic symptoms. Music is an established method for supporting auditory and speech processing, language, and literacy, but no previous studies have investigated its benefits for infants at risk for developmental language and reading disorders. In the longitudinal DyslexiaBaby study, we pseudo-randomized N~150 infants at risk for dyslexia to vocal or instrumental music listening interventions at 0–6 months, or to a no-intervention control group. We focused on music listening as an easy-to-administer, cost-effective intervention in early infancy. We surveyed the extent of other music activities at the ages of 6–24 months with regularly repeated parental questionnaires. Mismatch responses (MMRs) elicited by speech-sound changes were recorded with electroencephalogram (EEG) before (at birth) and after (at 6 months) the intervention and at 2 years' follow-up. Preliminary results demonstrate enhanced amplitudes of a positive MMR in the vocal music listening intervention group after the intervention and at follow-up. Music activities, which did not differ between the three groups, also showed associations to the MMR amplitudes. The results speak for the use of music to support speech processing and subsequent language and literacy already in infants at developmental risk.

Parental singing during kangaroo care affects ERPs at term

Eino Partanen1,6,10, Kaisamari Kostilainen1, Kaija Mikkola2, Minna Huotilainen1,5,10, Valtteri Wikström1, Satu Pakarinen1, Pernilla Hugoson7,8,9, Gustaf Mårtensson7, Ulrika Ådén7, Vineta Fellman3,4

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Perinatal risk factors, such as preterm birth, may affect auditory development. In comparison to healthy full-term infants, preterm infants show abnormal auditory brain responses at term age, which may have long-term detrimental outcomes. To alleviate these risks, various musical interventions have been developed for neonatal intensive care units (NICUs), and they have shown beneficial effects on vital functions and weight gain of preterm infants and might also influence basic auditory processing and thereby enhance outcomes. In this two-center Singing Kangaroo RCT study, we investigated if including parental singing activities in standard kangaroo care in NICU settings would have beneficial effects on auditory processing, measured using speech-related ERPs or ERFs at term. The families assigned to the singing intervention group were encouraged by a trained music therapist to sing or hum to their infant during kangaroo care while the control group received standard kangaroo care. Results from two separate cohorts suggest that ERP responses to speech-related changes was enhanced by the singing kangaroo intervention, and the enhancement was associated with the amount of singing. However, as the control group could not be

prevented from singing but similar ERP enhancement was not found in the control group, it may be that the beneficial effects from the intervention may not be due to singing itself, but instead from positive parenting, improved parental self-esteem and improved caregiver sensitivity.

Newborn infants show predictive inference of syllables in word-like items

Sari Ylinen[1,2], Emma Suppanen[2], Istvan Winkler[3] & Teija Kujala[2]

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To facilitate adaptive behavior, the brain aims to predict future sensory events. A recent study by Ylinen et al. (2017) showed that such predictive inference is linked with word recognition and learning in 12- and 24-month-old children. Negative-polarity auditory event-related potentials (ERP) were elicited when the preceding word context predicted familiar word endings, whereas word-expectancy violations generated prediction error (PE) responses of positive polarity. PE strength correlated with vocabulary scores at 12 months. Here we exposed newborn infants (N=45, mean age 7 days) with bisyllabic pseudowords AB and CD (p=0.5 for each) during ERP measurement. Then we presented the familiarized pseudoword AB (p=0.8), where A was expected to create predictions of B if learned, and occasional deviant pseudowords CD, CB, AD and AX (p=0.05 for each) in an oddball paradigm. The final syllables of AD and AX elicited significant positive PEs, the latter including novelty response contribution. In contrast, the final syllable of unexpected CB elicited a significant negative response differing from that to CD, to which the infants had been exposed earlier. This indicates that infants had learned the potential words as well as learned to predict D after C. Importantly, this index of learning correlated with expressive language ability (the mean length of utterance) at 24 months of age. In the future, such relationship may help early identification of infants at risk for language impairment.

