Auditory Expectations, Learning and Plasticity

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Christopher Petkov

Affiliation Newcastle University and University of Iowa

Participant(s) Christopher Petkov (Chair), Maria Geffen (Co-chair), Kerry Walker (Co-chair), Lori Holt (Presenter), Manuel Malmierca (Presenter), Zsuzsanna Kocsis (Presenter), Maria Chait (Presenter), Federico De Martino (Presenter), Maria Geffen (Presenter), Christopher Petkov (Presenter), Ryszard Auksztulewicz (Presenter)

SUBMISSION DETAILS

Session Description The auditory system constantly generates predictions about the sensory world based on prior experience, which creates expectations about upcoming future events. Auditory expectations powerfully shape sensation, perception and cognition, and a theoretical ‘predictive coding’ framework has advanced in large part from studies in the auditory domain. The expectancy process is thought to be mediated by neural interactions between feedforward and feedback processes all along the auditory pathway, using corticofugal projections from auditory cortex to the periphery, and back. However, until recently it had been unclear how different types of auditory expectations are detected and the role of different stages of the auditory pathway.

This symposium will provide a timely update to address:
• How do auditory expectations form, as an important basis for learning?
• What happens when expectations are not met and the system needs to adapt?
• In disorders that affect the auditory system how are expectancy signals affected?
• Is there plasticity that compensates for impact on the auditory system, and can auditory system impact be remediated?

The symposium will feature presentations from prominent early career and senior scientists, experts in the field of auditory expectancy, learning and plasticity. The presentations will cover a broad range of animal species, including murine models, nonhuman primates and humans. The speakers will showcase the latest neurophysiological approaches possible with each species, ranging from insights at the single neuron levels to mesoscopic and macroscopic studies of the auditory system in humans, including patients with auditory and communication impairments. The presentations will highlight cutting-edge approaches, including circuit-level optogenetic and pharmacological manipulations to identify causal elements involved in auditory expectancy and human intracranial recording and neuroimaging studies. The speakers will also provide insights on

how the auditory field is the leading modality helping to test and advance computational theories on predictive coding.

Presenter Diversity The symposium is gender balanced. The speakers represent five countries and a diversity of backgrounds. Six of the speakers are immigrants to the countries in which they are working.

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Signature Christopher Petkov

Auditory Expectations, Learning and Plasticity

Prediction, Attention, and Memory in the Auditory Cortex

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Ryszard Auksztulewicz

Affiliation European Neuroscience Institute Göttingen

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SUBMISSION DETAILS

Individual Abstract The brain is thought to generate internal predictions, based on the memory of past stimulation, to optimise behaviour. However, it is unclear to what extent these predictions are modulated by other top-down factors such as attention and task demands, and whether predictions of different sensory features are mediated by the same neural mechanisms. In this talk I will present results of studies combining human and rodent electrophysiology with computational modelling to identify the neural mechanisms of sensory predictions and their interactions with other cognitive factors. First, in non-invasive studies using MEG/EEG and direct recordings from humans using ECoG, analysis of behavioural and neural data showed that the effects of predictions are not automatic but are modulated by their contextual relevance. Second, computational modelling of the data suggested that these modulations could be linked to specific candidate mechanisms, including gain control in sensory regions. Finally, in a series of studies using invasive recordings in anaesthetised rodents, neural representations related to stimulus memory and predictions could be simultaneously decoded from auditory cortical activity, shedding light on the evolutionary conservation of predictive processing across species.

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Signature Ryszard Auksztulewicz

Auditory Expectations, Learning and Plasticity

Corticofugal Regulation of Predictive Coding

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Maria Geffen

Affiliation University of Pennsylvania School of Medicine

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SUBMISSION DETAILS

Individual Abstract Sensory systems must account for both contextual factors and prior experience to adaptively engage with the dynamic external environment. In the central auditory system, neurons modulate their responses to sounds based on statistical context. These response modulations can be understood through a hierarchical predictive coding lens: responses to repeated stimuli are progressively decreased, in a process known as repetition suppression, whereas unexpected stimuli produce a prediction error signal. Prediction error incrementally increases along the auditory hierarchy from the inferior colliculus (IC) to the auditory cortex (AC), suggesting that these regions may engage in hierarchical predictive coding. A potential substrate for top-down predictive cues is the massive set of descending projections from the AC to subcortical structures, although the role of this system in predictive processing has never been directly assessed. We tested the effect of optogenetic inactivation of the auditory cortico-collicular feedback in awake mice on responses of IC neurons to stimuli designed to test prediction error and repetition suppression. Inactivation of the cortico-collicular pathway led to a decrease in prediction error in IC. Repetition suppression was unaffected by cortico-collicular inactivation, suggesting that this metric may reflect fatigue of bottom-up sensory inputs rather than predictive processing. We also discovered populations of IC units that exhibit repetition enhancement, a sequential increase in firing with stimulus repetition. Cortico-collicular inactivation led to a decrease in repetition enhancement in the central nucleus of IC, suggesting that it is a top-down phenomenon. Negative prediction error, a stronger response to a tone in a predictable rather than unpredictable sequence, was suppressed in shell IC units during cortico-collicular inactivation. These changes in predictive coding metrics arose from bidirectional modulations in the response to the standard and deviant contexts, such that the units in IC responded more similarly to each context in the absence of cortical input. We also investigated how these metrics compare between the anesthetized and awake states by recording from the same units under both conditions. We found that metrics of

predictive coding and deviance detection differ depending on the anesthetic state of the animal, with negative prediction error emerging in the central IC and repetition enhancement and prediction error being more prevalent in the absence of anesthesia. Overall, our results demonstrate that the AC provides cues about the statistical context of sound to subcortical brain regions via direct feedback, regulating processing of both prediction and repetition.

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Signature Maria Geffen

Auditory Expectations, Learning and Plasticity

Precision in Predictive coding: The Role of Neuromodultion in Deviance Detection

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Manuel Malmierca

Affiliation Institute of Neuroscience Castilla y Leon, INCYL.

Participant(s) Christopher Petkov (Chair), Maria Geffen (Co-chair), Kerry Walker (Co-chair), Lori Holt (Presenter), Manuel Malmierca (Presenter), Zsuzsanna Kocsis (Presenter), Maria Chait (Presenter), Federico De Martino (Presenter), Maria Geffen (Presenter), Christopher Petkov (Presenter), Ryszard Auksztulewicz (Presenter)

SUBMISSION DETAILS

Individual Abstract Behaviour becomes more efficient when we can predict a stimulus. This is the basis of the enormous flexibility underlying interactions with our physical and social environment. Filtering out non-relevant stimuli is an important but understudied aspect of cognition. Today, there is rather universal agreement in neuroscience, that a major function of the brain is to constantly predict the environment on multiple levels and time scales (Friston, 2005), For example, one anticipates how a word of a friend will sound, and when and how a sentence will end, even before it has ended. This proposal is based on the assumption that the brain's neuronal circuitry is organized as a highly predictive machine.

The ability of the brain to recognize which prediction errors carry reliable information is critical in the process of prediction error minimization. For example, if a sensor is malfunctioning because of an impairment (e.g., hearing loss or tinnitus) or because it is operating out of its appropriate physical range, the sensory input it provides is not adequately reporting on real changes in the environment, which may generate misinformative prediction errors. According to the predictive coding theory, this distinction between signal and noise is based on an important element, the so-called precision, which weights the driving power of prediction errors according to how reliable they are estimated to be (Friston, 2005).

Neuromodulatory inputs not only gate plasticity (Martins and Froemke, 2015), but also change the balance of top-down versus bottom-up influence and it well known that neuromodulation strongly impacts sensory processing, learning and memory. 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). Therefore, 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. We have used single neuron recordings and microiontophoresis manipulation of the cholinergic system in the rat brain to study how these neuromodulators shape the predictive responses in cortical and subcortical brain regions in the rat brain

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Auditory Expectations, Learning and Plasticity

Transformations of Auditory Sequences into Neural Expectancy Signals

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Christopher Petkov

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SUBMISSION DETAILS

Individual Abstract There is considerable interest in understanding the neural transformations that occur at every stage in the auditory system. These are no longer thought to be simply feedforward or unidirectional, but rather are better conceived of as bidirectional processes and interactions that occur at every stage in the auditory system and influence sensory processing and expectation. A prime example of a system that efficiently transforms auditory sequences into higher-order structures is the human language system. However, because this system in humans is often thought to be special, the aspects of it that have parallels with the neural systems of other animals remains an open question. In this presentation, we overview work in human and nonhuman primates involving the processing of auditory sequences using statistical learning tasks that generate auditory expectancies. There is now evidence from comparative neuroimaging work that a broad auditory cortical system is involved in processing auditory dependencies separated in time. We also present data from neurophysiological recordings in nonhuman primates and human neurosurgery patients identifying auditory cortical expectancy signals and those that only appear when expectations are not met. This comparative research has generated hypotheses on the key neural transformations and neuronal codes that bind sequentially distributed auditory dependencies in time. We conclude the presentation by showing that there are now closer nonhuman animal parallels to the human auditory and language system, which bodes well for understanding fundamental aspects of it with animal models and more directly informing research with patients that have auditory disorders.

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Signature Christopher Petkov

Auditory Expectations, Learning and Plasticity

Immediate Neural Network Impact and Compensation after the Loss of a Semantic Hub

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Zsuzsanna Kocsis

Affiliation University of Iowa

Participant(s) Christopher Petkov (Chair), Maria Geffen (Co-chair), Kerry Walker (Co-chair), Lori Holt (Presenter), Manuel Malmierca (Presenter), Zsuzsanna Kocsis (Presenter), Maria Chait (Presenter), Federico De Martino (Presenter), Maria Geffen (Presenter), Christopher Petkov (Presenter), Ryszard Auksztulewicz (Presenter)

SUBMISSION DETAILS

Individual Abstract The human brain extracts meaning from the world using an extensive neural system for semantic knowledge. Whether such broadly distributed systems crucially depend on or can compensate for the loss of one of their highly interconnected hubs is controversial. The strongest level of causal evidence for the role of a brain hub is to evaluate its acute network-level impact following disconnection and any rapid functional compensation that ensues. We report rare neurophysiological data from two patients who underwent awake intracranial recordings during a speech prediction task immediately before and after neurosurgical treatment that required disconnection of the left anterior temporal lobe (ATL), a crucial hub for semantic knowledge. Informed by a predictive coding framework, we tested three sets of hypotheses including diaschisis causing disruption in interconnected sites and incomplete or complete compensation by other language-critical and speech processing sites. Immediately after ATL disconnection, we observed highly specific neurophysiological alterations in the recorded fronto-temporal network, including abnormally magnified high gamma responses to the speech sounds in auditory cortex. We also observed evidence for rapid compensation, seen as focal increases in effective connectivity involving language-critical sites in the inferior frontal gyrus and speech processing sites in auditory cortex. However, compensation was incomplete, in part because after ATL disconnection speech prediction signals were depleted in auditory cortex. This study provides direct causal evidence for a semantic hub in the human brain and shows striking neural impact and a rapid attempt at compensation in a neural network after the loss of one of its hubs.

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Signature Zsuzsanna Kocsis

Auditory Expectations, Learning and Plasticity

Laminar and High Spatial Resolution fMRI of Human Auditory Predictive Processing.

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Federico De Martino

Affiliation Maastricht University

Participant(s) Christopher Petkov (Chair), Maria Geffen (Co-chair), Kerry Walker (Co-chair), Lori Holt (Presenter), Manuel Malmierca (Presenter), Zsuzsanna Kocsis (Presenter), Maria Chait (Presenter), Federico De Martino (Presenter), Maria Geffen (Presenter), Christopher Petkov (Presenter), Ryszard Auksztulewicz (Presenter)

SUBMISSION DETAILS

Individual Abstract To deal with dynamic changes in the soundscape and adjust our behaviour accordingly, a key function of our brain is to predict future states of the world. This has led to a transformative way of thinking about brain function. That is, what we perceive does not reflect the sensory stimulus itself, but rather a combination of the stimulus and an internal (generative) model of its causes. This idea has led to several theoretical advances some of which are capitalized by Predictive Coding (PC). PC assumes that generative models are formed through the exchange of prediction errors (feedforward) and predictions (feedback) across hierarchical processing stages. In addition, PC assumes that prediction errors are modulated by the precision of currently available predictions. Results from invasive animal and human electrophysiological studies support the relevance of predictions for neural processing at different hierarchical levels. Nevertheless, especially in humans the evidence grounding PC principles onto fundamental neurocomputational units (i.e. cortical layers, subdivisions of subcortical structures) is limited and this hampers our understanding of how PC supports the processing of sounds in context in the human brain.
Ultra-high field fMRI at high spatial resolution offers a unique opportunity to investigate how computations are embedded in the mesoscopic (cortical) architecture of the human brain (in vivo and non-invasively). Laminar fMRI has already been used to investigate predictive processes in the human visual cortex. In this talk I will describe recent results from studies investigating how predictions and prediction errors are processed in auditory cortical layers. We combine ultra-high field fMRI with biophysical and computational approaches to gain further insights into the computations underlying these responses.

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Signature Federico De Martino

Auditory Expectations, Learning and Plasticity

Category Learning and Dimension-Selective Attention in Auditory Cortex

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Lori Holt

Affiliation Carnegie Mellon University

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SUBMISSION DETAILS

Individual Abstract Human listeners possess rich category representations for speech sounds and words. Yet speech input exhibits complexity across multiple acoustic dimensions, and short-term speech input regularities may not match long-term norms (as in foreign accents). Theoretical accounts of speech perception often have appealed to selective attention as a means by which to balance these demands. However, we do not yet understand how – and whether - listeners learn to selectively attend to informative acoustic dimensions during category learning, how selective attention impacts cortical representations of relevant dimensions, and whether selective attention involves suppression of irrelevant dimensions as well as enhancement of relevant dimensions.

We are examining these questions using novel non-speech auditory categories. Participants complete five days of stimulus-response-feedback training during which they learn four nonspeech categories to criterion. The categories are structured to require listeners to learn acoustic patterns positioned in either a high- or low-frequency band, with simultaneous irrelevant acoustic patterns in the opposite band. Thus, category learning requires reliance on – and perhaps selective attention to – the category-diagnostic acoustic patterns. Control trials involve categorization across an orthogonal dimension, stimulus amplitude (‘big’ or ‘small’ Category A). In a single post-training MRI session, listeners categorize sounds in a 2AFC task with categories differentiated by information in either high or low spectral bands, or on relative amplitude. Combined with tonotopic mapping and “attention-o-tonotopic” mapping driven by overt endogenous attention to high and low frequency bands, we examine how dimension-selective attention driven by implicit demands of categorization impact cortical activation.

This work illuminates the cortical mechanisms supporting dimension-based auditory selective

attention, providing a bridge to compare explicitly directed attention (i.e., “listen high”) and selective attention that emerges with learning. Comparison with our control (amplitude) condition allows for assessment of a putative role for suppression. Finally, the study links human studies with non-human animal studies of frequency-selective auditory attention with non-speech stimuli.

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Signature Lori L Holt

Auditory Expectations, Learning and Plasticity

Neural Mechanisms for Tracking Uncertainty in Rapidly Unfolding Sound Sequences.

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Maria Chait

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Participant(s) Christopher Petkov (Chair), Maria Geffen (Co-chair), Kerry Walker (Co-chair), Lori Holt (Presenter), Manuel Malmierca (Presenter), Zsuzsanna Kocsis (Presenter), Maria Chait (Presenter), Federico De Martino (Presenter), Maria Geffen (Presenter), Christopher Petkov (Presenter), Ryszard Auksztulewicz (Presenter)

SUBMISSION DETAILS

Individual Abstract The brain maintains a hierarchy of models to monitor the statistics of its surroundings and inform behaviour. Determining how such models are instantiated and updated is key to understanding the brain as a statistical learning machine.

The auditory system, supported by a network of auditory, hippocampal, and frontal sources, automatically discovers regularities in rapid tone sequences even when these are not behaviourally relevant. We have previously identified specific brain signatures of sequence structure tracking in humans. The transition from a random tone pattern to a structured pattern (RAN-REG) elicits a slow increase in tonic activity that is consistent with gradual evidence accumulation and instantiation of a new model. In contrast, the opposite transition (REG-RAN) evokes an ‘interrupt’ response’: a sharp drop in sustained activity, hypothesized to reflect immediate suppression of top-down prior expectations. The activity settles at a low sustained level, consistent with the weaker statistical constraints in the RAN pattern.

In this series of MEG experiments, we investigated how “model establishment” and “interrupt” responses are affected by information rate (by using sequences of identical statistical properties but halving tone-pip length; 25 vs 50 ms) and predictability of pattern transitions.

We examined responses to the following sequence transitions: REG1-REG2 (from one regular to a different regular pattern) REG-RAN (from a regular to a random pattern) REG1-RAN-REG1 (a regular pattern interrupted by a 500ms random pattern followed by the resuming of the original pattern). The probabilities of these transitions were varied to model a range of environmental volatilities. Naive participants performed a decoy task, while listening passively to the sounds.

We report the following key findings:
(1) The detailed dynamics of discovering, abandoning and learning new structure in sound sequences are observable in the MEG signal.
(2) The dynamics of “model establishment” roughly scaled with tone duration but with some evidence of increasing sluggishness with longer tones.
(3) In REG1-RAN-REG1 trials, post interruption model establishment occurred much faster than in REG1-REG2 trials, suggesting that a model of the original sequence was automatically preserved and re-activated.
(4) The “interrupt” response did not differ between high probably and low probability interruptions, suggesting an automatic process that (unlike what is expected from a Bayesian system) is not affected by volatility per se.

Ongoing EEG work comparing such brain responses in human and non-human primates explores how mnemonic systems may have evolved to support pattern sensitivity in humans.

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Signature Maria Chait

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Submitter Christopher Petkov

Affiliation Newcastle University and University of Iowa

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• In disorders that affect the auditory system how are expectancy signals affected?
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Presenter Diversity The symposium is gender balanced. The speakers represent five countries and a diversity of backgrounds. Six of the speakers are immigrants to the countries in which they are working.

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Signature Christopher Petkov

Auditory Expectations, Learning and Plasticity

Prediction, Attention, and Memory in the Auditory Cortex

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Ryszard Auksztulewicz

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SUBMISSION DETAILS

Individual Abstract The brain is thought to generate internal predictions, based on the memory of past stimulation, to optimise behaviour. However, it is unclear to what extent these predictions are modulated by other top-down factors such as attention and task demands, and whether predictions of different sensory features are mediated by the same neural mechanisms. In this talk I will present results of studies combining human and rodent electrophysiology with computational modelling to identify the neural mechanisms of sensory predictions and their interactions with other cognitive factors. First, in non-invasive studies using MEG/EEG and direct recordings from humans using ECoG, analysis of behavioural and neural data showed that the effects of predictions are not automatic but are modulated by their contextual relevance. Second, computational modelling of the data suggested that these modulations could be linked to specific candidate mechanisms, including gain control in sensory regions. Finally, in a series of studies using invasive recordings in anaesthetised rodents, neural representations related to stimulus memory and predictions could be simultaneously decoded from auditory cortical activity, shedding light on the evolutionary conservation of predictive processing across species.

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Auditory Expectations, Learning and Plasticity

Corticofugal Regulation of Predictive Coding

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Maria Geffen

Affiliation University of Pennsylvania School of Medicine

Participant(s) Christopher Petkov (Chair), Maria Geffen (Co-chair), Kerry Walker (Co-chair), Lori Holt (Presenter), Manuel Malmierca (Presenter), Zsuzsanna Kocsis (Presenter), Maria Chait (Presenter), Federico De Martino (Presenter), Maria Geffen (Presenter), Christopher Petkov (Presenter), Ryszard Auksztulewicz (Presenter)

SUBMISSION DETAILS

Individual Abstract Sensory systems must account for both contextual factors and prior experience to adaptively engage with the dynamic external environment. In the central auditory system, neurons modulate their responses to sounds based on statistical context. These response modulations can be understood through a hierarchical predictive coding lens: responses to repeated stimuli are progressively decreased, in a process known as repetition suppression, whereas unexpected stimuli produce a prediction error signal. Prediction error incrementally increases along the auditory hierarchy from the inferior colliculus (IC) to the auditory cortex (AC), suggesting that these regions may engage in hierarchical predictive coding. A potential substrate for top-down predictive cues is the massive set of descending projections from the AC to subcortical structures, although the role of this system in predictive processing has never been directly assessed. We tested the effect of optogenetic inactivation of the auditory cortico-collicular feedback in awake mice on responses of IC neurons to stimuli designed to test prediction error and repetition suppression. Inactivation of the cortico-collicular pathway led to a decrease in prediction error in IC. Repetition suppression was unaffected by cortico-collicular inactivation, suggesting that this metric may reflect fatigue of bottom-up sensory inputs rather than predictive processing. We also discovered populations of IC units that exhibit repetition enhancement, a sequential increase in firing with stimulus repetition. Cortico-collicular inactivation led to a decrease in repetition enhancement in the central nucleus of IC, suggesting that it is a top-down phenomenon. Negative prediction error, a stronger response to a tone in a predictable rather than unpredictable sequence, was suppressed in shell IC units during cortico-collicular inactivation. These changes in predictive coding metrics arose from bidirectional modulations in the response to the standard and deviant contexts, such that the units in IC responded more similarly to each context in the absence of cortical input. We also investigated how these metrics compare between the anesthetized and awake states by recording from the same units under both conditions. We found that metrics of

predictive coding and deviance detection differ depending on the anesthetic state of the animal, with negative prediction error emerging in the central IC and repetition enhancement and prediction error being more prevalent in the absence of anesthesia. Overall, our results demonstrate that the AC provides cues about the statistical context of sound to subcortical brain regions via direct feedback, regulating processing of both prediction and repetition.