Interaction between body, brain, and cognition across the human lifespan

PhD Jan Kujala[1,6], PhD, Assoc Prof Harri Piitulainen[1,2,4], PhD, Univ Researcher Tiina Parviainen[1,6], Professor Vesa Kiviniemi[3,5]

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In context of human neuroimaging, the functions of the brain and mind are often studied separately from the functions of the body. Although the representation and functional architecture of sensory-motor systems in the brain have been described at a general level, associations are rarely made between the more elaborated properties and capacity of motor system, and brain structural and functional measures. Moreover, the role of the motor system e.g. in language, emotion, and social interaction has been approached from the perspective of embodied cognition. However, these studies typically focus on principles of brain dynamics with respect to motor organization, rather than actual associations (and direct interaction) between bodily measures and brain measures underlying perception and cognition.

Recent years have brought interesting new evidence about the contribution and role of different body systems for the human brain and mind. In this symposium, we present different examples of the pathways from the body to the brain, including peripheral and autonomic nervous system, somatosensory system, muscular system and lymphatic system. First, we describe the influence of intervention combining cognitive and physical training for the brain basis of executive functions in elderly. As an example of the peripheral somatosensory function, we enlighten the importance of proprioception for a well-functioning motor system and how to quantify and follow proprioceptive functions across the lifespan. Besides the muscular system, we present findings on perceptual sensitivity to autonomic nervous system signals and its link with behavioral traits in adults. Finally, we will give an overview to the brain glymphatic system, the physiological factors contributing to its function and the future visions in this area of research.

Kujala: Effects of physical exercise intervention with and without cognitive training on brain basis of executive functions in elderly.

Elderly individuals demonstrate a decline in cognitive skills as a function of their age and this decline may be also a precursor to memory disorders. Thus, it is important to understand whether these impairments could be delayed or reversed through targeted interventions. Behavioural evidence suggests that physical activity and cognitive training, when applied separately, may improve working memory. However, physical training might affect neural function in a more general manner, whereas cognitive training is more domain-specific. We measured the task-related modulation in brain activation patterns in elderly individuals following a physical exercise intervention with and without additional cognitive training during 12 months. The effect of these two types of interventions on brain activation was quantified by recording brain signals using magnetoencephalography (MEG) while the participants performed a cognitive task requiring memory and distractor inhibition, and through behavioural measures. MEG data at baseline revealed task-related modulation of cortical oscillatory dynamics, reflecting the stages of encoding, inhibition and retrieval. Especially the gamma power at the encoding stage reflected the difference between the two intervention groups, accompanied by improved cognitive function for combined physical activity and cognitive training. Our results uncover the underlying brain dynamics of physical exercise and cognitive training -related improvements in executive functions in elderly. They highlighti that adding the domain-specific cognitive skill training is associated with distinct behavioural and brain activation patterns. The results will be discussed in broader context of (multimodal) interventions for improving executive functions and memory in elderly individuals.

Piitulainen: How and why to examine proprioception across lifespan

The motor control by the brain relies on vast sensory input from the environment and especially from the body itself. The proprioceptors ("movement sensors of the body") provide the brain crucial somatosensory information about the internal state of the locomotor system. The number of afferent somatosensory axons is tenfold compared to the efferent motor axons underlining the importance of this feedback. The proprioceptors are located in muscles and joints, and are sensing limb positions, movements and forces, but their function is challenging to measure in isolation compared to the exteroceptors, such as touch. Partly for this reason, the research on motor system has long been directed to the motor efference, while somatosensory—and especially proprioceptive—afference has largely been neglected. Thus, the bodily information driven mechanisms supporting cortical motor control, are still largely unknown in healthy humans, and even more so in diseased humans. Many movement disorders have historically been considered as dysfunction of the brain affecting planning and execution of voluntary movements. This notion has recently been challenged, as increasing evidence indicates that proprioceptive perception is often abnormal in many movement disorders such as Parkinsons, dystonia, chorea, cerebral palsy and stroke. We have developed behavioral and neuroimaging (MEG, EEG, fMRI) compatible tools and stimulators to objectively quantify the proprioceptive functions. These tools can be used to identify and follow normal and abnormal proprioceptive processing in the human cortex, that we have observed to be altered, e.g., in older population and patients with motor disorders.