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Signature Maria Geffen

Auditory Expectations, Learning and Plasticity

Precision in Predictive coding: The Role of Neuromodultion in Deviance Detection

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Manuel Malmierca

Affiliation Institute of Neuroscience Castilla y Leon, INCYL.

Participant(s) Christopher Petkov (Chair), Maria Geffen (Co-chair), Kerry Walker (Co-chair), Lori Holt (Presenter), Manuel Malmierca (Presenter), Zsuzsanna Kocsis (Presenter), Maria Chait (Presenter), Federico De Martino (Presenter), Maria Geffen (Presenter), Christopher Petkov (Presenter), Ryszard Auksztulewicz (Presenter)

SUBMISSION DETAILS

Individual Abstract Behaviour becomes more efficient when we can predict a stimulus. This is the basis of the enormous flexibility underlying interactions with our physical and social environment. Filtering out non-relevant stimuli is an important but understudied aspect of cognition. Today, there is rather universal agreement in neuroscience, that a major function of the brain is to constantly predict the environment on multiple levels and time scales (Friston, 2005), For example, one anticipates how a word of a friend will sound, and when and how a sentence will end, even before it has ended. This proposal is based on the assumption that the brain’s neuronal circuitry is organized as a highly predictive machine.

The ability of the brain to recognize which prediction errors carry reliable information is critical in the process of prediction error minimization. For example, if a sensor is malfunctioning because of an impairment (e.g., hearing loss or tinnitus) or because it is operating out of its appropriate physical range, the sensory input it provides is not adequately reporting on real changes in the environment, which may generate misinformative prediction errors. According to the predictive coding theory, this distinction between signal and noise is based on an important element, the so-called precision, which weights the driving power of prediction errors according to how reliable they are estimated to be (Friston, 2005).

Neuromodulatory inputs not only gate plasticity (Martins and Froemke, 2015), but also change the balance of top-down versus bottom-up influence and it well known that neuromodulation strongly impacts sensory processing, learning and memory. 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). Therefore, 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. We have used single neuron recordings and microiontophoresis manipulation of the cholinergic system in the rat brain to study how these neuromodulators shape the predictive responses in cortical and subcortical brain regions in the rat brain

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Auditory Expectations, Learning and Plasticity

Transformations of Auditory Sequences into Neural Expectancy Signals

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Christopher Petkov

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SUBMISSION DETAILS

Individual Abstract There is considerable interest in understanding the neural transformations that occur at every stage in the auditory system. These are no longer thought to be simply feedforward or unidirectional, but rather are better conceived of as bidirectional processes and interactions that occur at every stage in the auditory system and influence sensory processing and expectation. A prime example of a system that efficiently transforms auditory sequences into higher-order structures is the human language system. However, because this system in humans is often thought to be special, the aspects of it that have parallels with the neural systems of other animals remains an open question. In this presentation, we overview work in human and nonhuman primates involving the processing of auditory sequences using statistical learning tasks that generate auditory expectancies. There is now evidence from comparative neuroimaging work that a broad auditory cortical system is involved in processing auditory dependencies separated in time. We also present data from neurophysiological recordings in nonhuman primates and human neurosurgery patients identifying auditory cortical expectancy signals and those that only appear when expectations are not met. This comparative research has generated hypotheses on the key neural transformations and neuronal codes that bind sequentially distributed auditory dependencies in time. We conclude the presentation by showing that there are now closer nonhuman animal parallels to the human auditory and language system, which bodes well for understanding fundamental aspects of it with animal models and more directly informing research with patients that have auditory disorders.

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Signature Christopher Petkov

Auditory Expectations, Learning and Plasticity

Immediate Neural Network Impact and Compensation after the Loss of a Semantic Hub

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Zsuzsanna Kocsis

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SUBMISSION DETAILS

Individual Abstract The human brain extracts meaning from the world using an extensive neural system for semantic knowledge. Whether such broadly distributed systems crucially depend on or can compensate for the loss of one of their highly interconnected hubs is controversial. The strongest level of causal evidence for the role of a brain hub is to evaluate its acute network-level impact following disconnection and any rapid functional compensation that ensues. We report rare neurophysiological data from two patients who underwent awake intracranial recordings during a speech prediction task immediately before and after neurosurgical treatment that required disconnection of the left anterior temporal lobe (ATL), a crucial hub for semantic knowledge. Informed by a predictive coding framework, we tested three sets of hypotheses including diaschisis causing disruption in interconnected sites and incomplete or complete compensation by other language-critical and speech processing sites. Immediately after ATL disconnection, we observed highly specific neurophysiological alterations in the recorded fronto-temporal network, including abnormally magnified high gamma responses to the speech sounds in auditory cortex. We also observed evidence for rapid compensation, seen as focal increases in effective connectivity involving language-critical sites in the inferior frontal gyrus and speech processing sites in auditory cortex. However, compensation was incomplete, in part because after ATL disconnection speech prediction signals were depleted in auditory cortex. This study provides direct causal evidence for a semantic hub in the human brain and shows striking neural impact and a rapid attempt at compensation in a neural network after the loss of one of its hubs.

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Signature Zsuzsanna Kocsis

Auditory Expectations, Learning and Plasticity

Laminar and High Spatial Resolution fMRI of Human Auditory Predictive Processing.

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Federico De Martino

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SUBMISSION DETAILS

Individual Abstract To deal with dynamic changes in the soundscape and adjust our behaviour accordingly, a key function of our brain is to predict future states of the world. This has led to a transformative way of thinking about brain function. That is, what we perceive does not reflect the sensory stimulus itself, but rather a combination of the stimulus and an internal (generative) model of its causes. This idea has led to several theoretical advances some of which are capitalized by Predictive Coding (PC). PC assumes that generative models are formed through the exchange of prediction errors (feedforward) and predictions (feedback) across hierarchical processing stages. In addition, PC assumes that prediction errors are modulated by the precision of currently available predictions. Results from invasive animal and human electrophysiological studies support the relevance of predictions for neural processing at different hierarchical levels. Nevertheless, especially in humans the evidence grounding PC principles onto fundamental neurocomputational units (i.e. cortical layers, subdivisions of subcortical structures) is limited and this hampers our understanding of how PC supports the processing of sounds in context in the human brain. Ultra-high field fMRI at high spatial resolution offers a unique opportunity to investigate how computations are embedded in the mesoscopic (cortical) architecture of the human brain (in vivo and non-invasively). Laminar fMRI has already been used to investigate predictive processes in the human visual cortex. In this talk I will describe recent results from studies investigating how predictions and prediction errors are processed in auditory cortical layers. We combine ultra-high field fMRI with biophysical and computational approaches to gain further insights into the computations underlying these responses.

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Signature Federico De Martino

Auditory Expectations, Learning and Plasticity

Category Learning and Dimension-Selective Attention in Auditory Cortex

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Lori Holt

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SUBMISSION DETAILS

Individual Abstract Human listeners possess rich category representations for speech sounds and words. Yet speech input exhibits complexity across multiple acoustic dimensions, and short-term speech input regularities may not match long-term norms (as in foreign accents). Theoretical accounts of speech perception often have appealed to selective attention as a means by which to balance these demands. However, we do not yet understand how – and whether - listeners learn to selectively attend to informative acoustic dimensions during category learning, how selective attention impacts cortical representations of relevant dimensions, and whether selective attention involves suppression of irrelevant dimensions as well as enhancement of relevant dimensions.

We are examining these questions using novel non-speech auditory categories. Participants complete five days of stimulus-response-feedback training during which they learn four nonspeech categories to criterion. The categories are structured to require listeners to learn acoustic patterns positioned in either a high- or low-frequency band, with simultaneous irrelevant acoustic patterns in the opposite band. Thus, category learning requires reliance on – and perhaps selective attention to – the category-diagnostic acoustic patterns. Control trials involve categorization across an orthogonal dimension, stimulus amplitude ('big' or 'small' Category A). In a single post-training MRI session, listeners categorize sounds in a 2AFC task with categories differentiated by information in either high or low spectral bands, or on relative amplitude. Combined with tonotopic mapping and "attention-o-tonotopic" mapping driven by overt endogenous attention to high and low frequency bands, we examine how dimension-selective attention driven by implicit demands of categorization impact cortical activation.

This work illuminates the cortical mechanisms supporting dimension-based auditory selective

attention, providing a bridge to compare explicitly directed attention (i.e., “listen high”) and selective attention that emerges with learning. Comparison with our control (amplitude) condition allows for assessment of a putative role for suppression. Finally, the study links human studies with non-human animal studies of frequency-selective auditory attention with non-speech stimuli.

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Signature Lori L Holt

Auditory Expectations, Learning and Plasticity

Neural Mechanisms for Tracking Uncertainty in Rapidly Unfolding Sound Sequences.

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Maria Chait

Affiliation UCL Ear Institute

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SUBMISSION DETAILS

Individual Abstract The brain maintains a hierarchy of models to monitor the statistics of its surroundings and inform behaviour. Determining how such models are instantiated and updated is key to understanding the brain as a statistical learning machine.

The auditory system, supported by a network of auditory, hippocampal, and frontal sources, automatically discovers regularities in rapid tone sequences even when these are not behaviourally relevant. We have previously identified specific brain signatures of sequence structure tracking in humans. The transition from a random tone pattern to a structured pattern (RAN-REG) elicits a slow increase in tonic activity that is consistent with gradual evidence accumulation and instantiation of a new model. In contrast, the opposite transition (REG-RAN) evokes an ‘interrupt’ response’: a sharp drop in sustained activity, hypothesized to reflect immediate suppression of top-down prior expectations. The activity settles at a low sustained level, consistent with the weaker statistical constraints in the RAN pattern.

In this series of MEG experiments, we investigated how “model establishment” and “interrupt” responses are affected by information rate (by using sequences of identical statistical properties but halving tone-pip length; 25 vs 50 ms) and predictability of pattern transitions.

We examined responses to the following sequence transitions: REG1-REG2 (from one regular to a different regular pattern) REG-RAN (from a regular to a random pattern) REG1-RAN-REG1 (a regular pattern interrupted by a 500ms random pattern followed by the resuming of the original pattern). The probabilities of these transitions were varied to model a range of environmental volatilities. Naive participants performed a decoy task, while listening passively to the sounds.

We report the following key findings:
(1) The detailed dynamics of discovering, abandoning and learning new structure in sound sequences are observable in the MEG signal.
(2) The dynamics of “model establishment” roughly scaled with tone duration but with some evidence of increasing sluggishness with longer tones.
(3) In REG1-RAN-REG1 trials, post interruption model establishment occurred much faster than in REG1-REG2 trials, suggesting that a model of the original sequence was automatically preserved and re-activated.
(4) The “interrupt” response did not differ between high probably and low probability interruptions, suggesting an automatic process that (unlike what is expected from a Bayesian system) is not affected by volatility per se.