Parviainen: Attending your body: interoceptive sensitivity, behavioral traits and neural correlates of attention

The main function of autonomic nervous system is to regulate the homeostatic balance of the body, i.e. to adjust the body’s physiological systems to the ongoing needs, via functions of the visceral organs. Although this autonomic regulation mainly happens without conscious awareness, there are many situations when we are more aware of the information arising from the visceral system. This is evident for example in emotionally engaging situations, but increasing evidence suggests that this ‘interoceptive’ information has also important role for perception, memory and even self-awareness. Previous findings have indicated individual differences in the sensitivity to afferent visceral information. If the processing of afferent autonomic signals in the brain contributes to our experiences and awareness, differences in sensitivity to this information may significantly contribute to our characteristic way of experiencing the world and interacting with other people. I will review our recent data exploring this individual variability using both behavioural sensitivity measures and neural measures acquired using magnetoencephalography during interoceptive vs. exteroceptive attention tasks and rest. We correlated interoceptive sensitivity and the task-specific brain activations with temperament traits. In broader context, these findings demonstrate the importance of appreciating individual variability both in the body and brain measures.

Kiviniemi: Glymphatic system: a new aspect of water circulation in/out of the CNS

The recently described glymphatic brain clearance system convects both brain metabolites and waste materials using physiological pulsations. The glymphatic function has been measured by following contrast media injected into periarterial glymphatic space in both humans and animals. A recent human focused ultrasound study demonstrated how the glymphatic mechanisms also convects contrast agents from the interstitium in the human brain. In this talk, I will review the recent findings of the brain glymphatic system and its physiological driving factors. The glymphatic system pushes waste from the brain tissue into the perivenous space. The physiological pulsations move the waste into larger CSF spaces and the waste material is removed into paraspinal lymph nodes along the whole spinal canal. Where the glymphatic waste exits the CNS is currently under heavy research and at least part of the waste becomes removed near nerve root exits from the spinal canal and from certain areas around major venous sinuses. Early in vivo animal research has indicated that a main driving force of the glymphatic system is cardiovascular pulsations. However, in human brain there seems to be more driving forces involved, including respiration and vasomotor waves. Less invasive measures of the glymphatic function have been developed using ultrafast MRI technology to quantify pulsatory drivers of the brain.

Learning more from neural data: New methods to improve our understanding of perception and memory

Jelmer Borst[1], Elkan Akyürek[1], Linda Geerligs[2], Jochem Rieger[3], Diego Vidaurre[4]
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Introduction
Over the last decades, we have seen an enormous growth of the collection of neuroscientific data. However, these multidimensional data are difficult to fully account for with traditional analysis methods. Powerful new methods have therefore been introduced, chief among which are machine-learning decoding analyses. In this symposium we present five talks that highlight different approaches of combining neuroscience and machine learning to analyze complex datasets. The talks will show how we can apply these new methods, and how these methods yielded new insights in human perception and memory.
The first talk concerns the investigation of activity-quiescent brain states with EEG. Akyürek will showcase an impulse perturbation approach that allows the investigation of such brain states in memory tasks, which are otherwise effectively impossible to measure non-invasively. The next two talks examine the processing of naturalistic stimuli over time. Rieger will first discuss the application of machine learning to ultra-high-field fMRI data of perceiving movie soundtracks, in particular focusing on how such analyses can be performed across participants. Next, Geerligs reports on a data-driven fMRI analysis of how humans automatically segment an ongoing experience – watching movies – into subjective events, and how that links to functionally distinct brain networks and processes. The last two talks return to more simple tasks, to investigate processing of information with very high temporal resolution. Vidaurre and Borst discuss two different methods for tracking cognitive processing across time by analyzing MEG and EEG data with the help of hidden Markov models, and how these methods could lead to new insights in a wide variety of tasks.