Ongoing EEG work comparing such brain responses in human and non-human primates explores how mnemonic systems may have evolved to support pattern sensitivity in humans.

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Signature Maria Chait

Auditory Expectations, Learning and Plasticity

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Christopher Petkov

Affiliation Newcastle University and University of Iowa

Participant(s) Christopher Petkov (Chair), Maria Geffen (Co-chair), Kerry Walker (Co-chair), Lori Holt (Presenter), Manuel Malmierca (Presenter), Zsuzsanna Kocsis (Presenter), Maria Chait (Presenter), Federico De Martino (Presenter), Maria Geffen (Presenter), Christopher Petkov (Presenter), Ryszard Auksztulewicz (Presenter)

SUBMISSION DETAILS

Session Description The auditory system constantly generates predictions about the sensory world based on prior experience, which creates expectations about upcoming future events. Auditory expectations powerfully shape sensation, perception and cognition, and a theoretical 'predictive coding' framework has advanced in large part from studies in the auditory domain. The expectancy process is thought to be mediated by neural interactions between feedforward and feedback processes all along the auditory pathway, using corticofugal projections from auditory cortex to the periphery, and back. However, until recently it had been unclear how different types of auditory expectations are detected and the role of different stages of the auditory pathway.

This symposium will provide a timely update to address:
• How do auditory expectations form, as an important basis for learning?
• What happens when expectations are not met and the system needs to adapt?
• In disorders that affect the auditory system how are expectancy signals affected?
• Is there plasticity that compensates for impact on the auditory system, and can auditory system impact be remediated?

The symposium will feature presentations from prominent early career and senior scientists, experts in the field of auditory expectancy, learning and plasticity. The presentations will cover a broad range of animal species, including murine models, nonhuman primates and humans. The speakers will showcase the latest neurophysiological approaches possible with each species, ranging from insights at the single neuron levels to mesoscopic and macroscopic studies of the auditory system in humans, including patients with auditory and communication impairments. The presentations will highlight cutting-edge approaches, including circuit-level optogenetic and pharmacological manipulations to identify causal elements involved in auditory expectancy and human intracranial recording and neuroimaging studies. The speakers will also provide insights on

how the auditory field is the leading modality helping to test and advance computational theories on predictive coding.

Presenter Diversity The symposium is gender balanced. The speakers represent five countries and a diversity of backgrounds. Six of the speakers are immigrants to the countries in which they are working.

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Signature Christopher Petkov

Auditory Expectations, Learning and Plasticity

Prediction, Attention, and Memory in the Auditory Cortex

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Ryszard Auksztulewicz

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SUBMISSION DETAILS

Individual Abstract The brain is thought to generate internal predictions, based on the memory of past stimulation, to optimise behaviour. However, it is unclear to what extent these predictions are modulated by other top-down factors such as attention and task demands, and whether predictions of different sensory features are mediated by the same neural mechanisms. In this talk I will present results of studies combining human and rodent electrophysiology with computational modelling to identify the neural mechanisms of sensory predictions and their interactions with other cognitive factors. First, in non-invasive studies using MEG/EEG and direct recordings from humans using ECoG, analysis of behavioural and neural data showed that the effects of predictions are not automatic but are modulated by their contextual relevance. Second, computational modelling of the data suggested that these modulations could be linked to specific candidate mechanisms, including gain control in sensory regions. Finally, in a series of studies using invasive recordings in anaesthetised rodents, neural representations related to stimulus memory and predictions could be simultaneously decoded from auditory cortical activity, shedding light on the evolutionary conservation of predictive processing across species.

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Signature Ryszard Auksztulewicz

Auditory Expectations, Learning and Plasticity

Corticofugal Regulation of Predictive Coding

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Maria Geffen

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SUBMISSION DETAILS

Individual Abstract Sensory systems must account for both contextual factors and prior experience to adaptively engage with the dynamic external environment. In the central auditory system, neurons modulate their responses to sounds based on statistical context. These response modulations can be understood through a hierarchical predictive coding lens: responses to repeated stimuli are progressively decreased, in a process known as repetition suppression, whereas unexpected stimuli produce a prediction error signal. Prediction error incrementally increases along the auditory hierarchy from the inferior colliculus (IC) to the auditory cortex (AC), suggesting that these regions may engage in hierarchical predictive coding. A potential substrate for top-down predictive cues is the massive set of descending projections from the AC to subcortical structures, although the role of this system in predictive processing has never been directly assessed. We tested the effect of optogenetic inactivation of the auditory cortico-collicular feedback in awake mice on responses of IC neurons to stimuli designed to test prediction error and repetition suppression. Inactivation of the cortico-collicular pathway led to a decrease in prediction error in IC. Repetition suppression was unaffected by cortico-collicular inactivation, suggesting that this metric may reflect fatigue of bottom-up sensory inputs rather than predictive processing. We also discovered populations of IC units that exhibit repetition enhancement, a sequential increase in firing with stimulus repetition. Cortico-collicular inactivation led to a decrease in repetition enhancement in the central nucleus of IC, suggesting that it is a top-down phenomenon. Negative prediction error, a stronger response to a tone in a predictable rather than unpredictable sequence, was suppressed in shell IC units during cortico-collicular inactivation. These changes in predictive coding metrics arose from bidirectional modulations in the response to the standard and deviant contexts, such that the units in IC responded more similarly to each context in the absence of cortical input. We also investigated how these metrics compare between the anesthetized and awake states by recording from the same units under both conditions. We found that metrics of

predictive coding and deviance detection differ depending on the anesthetic state of the animal, with negative prediction error emerging in the central IC and repetition enhancement and prediction error being more prevalent in the absence of anesthesia. Overall, our results demonstrate that the AC provides cues about the statistical context of sound to subcortical brain regions via direct feedback, regulating processing of both prediction and repetition.

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Signature Maria Geffen

Auditory Expectations, Learning and Plasticity

Precision in Predictive coding: The Role of Neuromodultion in Deviance Detection

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Manuel Malmierca

Affiliation Institute of Neuroscience Castilla y Leon, INCYL.

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SUBMISSION DETAILS

Individual Abstract Behaviour becomes more efficient when we can predict a stimulus. This is the basis of the enormous flexibility underlying interactions with our physical and social environment. Filtering out non-relevant stimuli is an important but understudied aspect of cognition. Today, there is rather universal agreement in neuroscience, that a major function of the brain is to constantly predict the environment on multiple levels and time scales (Friston, 2005), For example, one anticipates how a word of a friend will sound, and when and how a sentence will end, even before it has ended. This proposal is based on the assumption that the brain's neuronal circuitry is organized as a highly predictive machine.

The ability of the brain to recognize which prediction errors carry reliable information is critical in the process of prediction error minimization. For example, if a sensor is malfunctioning because of an impairment (e.g., hearing loss or tinnitus) or because it is operating out of its appropriate physical range, the sensory input it provides is not adequately reporting on real changes in the environment, which may generate misinformative prediction errors. According to the predictive coding theory, this distinction between signal and noise is based on an important element, the so-called precision, which weights the driving power of prediction errors according to how reliable they are estimated to be (Friston, 2005).

Neuromodulatory inputs not only gate plasticity (Martins and Froemke, 2015), but also change the balance of top-down versus bottom-up influence and it well known that neuromodulation strongly impacts sensory processing, learning and memory. 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). Therefore, 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. We have used single neuron recordings and microiontophoresis manipulation of the cholinergic system in the rat brain to study how these neuromodulators shape the predictive responses in cortical and subcortical brain regions in the rat brain

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Auditory Expectations, Learning and Plasticity

Transformations of Auditory Sequences into Neural Expectancy Signals

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Christopher Petkov

Affiliation Newcastle University and University of Iowa

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SUBMISSION DETAILS

Individual Abstract There is considerable interest in understanding the neural transformations that occur at every stage in the auditory system. These are no longer thought to be simply feedforward or unidirectional, but rather are better conceived of as bidirectional processes and interactions that occur at every stage in the auditory system and influence sensory processing and expectation. A prime example of a system that efficiently transforms auditory sequences into higher-order structures is the human language system. However, because this system in humans is often thought to be special, the aspects of it that have parallels with the neural systems of other animals remains an open question. In this presentation, we overview work in human and nonhuman primates involving the processing of auditory sequences using statistical learning tasks that generate auditory expectancies. There is now evidence from comparative neuroimaging work that a broad auditory cortical system is involved in processing auditory dependencies separated in time. We also present data from neurophysiological recordings in nonhuman primates and human neurosurgery patients identifying auditory cortical expectancy signals and those that only appear when expectations are not met. This comparative research has generated hypotheses on the key neural transformations and neuronal codes that bind sequentially distributed auditory dependencies in time. We conclude the presentation by showing that there are now closer nonhuman animal parallels to the human auditory and language system, which bodes well for understanding fundamental aspects of it with animal models and more directly informing research with patients that have auditory disorders.

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Signature Christopher Petkov

Auditory Expectations, Learning and Plasticity

Immediate Neural Network Impact and Compensation after the Loss of a Semantic Hub

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Zsuzsanna Kocsis

Affiliation University of Iowa

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SUBMISSION DETAILS

Individual Abstract The human brain extracts meaning from the world using an extensive neural system for semantic knowledge. Whether such broadly distributed systems crucially depend on or can compensate for the loss of one of their highly interconnected hubs is controversial. The strongest level of causal evidence for the role of a brain hub is to evaluate its acute network-level impact following disconnection and any rapid functional compensation that ensues. We report rare neurophysiological data from two patients who underwent awake intracranial recordings during a speech prediction task immediately before and after neurosurgical treatment that required disconnection of the left anterior temporal lobe (ATL), a crucial hub for semantic knowledge. Informed by a predictive coding framework, we tested three sets of hypotheses including diaschisis causing disruption in interconnected sites and incomplete or complete compensation by other language-critical and speech processing sites. Immediately after ATL disconnection, we observed highly specific neurophysiological alterations in the recorded fronto-temporal network, including abnormally magnified high gamma responses to the speech sounds in auditory cortex. We also observed evidence for rapid compensation, seen as focal increases in effective connectivity involving language-critical sites in the inferior frontal gyrus and speech processing sites in auditory cortex. However, compensation was incomplete, in part because after ATL disconnection speech prediction signals were depleted in auditory cortex. This study provides direct causal evidence for a semantic hub in the human brain and shows striking neural impact and a rapid attempt at compensation in a neural network after the loss of one of its hubs.

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Signature Zsuzsanna Kocsis

Auditory Expectations, Learning and Plasticity

Laminar and High Spatial Resolution fMRI of Human Auditory Predictive Processing.