Symposium Abstracts

Probing representations in activity-quiescent brain states
Elkan Akyürek
For most if not all cognitive processes, it is necessary to retain some information, at least for a short period of time, while it is being accessed and manipulated. Working memory serves precisely this purpose and thereby provides the backbone of intelligent, adaptive behavior. Our understanding of the neural mechanisms that support working memory has recently shifted significantly: Rather than relying exclusively on an unbroken chain of neural activity, working memory may also rely on transient changes in neuronal connectivity, which can be maintained efficiently in activity-quiescent or even activity-silent brain states. This poses a problem, since such brain states are effectively invisible to standard measures in cognitive neuroscience (EEG, fMRI, etc.).
By presenting a visual impulse to perturb the underlying brain network, in combination with multivariate pattern analysis of the resultant impulse response signal, we showed it is possible to reveal the hidden state of the network. Using this method has provided important new insights into the nature of representations in working memory. Recent experiments have shown how representations are maintained while evolving dynamically over time, and how they are discarded when needed. Finally, by using bi-modal impulse signals we showed that working memory networks may be triggered by modality-specific and -unspecific impulse signals, depending on prior learning.

Discovering functional dimensions of speech processing in natural soundscapes that generalize over individuals
Jochem Rieger

In natural environments human perception must reliably function in largely unconstrained contexts. Speech perception in natural soundscapes depends on the ability of the auditory system to extract speech information from a complex acoustic signal with overlapping contributions from many sound sources. In the work presented here participants listened to an audio soundtrack of a movie while their brain activity was recorded with ultra-high-field fMRI. Our data driven approach used minimal a priori assumptions and revealed three canonical processing networks of speech processing in natural soundscapes that generalized functionally well over individual brains. This indicates that at the functional level the neuronal processing of speech in natural soundscapes can be surprisingly low dimensional in the human cortex, highlighting the functional efficiency of the auditory system for seemingly complex tasks. We further demonstrate that the three functional dimensions are implemented in anatomically overlapping networks that can vary in their anatomical implementation across individual brains and characterize their functional specificity.
This observed generalization of functional dimensions over individuals is critical for combining data over participants in large multi-participant datasets. However, to date, most machine learning approaches start from individual data. In the second part of my talk I will present further machine approaches to reveal functional dimensions of brain from datasets combined over participants and demonstrate that the functional dimensions derived from a group can transfer to data from novel participants. In the future, such approaches could help to exploit the potential of large multi-participant datasets in cognitive neuroscience and brain computer interfacing research.

Event segmentation and the temporal hierarchy of neural states in the human brain
Linda Geerligs
Humans automatically segment their ongoing experience into discrete events. This segmentation is an essential component of understanding, memory and future learning. Event segmentation has been frequently studied in behavioral experiments, but little is known about its neural mechanisms. Recently it has been shown that event segmentation may be underpinned by transitions between distinct neural states. Using an innovative data-driven state segmentation method, we investigate how neural states are organized across the cortical hierarchy and where in cortex neural state and perceived event boundaries overlap. Our results show that neural state boundaries are organized in a temporal cortical hierarchy, with short states in primary sensory regions and long states in anterior temporal pole and lateral and medial prefrontal cortex. Neural state boundaries overlap with event boundaries across large parts of this hierarchy and state boundaries are shared within and between groups of brain regions that resemble well known functional networks. Together these findings suggest that a nested cortical hierarchy of neural states forms the basis of event segmentation.

Variability of neural responses and the Hidden Markov model
Diego Vidaurre
Perceptions and decisions are implemented in the brain by rapid patterns of activity and communication in the brain. Not only across subjects but also across experimental repetitions or trials, these show a great variability that traditional methods are often limited to accommodate.
In this talk, I will introduce a technique designed to track trial-specific neural dynamics of stimulus processing and decision making with high temporal precision. Based on the use of decoding analysis and the Hidden Markov model, this method addresses a major limitation of the traditional decoding approach – which is that it relies on consistent timing of these processes over trials. Using a temporally-unconstrained approach, the temporal differences in neural processing between presentations of the stimulus (or decisions to make) are explicitly accounted for.
By applying this novel method to a perceptual template-matching task, we tracked representational brain states associated with the cascade of neural processing, from early sensory areas to higher order areas, that are involved in integration and decision making. This way, we found that the timing of the cognitive processes involved in perceptual judgments can vary considerably over trials, even though the sequence of processing states was consistent for all subjects and trials. Furthermore, we found that the specific timing of

states on each trial was related to the quality of performance over trials. To summarise, I will discuss how this type of analysis could open avenues to investigate learning, memory consolidation and plasticity.