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Federico De Martino

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SUBMISSION DETAILS

Individual Abstract To deal with dynamic changes in the soundscape and adjust our behaviour accordingly, a key function of our brain is to predict future states of the world. This has led to a transformative way of thinking about brain function. That is, what we perceive does not reflect the sensory stimulus itself, but rather a combination of the stimulus and an internal (generative) model of its causes. This idea has led to several theoretical advances some of which are capitalized by Predictive Coding (PC). PC assumes that generative models are formed through the exchange of prediction errors (feedforward) and predictions (feedback) across hierarchical processing stages. In addition, PC assumes that prediction errors are modulated by the precision of currently available predictions. Results from invasive animal and human electrophysiological studies support the relevance of predictions for neural processing at different hierarchical levels. Nevertheless, especially in humans the evidence grounding PC principles onto fundamental neurocomputational units (i.e. cortical layers, subdivisions of subcortical structures) is limited and this hampers our understanding of how PC supports the processing of sounds in context in the human brain.
Ultra-high field fMRI at high spatial resolution offers a unique opportunity to investigate how computations are embedded in the mesoscopic (cortical) architecture of the human brain (in vivo and non-invasively). Laminar fMRI has already been used to investigate predictive processes in the human visual cortex. In this talk I will describe recent results from studies investigating how predictions and prediction errors are processed in auditory cortical layers. We combine ultra-high field fMRI with biophysical and computational approaches to gain further insights into the computations underlying these responses.

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Signature Federico De Martino

Auditory Expectations, Learning and Plasticity

Category Learning and Dimension-Selective Attention in Auditory Cortex

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Lori Holt

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SUBMISSION DETAILS

Individual Abstract Human listeners possess rich category representations for speech sounds and words. Yet speech input exhibits complexity across multiple acoustic dimensions, and short-term speech input regularities may not match long-term norms (as in foreign accents). Theoretical accounts of speech perception often have appealed to selective attention as a means by which to balance these demands. However, we do not yet understand how – and whether - listeners learn to selectively attend to informative acoustic dimensions during category learning, how selective attention impacts cortical representations of relevant dimensions, and whether selective attention involves suppression of irrelevant dimensions as well as enhancement of relevant dimensions.

We are examining these questions using novel non-speech auditory categories. Participants complete five days of stimulus-response-feedback training during which they learn four nonspeech categories to criterion. The categories are structured to require listeners to learn acoustic patterns positioned in either a high- or low-frequency band, with simultaneous irrelevant acoustic patterns in the opposite band. Thus, category learning requires reliance on – and perhaps selective attention to – the category-diagnostic acoustic patterns. Control trials involve categorization across an orthogonal dimension, stimulus amplitude ('big' or 'small' Category A). In a single post-training MRI session, listeners categorize sounds in a 2AFC task with categories differentiated by information in either high or low spectral bands, or on relative amplitude. Combined with tonotopic mapping and "attention-o-tonotopic" mapping driven by overt endogenous attention to high and low frequency bands, we examine how dimension-selective attention driven by implicit demands of categorization impact cortical activation.

This work illuminates the cortical mechanisms supporting dimension-based auditory selective

attention, providing a bridge to compare explicitly directed attention (i.e., “listen high”) and selective attention that emerges with learning. Comparison with our control (amplitude) condition allows for assessment of a putative role for suppression. Finally, the study links human studies with non-human animal studies of frequency-selective auditory attention with non-speech stimuli.

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Signature Lori L Holt

Auditory Expectations, Learning and Plasticity

Neural Mechanisms for Tracking Uncertainty in Rapidly Unfolding Sound Sequences.

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Maria Chait

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SUBMISSION DETAILS

Individual Abstract The brain maintains a hierarchy of models to monitor the statistics of its surroundings and inform behaviour. Determining how such models are instantiated and updated is key to understanding the brain as a statistical learning machine.

The auditory system, supported by a network of auditory, hippocampal, and frontal sources, automatically discovers regularities in rapid tone sequences even when these are not behaviourally relevant. We have previously identified specific brain signatures of sequence structure tracking in humans. The transition from a random tone pattern to a structured pattern (RAN-REG) elicits a slow increase in tonic activity that is consistent with gradual evidence accumulation and instantiation of a new model. In contrast, the opposite transition (REG-RAN) evokes an ‘interrupt’ response’: a sharp drop in sustained activity, hypothesized to reflect immediate suppression of top-down prior expectations. The activity settles at a low sustained level, consistent with the weaker statistical constraints in the RAN pattern.

In this series of MEG experiments, we investigated how “model establishment” and “interrupt” responses are affected by information rate (by using sequences of identical statistical properties but halving tone-pip length; 25 vs 50 ms) and predictability of pattern transitions.

We examined responses to the following sequence transitions: REG1-REG2 (from one regular to a different regular pattern) REG-RAN (from a regular to a random pattern) REG1-RAN-REG1 (a regular pattern interrupted by a 500ms random pattern followed by the resuming of the original pattern). The probabilities of these transitions were varied to model a range of environmental volatilities. Naive participants performed a decoy task, while listening passively to the sounds.

We report the following key findings:
(1) The detailed dynamics of discovering, abandoning and learning new structure in sound sequences are observable in the MEG signal.
(2) The dynamics of “model establishment” roughly scaled with tone duration but with some evidence of increasing sluggishness with longer tones.
(3) In REG1-RAN-REG1 trials, post interruption model establishment occurred much faster than in REG1-REG2 trials, suggesting that a model of the original sequence was automatically preserved and re-activated.
(4) The “interrupt” response did not differ between high probably and low probability interruptions, suggesting an automatic process that (unlike what is expected from a Bayesian system) is not affected by volatility per se.

Ongoing EEG work comparing such brain responses in human and non-human primates explores how mnemonic systems may have evolved to support pattern sensitivity in humans.

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Signature Maria Chait

Auditory Expectations, Learning and Plasticity

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Christopher Petkov

Affiliation Newcastle University and University of Iowa

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SUBMISSION DETAILS

Session Description The auditory system constantly generates predictions about the sensory world based on prior experience, which creates expectations about upcoming future events. Auditory expectations powerfully shape sensation, perception and cognition, and a theoretical ‘predictive coding’ framework has advanced in large part from studies in the auditory domain. The expectancy process is thought to be mediated by neural interactions between feedforward and feedback processes all along the auditory pathway, using corticofugal projections from auditory cortex to the periphery, and back. However, until recently it had been unclear how different types of auditory expectations are detected and the role of different stages of the auditory pathway.

This symposium will provide a timely update to address:
• How do auditory expectations form, as an important basis for learning?
• What happens when expectations are not met and the system needs to adapt?
• In disorders that affect the auditory system how are expectancy signals affected?
• Is there plasticity that compensates for impact on the auditory system, and can auditory system impact be remediated?

The symposium will feature presentations from prominent early career and senior scientists, experts in the field of auditory expectancy, learning and plasticity. The presentations will cover a broad range of animal species, including murine models, nonhuman primates and humans. The speakers will showcase the latest neurophysiological approaches possible with each species, ranging from insights at the single neuron levels to mesoscopic and macroscopic studies of the auditory system in humans, including patients with auditory and communication impairments. The presentations will highlight cutting-edge approaches, including circuit-level optogenetic and pharmacological manipulations to identify causal elements involved in auditory expectancy and human intracranial recording and neuroimaging studies. The speakers will also provide insights on

how the auditory field is the leading modality helping to test and advance computational theories on predictive coding.

Presenter Diversity The symposium is gender balanced. The speakers represent five countries and a diversity of backgrounds. Six of the speakers are immigrants to the countries in which they are working.

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Signature Christopher Petkov

Auditory Expectations, Learning and Plasticity

Prediction, Attention, and Memory in the Auditory Cortex

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Ryszard Auksztulewicz

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SUBMISSION DETAILS

Individual Abstract The brain is thought to generate internal predictions, based on the memory of past stimulation, to optimise behaviour. However, it is unclear to what extent these predictions are modulated by other top-down factors such as attention and task demands, and whether predictions of different sensory features are mediated by the same neural mechanisms. In this talk I will present results of studies combining human and rodent electrophysiology with computational modelling to identify the neural mechanisms of sensory predictions and their interactions with other cognitive factors. First, in non-invasive studies using MEG/EEG and direct recordings from humans using ECoG, analysis of behavioural and neural data showed that the effects of predictions are not automatic but are modulated by their contextual relevance. Second, computational modelling of the data suggested that these modulations could be linked to specific candidate mechanisms, including gain control in sensory regions. Finally, in a series of studies using invasive recordings in anaesthetised rodents, neural representations related to stimulus memory and predictions could be simultaneously decoded from auditory cortical activity, shedding light on the evolutionary conservation of predictive processing across species.

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Signature Ryszard Auksztulewicz

Auditory Expectations, Learning and Plasticity

Corticofugal Regulation of Predictive Coding

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Maria Geffen

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SUBMISSION DETAILS

Individual Abstract Sensory systems must account for both contextual factors and prior experience to adaptively engage with the dynamic external environment. In the central auditory system, neurons modulate their responses to sounds based on statistical context. These response modulations can be understood through a hierarchical predictive coding lens: responses to repeated stimuli are progressively decreased, in a process known as repetition suppression, whereas unexpected stimuli produce a prediction error signal. Prediction error incrementally increases along the auditory hierarchy from the inferior colliculus (IC) to the auditory cortex (AC), suggesting that these regions may engage in hierarchical predictive coding. A potential substrate for top-down predictive cues is the massive set of descending projections from the AC to subcortical structures, although the role of this system in predictive processing has never been directly assessed. We tested the effect of optogenetic inactivation of the auditory cortico-collicular feedback in awake mice on responses of IC neurons to stimuli designed to test prediction error and repetition suppression. Inactivation of the cortico-collicular pathway led to a decrease in prediction error in IC. Repetition suppression was unaffected by cortico-collicular inactivation, suggesting that this metric may reflect fatigue of bottom-up sensory inputs rather than predictive processing. We also discovered populations of IC units that exhibit repetition enhancement, a sequential increase in firing with stimulus repetition. Cortico-collicular inactivation led to a decrease in repetition enhancement in the central nucleus of IC, suggesting that it is a top-down phenomenon. Negative prediction error, a stronger response to a tone in a predictable rather than unpredictable sequence, was suppressed in shell IC units during cortico-collicular inactivation. These changes in predictive coding metrics arose from bidirectional modulations in the response to the standard and deviant contexts, such that the units in IC responded more similarly to each context in the absence of cortical input. We also investigated how these metrics compare between the anesthetized and awake states by recording from the same units under both conditions. We found that metrics of

predictive coding and deviance detection differ depending on the anesthetic state of the animal, with negative prediction error emerging in the central IC and repetition enhancement and prediction error being more prevalent in the absence of anesthesia. Overall, our results demonstrate that the AC provides cues about the statistical context of sound to subcortical brain regions via direct feedback, regulating processing of both prediction and repetition.