Discovering processing stages on single trials: Combining MVPA with Hidden semi-Markov models
Jelmer Borst
Cognitive science has long investigated processing stages. Where the traditional methods of Donders and Sternberg were limited by behavioral measures, new methods use neuroscience to track processing continuously.
Here I will present such a method, which is founded on two theories of EEG generation. Both the classical theory and the synchronized oscillation theory state that significant cognitive events cause multivariate voltage peaks that are added to the ongoing oscillations. If one could measure such peaks, one could identify the onset of cognitive stages. For example, if one averages across trials, the uncorrelated EEG signal will go to zero, and a peak will be identified (ERP analysis). However, the further away from a fixed time point, the larger the variation in timing of the peaks, making them hard to identify and impossible to define precisely in time.
The HsMM-MVPA method solves this problem by using hidden semi-Markov models to analyze EEG or MEG data. It integrates the information present across all trials of all participants, to ultimately identify multivariate peaks on single trials. I will first show that this method can identify processing stages in simple decision and memory tasks, and that it can track which cognitive stages are affected by experimental conditions. Next, I will show that we can measure the onsets of cognitive stages at the single-trial level, allowing for the identification of more precise ERP-like components, as well as the analysis of longer trials.

New Frontiers in Vision Rehabilitation: From Implants to Sensory Substitution

Dr. Benedetta Franceschiello[1,2,7], Dr. Ruxandra Tivadar[2,3,7], Prof. Serge Picaud[4], Prof. Monica Gori[5], Prof. Micah Murray[1,2,6]

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Organisers: Dr. Benedetta Franceschiello and Dr. Ruxandra Tivadar

Summary of the symposium:
According to the World Health Organisation, 2.2 billion people live with a vision impairment or with blindness, and preventable causes account for 80% of the total global burden. Therefore, visual neuroscience and vision rehabilitation constitute frontier areas with significant opportunities and implications for applied, basic, and clinical domains. This symposium brings together researchers whose work spans cutting-edge laboratory-based and field research on the development of new technologies and protocols for understanding vision, its breakdown, and its rehabilitation. The research covered in the symposium spans 1) the development of MRI-based tools for studying the structural-functional integrity of the visual system from eye to brain, 2) innovations in retinal prostheses, 3) the development and application of digital haptics, 4) the application of vision rehabilitation strategies with children, and 5) the mechanisms of brain plasticity promoting 'visual' functions in visually-impaired and sight-restored individuals. These advancements in the field will be presented and discussed in terms of the hurdles already overcome and the challenges ahead for widespread application in public health.

Title: DEBI – Dynamic Eye Brain Imaging
Speaker: Dr. Benedetta Franceschiello

Abstract: The interplay between eye and brain and the interdependence between the loss of functionality in the eye and its effect in the brain are research domains that have not been systematically explored. A lack of adequate methods is likely a major contributor to this knowledge gap. Magnetic Resonance Imaging (MRI) is a particularly promising non-invasive technique, because it can provide measurements related both to the tissue/organ structure and to the regional neural activity. MRI can also inform about particle deposits within the tissues, such as iron, considered a risk factor for eye and brain diseases. However, eye motion and its artefacts prevent the applicability of MR techniques to image the eye, therefore impeding the simultaneous imaging of the eye and brain. In this talk I will describe a recent technology our group successfully introduced, DEBI: a comprehensive, non-invasive research and assessment tool that can yield both structural and oculomotor information about the integrity of the eye and brain circuit (eye-brain) while the eye freely moves, overcoming motion artefacts through the application of motion-resolved techniques and a "free-running" approach.