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Signature Maria Geffen

Auditory Expectations, Learning and Plasticity

Precision in Predictive coding: The Role of Neuromodultion in Deviance Detection

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Manuel Malmierca

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Participant(s) Christopher Petkov (Chair), Maria Geffen (Co-chair), Kerry Walker (Co-chair), Lori Holt (Presenter), Manuel Malmierca (Presenter), Zsuzsanna Kocsis (Presenter), Maria Chait (Presenter), Federico De Martino (Presenter), Maria Geffen (Presenter), Christopher Petkov (Presenter), Ryszard Auksztulewicz (Presenter)

SUBMISSION DETAILS

Individual Abstract Behaviour becomes more efficient when we can predict a stimulus. This is the basis of the enormous flexibility underlying interactions with our physical and social environment. Filtering out non-relevant stimuli is an important but understudied aspect of cognition. Today, there is rather universal agreement in neuroscience, that a major function of the brain is to constantly predict the environment on multiple levels and time scales (Friston, 2005), For example, one anticipates how a word of a friend will sound, and when and how a sentence will end, even before it has ended. This proposal is based on the assumption that the brain's neuronal circuitry is organized as a highly predictive machine.

The ability of the brain to recognize which prediction errors carry reliable information is critical in the process of prediction error minimization. For example, if a sensor is malfunctioning because of an impairment (e.g., hearing loss or tinnitus) or because it is operating out of its appropriate physical range, the sensory input it provides is not adequately reporting on real changes in the environment, which may generate misinformative prediction errors. According to the predictive coding theory, this distinction between signal and noise is based on an important element, the so-called precision, which weights the driving power of prediction errors according to how reliable they are estimated to be (Friston, 2005).

Neuromodulatory inputs not only gate plasticity (Martins and Froemke, 2015), but also change the balance of top-down versus bottom-up influence and it well known that neuromodulation strongly impacts sensory processing, learning and memory. 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). Therefore, 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. We have used single neuron recordings and microiontophoresis manipulation of the cholinergic system in the rat brain to study how these neuromodulators shape the predictive responses in cortical and subcortical brain regions in the rat brain

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Auditory Expectations, Learning and Plasticity

Transformations of Auditory Sequences into Neural Expectancy Signals

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Christopher Petkov

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Participant(s) Christopher Petkov (Chair), Maria Geffen (Co-chair), Kerry Walker (Co-chair), Lori Holt (Presenter), Manuel Malmierca (Presenter), Zsuzsanna Kocsis (Presenter), Maria Chait (Presenter), Federico De Martino (Presenter), Maria Geffen (Presenter), Christopher Petkov (Presenter), Ryszard Auksztulewicz (Presenter)

SUBMISSION DETAILS

Individual Abstract There is considerable interest in understanding the neural transformations that occur at every stage in the auditory system. These are no longer thought to be simply feedforward or unidirectional, but rather are better conceived of as bidirectional processes and interactions that occur at every stage in the auditory system and influence sensory processing and expectation. A prime example of a system that efficiently transforms auditory sequences into higher-order structures is the human language system. However, because this system in humans is often thought to be special, the aspects of it that have parallels with the neural systems of other animals remains an open question. In this presentation, we overview work in human and nonhuman primates involving the processing of auditory sequences using statistical learning tasks that generate auditory expectancies. There is now evidence from comparative neuroimaging work that a broad auditory cortical system is involved in processing auditory dependencies separated in time. We also present data from neurophysiological recordings in nonhuman primates and human neurosurgery patients identifying auditory cortical expectancy signals and those that only appear when expectations are not met. This comparative research has generated hypotheses on the key neural transformations and neuronal codes that bind sequentially distributed auditory dependencies in time. We conclude the presentation by showing that there are now closer nonhuman animal parallels to the human auditory and language system, which bodes well for understanding fundamental aspects of it with animal models and more directly informing research with patients that have auditory disorders.

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Signature Christopher Petkov

Auditory Expectations, Learning and Plasticity

Immediate Neural Network Impact and Compensation after the Loss of a Semantic Hub

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Zsuzsanna Kocsis

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SUBMISSION DETAILS

Individual Abstract The human brain extracts meaning from the world using an extensive neural system for semantic knowledge. Whether such broadly distributed systems crucially depend on or can compensate for the loss of one of their highly interconnected hubs is controversial. The strongest level of causal evidence for the role of a brain hub is to evaluate its acute network-level impact following disconnection and any rapid functional compensation that ensues. We report rare neurophysiological data from two patients who underwent awake intracranial recordings during a speech prediction task immediately before and after neurosurgical treatment that required disconnection of the left anterior temporal lobe (ATL), a crucial hub for semantic knowledge. Informed by a predictive coding framework, we tested three sets of hypotheses including diaschisis causing disruption in interconnected sites and incomplete or complete compensation by other language-critical and speech processing sites. Immediately after ATL disconnection, we observed highly specific neurophysiological alterations in the recorded fronto-temporal network, including abnormally magnified high gamma responses to the speech sounds in auditory cortex. We also observed evidence for rapid compensation, seen as focal increases in effective connectivity involving language-critical sites in the inferior frontal gyrus and speech processing sites in auditory cortex. However, compensation was incomplete, in part because after ATL disconnection speech prediction signals were depleted in auditory cortex. This study provides direct causal evidence for a semantic hub in the human brain and shows striking neural impact and a rapid attempt at compensation in a neural network after the loss of one of its hubs.

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Signature Zsuzsanna Kocsis

Auditory Expectations, Learning and Plasticity

Laminar and High Spatial Resolution fMRI of Human Auditory Predictive Processing.

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Federico De Martino

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SUBMISSION DETAILS

Individual Abstract To deal with dynamic changes in the soundscape and adjust our behaviour accordingly, a key function of our brain is to predict future states of the world. This has led to a transformative way of thinking about brain function. That is, what we perceive does not reflect the sensory stimulus itself, but rather a combination of the stimulus and an internal (generative) model of its causes. This idea has led to several theoretical advances some of which are capitalized by Predictive Coding (PC). PC assumes that generative models are formed through the exchange of prediction errors (feedforward) and predictions (feedback) across hierarchical processing stages. In addition, PC assumes that prediction errors are modulated by the precision of currently available predictions. Results from invasive animal and human electrophysiological studies support the relevance of predictions for neural processing at different hierarchical levels. Nevertheless, especially in humans the evidence grounding PC principles onto fundamental neurocomputational units (i.e. cortical layers, subdivisions of subcortical structures) is limited and this hampers our understanding of how PC supports the processing of sounds in context in the human brain. Ultra-high field fMRI at high spatial resolution offers a unique opportunity to investigate how computations are embedded in the mesoscopic (cortical) architecture of the human brain (in vivo and non-invasively). Laminar fMRI has already been used to investigate predictive processes in the human visual cortex. In this talk I will describe recent results from studies investigating how predictions and prediction errors are processed in auditory cortical layers. We combine ultra-high field fMRI with biophysical and computational approaches to gain further insights into the computations underlying these responses.

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Auditory Expectations, Learning and Plasticity

Category Learning and Dimension-Selective Attention in Auditory Cortex

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Lori Holt

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SUBMISSION DETAILS

Individual Abstract Human listeners possess rich category representations for speech sounds and words. Yet speech input exhibits complexity across multiple acoustic dimensions, and short-term speech input regularities may not match long-term norms (as in foreign accents). Theoretical accounts of speech perception often have appealed to selective attention as a means by which to balance these demands. However, we do not yet understand how – and whether - listeners learn to selectively attend to informative acoustic dimensions during category learning, how selective attention impacts cortical representations of relevant dimensions, and whether selective attention involves suppression of irrelevant dimensions as well as enhancement of relevant dimensions.

We are examining these questions using novel non-speech auditory categories. Participants complete five days of stimulus-response-feedback training during which they learn four nonspeech categories to criterion. The categories are structured to require listeners to learn acoustic patterns positioned in either a high- or low-frequency band, with simultaneous irrelevant acoustic patterns in the opposite band. Thus, category learning requires reliance on – and perhaps selective attention to – the category-diagnostic acoustic patterns. Control trials involve categorization across an orthogonal dimension, stimulus amplitude ('big' or 'small' Category A). In a single post-training MRI session, listeners categorize sounds in a 2AFC task with categories differentiated by information in either high or low spectral bands, or on relative amplitude. Combined with tonotopic mapping and "attention-o-tonotopic" mapping driven by overt endogenous attention to high and low frequency bands, we examine how dimension-selective attention driven by implicit demands of categorization impact cortical activation.

This work illuminates the cortical mechanisms supporting dimension-based auditory selective

attention, providing a bridge to compare explicitly directed attention (i.e., “listen high”) and selective attention that emerges with learning. Comparison with our control (amplitude) condition allows for assessment of a putative role for suppression. Finally, the study links human studies with non-human animal studies of frequency-selective auditory attention with non-speech stimuli.

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Signature Lori L Holt

Auditory Expectations, Learning and Plasticity

Neural Mechanisms for Tracking Uncertainty in Rapidly Unfolding Sound Sequences.

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Maria Chait

Affiliation UCL Ear Institute

Participant(s) Christopher Petkov (Chair), Maria Geffen (Co-chair), Kerry Walker (Co-chair), Lori Holt (Presenter), Manuel Malmierca (Presenter), Zsuzsanna Kocsis (Presenter), Maria Chait (Presenter), Federico De Martino (Presenter), Maria Geffen (Presenter), Christopher Petkov (Presenter), Ryszard Auksztulewicz (Presenter)

SUBMISSION DETAILS

Individual Abstract The brain maintains a hierarchy of models to monitor the statistics of its surroundings and inform behaviour. Determining how such models are instantiated and updated is key to understanding the brain as a statistical learning machine.

The auditory system, supported by a network of auditory, hippocampal, and frontal sources, automatically discovers regularities in rapid tone sequences even when these are not behaviourally relevant. We have previously identified specific brain signatures of sequence structure tracking in humans. The transition from a random tone pattern to a structured pattern (RAN-REG) elicits a slow increase in tonic activity that is consistent with gradual evidence accumulation and instantiation of a new model. In contrast, the opposite transition (REG-RAN) evokes an 'interrupt' response': a sharp drop in sustained activity, hypothesized to reflect immediate suppression of top-down prior expectations. The activity settles at a low sustained level, consistent with the weaker statistical constraints in the RAN pattern.

In this series of MEG experiments, we investigated how "model establishment" and "interrupt" responses are affected by information rate (by using sequences of identical statistical properties but halving tone-pip length; 25 vs 50 ms) and predictability of pattern transitions.

We examined responses to the following sequence transitions: REG1-REG2 (from one regular to a different regular pattern) REG-RAN (from a regular to a random pattern) REG1-RAN-REG1 (a regular pattern interrupted by a 500ms random pattern followed by the resuming of the original pattern). The probabilities of these transitions were varied to model a range of environmental volatilities. Naive participants performed a decoy task, while listening passively to the sounds.