Title: Visual restoration: from prosthesis and optogenetic therapy to sonogenetic therapy.
Speaker: Prof. Serge Picaud

Abstract: Following retinal degeneration, visual prostheses can restore some visual perception by stimulating residual neurons of the visual system but current devices fail to provide face recognition or autonomous motion in an unknown environment. We here tested the spatio-temporal resolutions of a

novel photovoltaic prosthesis and of optogenetic therapy at the retinal level in addition to sonogenetic therapy at the cortical level.
Following their validation in non-human primates, the retinal prostheses, PRIMA, showed the best visual acuity for a prosthesis in patients affected by age-related macular degeneration. In parallel, we selected the best AAV viral vector coding for ChrimsonR-tdTomato, a microbial opsin, in living primates, and this vector was found to generate a partial recovery of vision in a patient affected by retinitis pigmentosa. Finally, we showed that expression of a mechanosensitive channel in rat cortical neurons can produce a sensitivity to ultrasound waves with a spatiotemporal resolution compatible for visual restoration.
These results demonstrated the functional efficacy of the PRIMA photovoltaic retinal prosthesis and of optogenetic therapy using ChrimsonR up to clinical trials. Following these strategies at the retinal level, sonogenetic therapy will likely offer a novel brain machine interface at the cortical level.

Title: Digital Haptics in Vision Rehabilitation
Speaker: Dr. Ruxandra Tivadar

Abstract: Digital haptics are relevant as a sensory substitution and visual rehabilitation tool. Digital haptics use ultrasonic vibrations on screens to render textures through reduction of the local friction felt by an actively exploring finger. Digital haptics are a significant advance over existing approaches because they require less training time and are non-invasive and more ergonomic. First, we show how sighted and visually impaired participants quickly learn to interact with the device and in turn use digital haptics to generate mental representations of objects that they can then mentally manipulate in a mental rotation paradigm. Second, we show that digital haptics can also be applied in more naturalistic circumstances. In navigation experiments, digital haptics can confer the spatial layout of an environment and assist individuals in reconstruction and navigation of this space. In visual dual-task settings, haptic feedback significantly biases attention towards and improves performance on a central visual task, as compared to visual and multisensory (i.e. visual and haptic) feedback. This impacts dashboard designs in automobiles and other control panels. Collectively, our work shows how digital haptics provide an accessible approach for the benefit of visually impaired as well as sighted individuals alike, offering an ergonomic solution for sensory substitution.

Title: Multisensory integration development for rehabilitation
Speaker: Prof. Monica Gori

Abstract: In 2014 the number of blind children below the age of 15 years was estimated to be 19 million. It has long been known that visually impaired children tend to manifest impairments in the motor, perceptive, and social domains. The creation of new technological devices to be used early in life is a must.
However, despite the massive improvement of technological solutions specifically designed for visually impaired users, we find that adults do not widely accept many of these solutions, and these are not suitable for young children.
When the visual information is unavailable, the natural visual sensory feedback associated with body movement that is crucial for the development of spatial representation is missing. To restore this significant sensory-motor association, we recently developed and validated a new rehabilitation device called ABBI (Audio Bracelet for Blind Interaction; www.abbiproject.eu) to be used by children and adults with visual impairments starting from the first years of age. Our results suggest that three months of training with this device in 42 visually impaired children between 6 and 15 years of age rehabilitate space representation and social skills. The training was also effective in adults and younger, visually impaired children. In the presentation, I'll show the rehabilitation results obtained with the ABBI
device and with other tools we have recently developed and validated in young, visually impaired children.

Title: Multisensory plasticity supporting vision rehabilitation

Speaker: Prof. Micah Murray

Abstract: The 21st century has witnessed a paradigm shift in conceptions of the brain's functional organization. This talk first overviews evidence that instead of sensory systems operating in relative isolation, multisensory processes transpire at early and low-level stages; primary visual cortices are inherently multisensory. Two further lines of evidence show that multisensory processes also benefit vision rehabilitation. First, sounds enhance visual completion; a laboratory example of which is illusory contours (ICs) or borders perceived in the absence of contrast gradients. Hitherto, IC processes were considered exclusively visual in nature and unaffected by other sensory information. Not only is IC discrimination enhanced, but sounds also functionally couple brain responses within a network of primary visual, inferior parietal and lateral occipital cortices within the initial 100-150ms of stimulus processing. These findings impact visual rehabilitation strategies, because IC processes are impaired in sight-restored individuals despite intact low-level vision. Second, we detail the spatio-temporal brain dynamics of sensory substitution in the congenitally blind and the perceptual qualia they confer. The fusiform face area differentiates soundscapes of faces within ~400ms, and primary visual cortices retain vertical vs. horizontal line orientation sensitivity within ~270ms. The functional utility of multisensory plasticity in visual rehabilitation is widespread and cost-effective.

Beyond a single brain imaging modality and lab measure to enhance prediction of spontaneous behaviors and outcomes in drug addiction

Dr. Vince Calhoun[1], Dr. Conor Liston[2], Dr. Rita Goldstein[3], Prof. Dr. Daniel Durstewitz[4]
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Measuring brain responses using distinct yet complementary modalities, integrated with novel analyses to enhance modeling of naturalistic behaviors, may shed new light on higher-order human emotion and cognition with implications to psychopathology. We will focus on novel analyses and approaches applied to large-scale data encompassing free speech and mobile-sensor/electronic momentary assessment (EMA) and using various neural measures (spanning structural MRI, functional MRI and EEG/ERPs) to enhance understanding of the human brain in drug addiction and related disorders of inhibitory control and salience attribution. This symposium will start by presentation of novel machine-learning analyses applied to multivariate brain network features from several neuroimaging modalities to enhance prediction and understanding across human mental illness and specifically substance use disorders (Calhoun). The next speaker will proceed to the identification of the patterns and circuits in resting-state functional MRI signals and in structural MRI to dissect diagnostic heterogeneity and individual differences in drug addiction (Liston). The next one will demonstrate the use of brain responses to discreet neuropsychological tasks and/or naturalistic stimuli (movies) in predicting spontaneous behaviors (e.g., features in free speech, gaze duration, habit formation and craving, daily sleep/mobility patterns) to identify the underlying effects of drug stimuli on psychophysiological, cognitive and emotional functions in drug addicted individuals, as predictive of longitudinal clinical outcomes (Goldstein). The symposium will conclude by discussing new ongoing research and advanced machine-learning methods (e.g., deep learning) applied to model large-scale mobile-sensor/EMA data acquired in naturalistic settings, to further shed light on alcohol addiction and other psychiatric illnesses as disorders of network dynamics (Durstewitz).
Calhoun abstract: The neuroimaging community has seen a number of large open data collection efforts, which have vastly increased the amount of data available to the community. However, the use of such data for studying brain disorders is not trivial and comes with major challenges including 1) balancing computational resources and analytic flexibility, 2) harmonization/standardization across studies, 3) integrating categorical versus dimensional approaches to (multimodal) data. In this session I will present specific examples of strategies to address each of these points, with a focus on leveraging big data without 'losing the forest for the trees'. We will discuss three computationally efficient data-driven approaches [spatially constrained independent component analysis (ICA), constrained joint ICA, and a pre-trained deep neural network] to capture information about resting fMRI, structural MRI, and polygenic risk score (PRS) data in the large UK Biobank and ABCD datasets. We evaluate results relative to several transdiagnostic multisite clinical datasets including mental illness and substance use. Results show that PRS associated neuroimaging patterns derived from the typical data were associated with robustly decreased function and volume in frontotemporal, hippocampus complex, thalamus and insula. These patterns predict schizophrenia from controls with high accuracy, and predict cognition and symptoms for schizophrenia across four independent cohorts. A federated analysis of functional network connectivity using cohorts from India, the UK, and the US, reveals similar functional network connectivity patterns associated with drinkers and smokers relative to controls. ABCD neuroimaging data show a dimensional relationship in functional network connectivity patterns relative to clinical vs. control extremes. Strategies for working with large heterogeneous multimodal neuroimaging data are numerous and fraught with trade-offs. Here we show several ways to efficiently work with large typically developing or aging datasets in combination with clinical data. Results highlight potentially important relationships between neuroimaging genomics data and brain disorders.
Liston abstract: Substance use disorders (SUDs) are increasing in prevalence, particularly during the COVID-19 pandemic, and are already a leading cause of disability, due in part to our incomplete understanding of