We report the following key findings:
(1) The detailed dynamics of discovering, abandoning and learning new structure in sound sequences are observable in the MEG signal.
(2) The dynamics of “model establishment” roughly scaled with tone duration but with some evidence of increasing sluggishness with longer tones.
(3) In REG1-RAN-REG1 trials, post interruption model establishment occurred much faster than in REG1-REG2 trials, suggesting that a model of the original sequence was automatically preserved and re-activated.
(4) The “interrupt” response did not differ between high probably and low probability interruptions, suggesting an automatic process that (unlike what is expected from a Bayesian system) is not affected by volatility per se.

Ongoing EEG work comparing such brain responses in human and non-human primates explores how mnemonic systems may have evolved to support pattern sensitivity in humans.

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Signature Maria Chait

Auditory Expectations, Learning and Plasticity

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Christopher Petkov

Affiliation Newcastle University and University of Iowa

Participant(s) Christopher Petkov (Chair), Maria Geffen (Co-chair), Kerry Walker (Co-chair), Lori Holt (Presenter), Manuel Malmierca (Presenter), Zsuzsanna Kocsis (Presenter), Maria Chait (Presenter), Federico De Martino (Presenter), Maria Geffen (Presenter), Christopher Petkov (Presenter), Ryszard Auksztulewicz (Presenter)

SUBMISSION DETAILS

Session Description The auditory system constantly generates predictions about the sensory world based on prior experience, which creates expectations about upcoming future events. Auditory expectations powerfully shape sensation, perception and cognition, and a theoretical 'predictive coding' framework has advanced in large part from studies in the auditory domain. The expectancy process is thought to be mediated by neural interactions between feedforward and feedback processes all along the auditory pathway, using corticofugal projections from auditory cortex to the periphery, and back. However, until recently it had been unclear how different types of auditory expectations are detected and the role of different stages of the auditory pathway.

This symposium will provide a timely update to address:
• How do auditory expectations form, as an important basis for learning?
• What happens when expectations are not met and the system needs to adapt?
• In disorders that affect the auditory system how are expectancy signals affected?
• Is there plasticity that compensates for impact on the auditory system, and can auditory system impact be remediated?

The symposium will feature presentations from prominent early career and senior scientists, experts in the field of auditory expectancy, learning and plasticity. The presentations will cover a broad range of animal species, including murine models, nonhuman primates and humans. The speakers will showcase the latest neurophysiological approaches possible with each species, ranging from insights at the single neuron levels to mesoscopic and macroscopic studies of the auditory system in humans, including patients with auditory and communication impairments. The presentations will highlight cutting-edge approaches, including circuit-level optogenetic and pharmacological manipulations to identify causal elements involved in auditory expectancy and human intracranial recording and neuroimaging studies. The speakers will also provide insights on

how the auditory field is the leading modality helping to test and advance computational theories on predictive coding.

Presenter Diversity The symposium is gender balanced. The speakers represent five countries and a diversity of backgrounds. Six of the speakers are immigrants to the countries in which they are working.

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Signature Christopher Petkov

Auditory Expectations, Learning and Plasticity

Prediction, Attention, and Memory in the Auditory Cortex

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Ryszard Auksztulewicz

Affiliation European Neuroscience Institute Göttingen

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SUBMISSION DETAILS

Individual Abstract The brain is thought to generate internal predictions, based on the memory of past stimulation, to optimise behaviour. However, it is unclear to what extent these predictions are modulated by other top-down factors such as attention and task demands, and whether predictions of different sensory features are mediated by the same neural mechanisms. In this talk I will present results of studies combining human and rodent electrophysiology with computational modelling to identify the neural mechanisms of sensory predictions and their interactions with other cognitive factors. First, in non-invasive studies using MEG/EEG and direct recordings from humans using ECoG, analysis of behavioural and neural data showed that the effects of predictions are not automatic but are modulated by their contextual relevance. Second, computational modelling of the data suggested that these modulations could be linked to specific candidate mechanisms, including gain control in sensory regions. Finally, in a series of studies using invasive recordings in anaesthetised rodents, neural representations related to stimulus memory and predictions could be simultaneously decoded from auditory cortical activity, shedding light on the evolutionary conservation of predictive processing across species.

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Signature Ryszard Auksztulewicz

Auditory Expectations, Learning and Plasticity

Corticofugal Regulation of Predictive Coding

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Maria Geffen

Affiliation University of Pennsylvania School of Medicine

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SUBMISSION DETAILS

Individual Abstract Sensory systems must account for both contextual factors and prior experience to adaptively engage with the dynamic external environment. In the central auditory system, neurons modulate their responses to sounds based on statistical context. These response modulations can be understood through a hierarchical predictive coding lens: responses to repeated stimuli are progressively decreased, in a process known as repetition suppression, whereas unexpected stimuli produce a prediction error signal. Prediction error incrementally increases along the auditory hierarchy from the inferior colliculus (IC) to the auditory cortex (AC), suggesting that these regions may engage in hierarchical predictive coding. A potential substrate for top-down predictive cues is the massive set of descending projections from the AC to subcortical structures, although the role of this system in predictive processing has never been directly assessed. We tested the effect of optogenetic inactivation of the auditory cortico-collicular feedback in awake mice on responses of IC neurons to stimuli designed to test prediction error and repetition suppression. Inactivation of the cortico-collicular pathway led to a decrease in prediction error in IC. Repetition suppression was unaffected by cortico-collicular inactivation, suggesting that this metric may reflect fatigue of bottom-up sensory inputs rather than predictive processing. We also discovered populations of IC units that exhibit repetition enhancement, a sequential increase in firing with stimulus repetition. Cortico-collicular inactivation led to a decrease in repetition enhancement in the central nucleus of IC, suggesting that it is a top-down phenomenon. Negative prediction error, a stronger response to a tone in a predictable rather than unpredictable sequence, was suppressed in shell IC units during cortico-collicular inactivation. These changes in predictive coding metrics arose from bidirectional modulations in the response to the standard and deviant contexts, such that the units in IC responded more similarly to each context in the absence of cortical input. We also investigated how these metrics compare between the anesthetized and awake states by recording from the same units under both conditions. We found that metrics of

predictive coding and deviance detection differ depending on the anesthetic state of the animal, with negative prediction error emerging in the central IC and repetition enhancement and prediction error being more prevalent in the absence of anesthesia. Overall, our results demonstrate that the AC provides cues about the statistical context of sound to subcortical brain regions via direct feedback, regulating processing of both prediction and repetition.

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Signature Maria Geffen

Auditory Expectations, Learning and Plasticity

Precision in Predictive coding: The Role of Neuromodultion in Deviance Detection

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

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SUBMISSION DETAILS

Individual Abstract Behaviour becomes more efficient when we can predict a stimulus. This is the basis of the enormous flexibility underlying interactions with our physical and social environment. Filtering out non-relevant stimuli is an important but understudied aspect of cognition. Today, there is rather universal agreement in neuroscience, that a major function of the brain is to constantly predict the environment on multiple levels and time scales (Friston, 2005), For example, one anticipates how a word of a friend will sound, and when and how a sentence will end, even before it has ended. This proposal is based on the assumption that the brain's neuronal circuitry is organized as a highly predictive machine.

The ability of the brain to recognize which prediction errors carry reliable information is critical in the process of prediction error minimization. For example, if a sensor is malfunctioning because of an impairment (e.g., hearing loss or tinnitus) or because it is operating out of its appropriate physical range, the sensory input it provides is not adequately reporting on real changes in the environment, which may generate misinformative prediction errors. According to the predictive coding theory, this distinction between signal and noise is based on an important element, the so-called precision, which weights the driving power of prediction errors according to how reliable they are estimated to be (Friston, 2005).

Neuromodulatory inputs not only gate plasticity (Martins and Froemke, 2015), but also change the balance of top-down versus bottom-up influence and it well known that neuromodulation strongly impacts sensory processing, learning and memory. 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). Therefore, 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. We have used single neuron recordings and microiontophoresis manipulation of the cholinergic system in the rat brain to study how these neuromodulators shape the predictive responses in cortical and subcortical brain regions in the rat brain

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Auditory Expectations, Learning and Plasticity

Transformations of Auditory Sequences into Neural Expectancy Signals

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

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SUBMISSION DETAILS

Individual Abstract There is considerable interest in understanding the neural transformations that occur at every stage in the auditory system. These are no longer thought to be simply feedforward or unidirectional, but rather are better conceived of as bidirectional processes and interactions that occur at every stage in the auditory system and influence sensory processing and expectation. A prime example of a system that efficiently transforms auditory sequences into higher-order structures is the human language system. However, because this system in humans is often thought to be special, the aspects of it that have parallels with the neural systems of other animals remains an open question. In this presentation, we overview work in human and nonhuman primates involving the processing of auditory sequences using statistical learning tasks that generate auditory expectancies. There is now evidence from comparative neuroimaging work that a broad auditory cortical system is involved in processing auditory dependencies separated in time. We also present data from neurophysiological recordings in nonhuman primates and human neurosurgery patients identifying auditory cortical expectancy signals and those that only appear when expectations are not met. This comparative research has generated hypotheses on the key neural transformations and neuronal codes that bind sequentially distributed auditory dependencies in time. We conclude the presentation by showing that there are now closer nonhuman animal parallels to the human auditory and language system, which bodes well for understanding fundamental aspects of it with animal models and more directly informing research with patients that have auditory disorders.

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Signature Christopher Petkov

Auditory Expectations, Learning and Plasticity

Immediate Neural Network Impact and Compensation after the Loss of a Semantic Hub

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Zsuzsanna Kocsis

Affiliation University of Iowa

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SUBMISSION DETAILS

Individual Abstract The human brain extracts meaning from the world using an extensive neural system for semantic knowledge. Whether such broadly distributed systems crucially depend on or can compensate for the loss of one of their highly interconnected hubs is controversial. The strongest level of causal evidence for the role of a brain hub is to evaluate its acute network-level impact following disconnection and any rapid functional compensation that ensues. We report rare neurophysiological data from two patients who underwent awake intracranial recordings during a speech prediction task immediately before and after neurosurgical treatment that required disconnection of the left anterior temporal lobe (ATL), a crucial hub for semantic knowledge. Informed by a predictive coding framework, we tested three sets of hypotheses including diaschisis causing disruption in interconnected sites and incomplete or complete compensation by other language-critical and speech processing sites. Immediately after ATL disconnection, we observed highly specific neurophysiological alterations in the recorded fronto-temporal network, including abnormally magnified high gamma responses to the speech sounds in auditory cortex. We also observed evidence for rapid compensation, seen as focal increases in effective connectivity involving language-critical sites in the inferior frontal gyrus and speech processing sites in auditory cortex. However, compensation was incomplete, in part because after ATL disconnection speech prediction signals were depleted in auditory cortex. This study provides direct causal evidence for a semantic hub in the human brain and shows striking neural impact and a rapid attempt at compensation in a neural network after the loss of one of its hubs.