the underlying pathophysiology. Like most neuropsychiatric syndromes, SUDs are highly heterogeneous, and distinct mechanisms may be operative in some individuals but not in others, even within a single diagnostic category. Furthermore, SUDs frequently co-occur with depression, anxiety, and other psychiatric syndromes, complicating efforts to identify molecular and circuit-level mechanisms, and disentangle them from those involved in mood and anxiety disorders. Diagnostic heterogeneity is thus a fundamental obstacle to developing better treatments, identifying biomarkers for quantifying risk for different forms of addiction, and predicting treatment response and relapse. Recently, we developed and validated an approach to discovering and diagnosing subtypes of depression using fMRI measures of functional connectivity, which in turn predicted subtype-specific clinical symptom profiles and treatment outcomes. Here, I will present the initial results of a multi-investigator collaboration to test the hypothesis that individual differences in mechanisms underlying impairments in response inhibition and salience attribution (iRISA) are mediated by distinct forms of dysfunctional connectivity in addiction-related circuits, which in turn interact and give rise to distinct neurophysiological addiction subtypes. Our initial findings in two large samples reveal at least two brain-behavior dimensions explaining individual differences in addiction- and mood-related symptoms and behaviors. They also identify clusters of SUD patients in this two dimensional space that transcend conventional diagnostic boundaries and are associated with distinct patterns of abnormal functional connectivity in iRISA-related networks.

Goldstein abstract: Drug addiction is a chronically relapsing disorder, with a clear set of clinical symptoms, encompassing repeat intoxication, craving, withdrawal, and relapse. The underlying cognitive, emotional and neurobiological substrates include enhanced salience attributed to the drug at the expense of non-drug related reinforcers with concomitant impairments in inhibitory control as attributed to deficits in the mesolimbic corticostriatal circuits innervated by dopamine. Recent advances in the field emphasize the importance of predicting clinical outcomes including relapse vs. abstinence and treatment success, encouraging the use of machine learning/artificial intelligence to identify important brain-behavior bio-markers from data obtained before treatment. In this talk we will focus on such bio-markers in individuals addicted to cocaine and/or heroin, providing empirical evidence from currently ongoing clinical trials, where neuroimaging and neuropsychological testing are conducted before (and after) randomization of subjects intro select treatments (e.g., mindfulness, tDCS) with the goal of ultimately improving diagnostics and for tailored treatment delivery. Throughout this talk, I will discuss the importance of prediction to enhancing understanding of the complex nature of human drug addiction. Specifically, I will explore issues pertaining to the severity of addiction (e.g., is it easier to predict a more severe state; are we missing out on predictive variability by excluding those who are resilient?), phenomenology of addiction (e.g., is craving/wanting more predictable than liking/hedonic responses? Can we identify different patterns of drug use and differentiate not only addicted individuals from healthy control subjects but also, within the addicted individuals, those who use different drugs of abuse; show treatment-seeking vs. current use; binge use vs. more low-grade yet constant use; use associated with the revolving door of detoxification, rehabilitation, jail; effects of menstrual cycle on drug use and craving in women) and course of addiction (e.g., modeling non-linear relationship patterns such as those between abstinence length and cue-induced reactivity termed incubation of craving).

Durstewitz Abstract: Like many other phenomena in physics and biology, cognitive and neural processes can be formally described, predicted, or explained using the mathematical framework of dynamical systems theory (DST). For instance, reinforcement learning models (among many others) are formally discrete-time dynamical systems (DSs), as are recurrent neural networks (RNNs). Likewise, any Turing machine (and hence computational process) can be reformulated or represented as a DS. In recent years there have been tremendous efforts in scientific machine learning to harvest recent progress in AI to infer the underlying DS directly from time series observations. One major branch of DS reconstruction approaches, to which we have contributed, is based on (deep) RNNs, which are universal approximators of DSs (i.e., can essentially represent any DS in their own governing equations). My talk will first cover these methodological developments, i.e. will review RNN architectures and training algorithms for DS reconstruction. I will then illustrate these methods on various examples from neuroscience and psychiatry, specifically neuroimaging and Smartphone-based mobile data. Applying RNN-based DS reconstruction to fMRI data, we can derive novel dynamical signatures of psychiatric or neurological conditions that may be utilized both for diagnosis and prediction, and for mechanistic insight into the nature of the disturbances in underlying network dynamics. Applying them to Ecological Momentary Assessments (EMAs) and other mobile data, we can build subject-level models of the individual behavioral dynamics that can be simulated to predict, for instance, the effect of potential interventions.