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Signature Zsuzsanna Kocsis

Auditory Expectations, Learning and Plasticity

Laminar and High Spatial Resolution fMRI of Human Auditory Predictive Processing.

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Federico De Martino

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SUBMISSION DETAILS

Individual Abstract To deal with dynamic changes in the soundscape and adjust our behaviour accordingly, a key function of our brain is to predict future states of the world. This has led to a transformative way of thinking about brain function. That is, what we perceive does not reflect the sensory stimulus itself, but rather a combination of the stimulus and an internal (generative) model of its causes. This idea has led to several theoretical advances some of which are capitalized by Predictive Coding (PC). PC assumes that generative models are formed through the exchange of prediction errors (feedforward) and predictions (feedback) across hierarchical processing stages. In addition, PC assumes that prediction errors are modulated by the precision of currently available predictions. Results from invasive animal and human electrophysiological studies support the relevance of predictions for neural processing at different hierarchical levels. Nevertheless, especially in humans the evidence grounding PC principles onto fundamental neurocomputational units (i.e. cortical layers, subdivisions of subcortical structures) is limited and this hampers our understanding of how PC supports the processing of sounds in context in the human brain.
Ultra-high field fMRI at high spatial resolution offers a unique opportunity to investigate how computations are embedded in the mesoscopic (cortical) architecture of the human brain (in vivo and non-invasively). Laminar fMRI has already been used to investigate predictive processes in the human visual cortex. In this talk I will describe recent results from studies investigating how predictions and prediction errors are processed in auditory cortical layers. We combine ultra-high field fMRI with biophysical and computational approaches to gain further insights into the computations underlying these responses.

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Signature Federico De Martino

Auditory Expectations, Learning and Plasticity

Category Learning and Dimension-Selective Attention in Auditory Cortex

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Lori Holt

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SUBMISSION DETAILS

Individual Abstract Human listeners possess rich category representations for speech sounds and words. Yet speech input exhibits complexity across multiple acoustic dimensions, and short-term speech input regularities may not match long-term norms (as in foreign accents). Theoretical accounts of speech perception often have appealed to selective attention as a means by which to balance these demands. However, we do not yet understand how – and whether - listeners learn to selectively attend to informative acoustic dimensions during category learning, how selective attention impacts cortical representations of relevant dimensions, and whether selective attention involves suppression of irrelevant dimensions as well as enhancement of relevant dimensions.

We are examining these questions using novel non-speech auditory categories. Participants complete five days of stimulus-response-feedback training during which they learn four nonspeech categories to criterion. The categories are structured to require listeners to learn acoustic patterns positioned in either a high- or low-frequency band, with simultaneous irrelevant acoustic patterns in the opposite band. Thus, category learning requires reliance on – and perhaps selective attention to – the category-diagnostic acoustic patterns. Control trials involve categorization across an orthogonal dimension, stimulus amplitude (‘big’ or ‘small’ Category A). In a single post-training MRI session, listeners categorize sounds in a 2AFC task with categories differentiated by information in either high or low spectral bands, or on relative amplitude. Combined with tonotopic mapping and “attention-o-tonotopic” mapping driven by overt endogenous attention to high and low frequency bands, we examine how dimension-selective attention driven by implicit demands of categorization impact cortical activation.

This work illuminates the cortical mechanisms supporting dimension-based auditory selective

attention, providing a bridge to compare explicitly directed attention (i.e., “listen high”) and selective attention that emerges with learning. Comparison with our control (amplitude) condition allows for assessment of a putative role for suppression. Finally, the study links human studies with non-human animal studies of frequency-selective auditory attention with non-speech stimuli.

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Signature Lori L Holt

Auditory Expectations, Learning and Plasticity

Neural Mechanisms for Tracking Uncertainty in Rapidly Unfolding Sound Sequences.

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Maria Chait

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SUBMISSION DETAILS

Individual Abstract The brain maintains a hierarchy of models to monitor the statistics of its surroundings and inform behaviour. Determining how such models are instantiated and updated is key to understanding the brain as a statistical learning machine.

The auditory system, supported by a network of auditory, hippocampal, and frontal sources, automatically discovers regularities in rapid tone sequences even when these are not behaviourally relevant. We have previously identified specific brain signatures of sequence structure tracking in humans. The transition from a random tone pattern to a structured pattern (RAN-REG) elicits a slow increase in tonic activity that is consistent with gradual evidence accumulation and instantiation of a new model. In contrast, the opposite transition (REG-RAN) evokes an 'interrupt' response': a sharp drop in sustained activity, hypothesized to reflect immediate suppression of top-down prior expectations. The activity settles at a low sustained level, consistent with the weaker statistical constraints in the RAN pattern.

In this series of MEG experiments, we investigated how "model establishment" and "interrupt" responses are affected by information rate (by using sequences of identical statistical properties but halving tone-pip length; 25 vs 50 ms) and predictability of pattern transitions.

We examined responses to the following sequence transitions: REG1-REG2 (from one regular to a different regular pattern) REG-RAN (from a regular to a random pattern) REG1-RAN-REG1 (a regular pattern interrupted by a 500ms random pattern followed by the resuming of the original pattern). The probabilities of these transitions were varied to model a range of environmental volatilities. Naive participants performed a decoy task, while listening passively to the sounds.

We report the following key findings:
(1) The detailed dynamics of discovering, abandoning and learning new structure in sound sequences are observable in the MEG signal.
(2) The dynamics of “model establishment” roughly scaled with tone duration but with some evidence of increasing sluggishness with longer tones.
(3) In REG1-RAN-REG1 trials, post interruption model establishment occurred much faster than in REG1-REG2 trials, suggesting that a model of the original sequence was automatically preserved and re-activated.
(4) The “interrupt” response did not differ between high probably and low probability interruptions, suggesting an automatic process that (unlike what is expected from a Bayesian system) is not affected by volatility per se.

Ongoing EEG work comparing such brain responses in human and non-human primates explores how mnemonic systems may have evolved to support pattern sensitivity in humans.

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Signature Maria Chait

Auditory Expectations, Learning and Plasticity

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Christopher Petkov

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SUBMISSION DETAILS

Session Description The auditory system constantly generates predictions about the sensory world based on prior experience, which creates expectations about upcoming future events. Auditory expectations powerfully shape sensation, perception and cognition, and a theoretical ‘predictive coding’ framework has advanced in large part from studies in the auditory domain. The expectancy process is thought to be mediated by neural interactions between feedforward and feedback processes all along the auditory pathway, using corticofugal projections from auditory cortex to the periphery, and back. However, until recently it had been unclear how different types of auditory expectations are detected and the role of different stages of the auditory pathway.

This symposium will provide a timely update to address:
• How do auditory expectations form, as an important basis for learning?
• What happens when expectations are not met and the system needs to adapt?
• In disorders that affect the auditory system how are expectancy signals affected?
• Is there plasticity that compensates for impact on the auditory system, and can auditory system impact be remediated?

The symposium will feature presentations from prominent early career and senior scientists, experts in the field of auditory expectancy, learning and plasticity. The presentations will cover a broad range of animal species, including murine models, nonhuman primates and humans. The speakers will showcase the latest neurophysiological approaches possible with each species, ranging from insights at the single neuron levels to mesoscopic and macroscopic studies of the auditory system in humans, including patients with auditory and communication impairments. The presentations will highlight cutting-edge approaches, including circuit-level optogenetic and pharmacological manipulations to identify causal elements involved in auditory expectancy and human intracranial recording and neuroimaging studies. The speakers will also provide insights on

how the auditory field is the leading modality helping to test and advance computational theories on predictive coding.

Presenter Diversity The symposium is gender balanced. The speakers represent five countries and a diversity of backgrounds. Six of the speakers are immigrants to the countries in which they are working.

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Signature Christopher Petkov

Auditory Expectations, Learning and Plasticity

Prediction, Attention, and Memory in the Auditory Cortex

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Ryszard Auksztulewicz

Affiliation European Neuroscience Institute Göttingen

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SUBMISSION DETAILS

Individual Abstract The brain is thought to generate internal predictions, based on the memory of past stimulation, to optimise behaviour. However, it is unclear to what extent these predictions are modulated by other top-down factors such as attention and task demands, and whether predictions of different sensory features are mediated by the same neural mechanisms. In this talk I will present results of studies combining human and rodent electrophysiology with computational modelling to identify the neural mechanisms of sensory predictions and their interactions with other cognitive factors. First, in non-invasive studies using MEG/EEG and direct recordings from humans using ECoG, analysis of behavioural and neural data showed that the effects of predictions are not automatic but are modulated by their contextual relevance. Second, computational modelling of the data suggested that these modulations could be linked to specific candidate mechanisms, including gain control in sensory regions. Finally, in a series of studies using invasive recordings in anaesthetised rodents, neural representations related to stimulus memory and predictions could be simultaneously decoded from auditory cortical activity, shedding light on the evolutionary conservation of predictive processing across species.

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Auditory Expectations, Learning and Plasticity

Corticofugal Regulation of Predictive Coding

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Maria Geffen

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SUBMISSION DETAILS

Individual Abstract Sensory systems must account for both contextual factors and prior experience to adaptively engage with the dynamic external environment. In the central auditory system, neurons modulate their responses to sounds based on statistical context. These response modulations can be understood through a hierarchical predictive coding lens: responses to repeated stimuli are progressively decreased, in a process known as repetition suppression, whereas unexpected stimuli produce a prediction error signal. Prediction error incrementally increases along the auditory hierarchy from the inferior colliculus (IC) to the auditory cortex (AC), suggesting that these regions may engage in hierarchical predictive coding. A potential substrate for top-down predictive cues is the massive set of descending projections from the AC to subcortical structures, although the role of this system in predictive processing has never been directly assessed. We tested the effect of optogenetic inactivation of the auditory cortico-collicular feedback in awake mice on responses of IC neurons to stimuli designed to test prediction error and repetition suppression. Inactivation of the cortico-collicular pathway led to a decrease in prediction error in IC. Repetition suppression was unaffected by cortico-collicular inactivation, suggesting that this metric may reflect fatigue of bottom-up sensory inputs rather than predictive processing. We also discovered populations of IC units that exhibit repetition enhancement, a sequential increase in firing with stimulus repetition. Cortico-collicular inactivation led to a decrease in repetition enhancement in the central nucleus of IC, suggesting that it is a top-down phenomenon. Negative prediction error, a stronger response to a tone in a predictable rather than unpredictable sequence, was suppressed in shell IC units during cortico-collicular inactivation. These changes in predictive coding metrics arose from bidirectional modulations in the response to the standard and deviant contexts, such that the units in IC responded more similarly to each context in the absence of cortical input. We also investigated how these metrics compare between the anesthetized and awake states by recording from the same units under both conditions. We found that metrics of

predictive coding and deviance detection differ depending on the anesthetic state of the animal, with negative prediction error emerging in the central IC and repetition enhancement and prediction error being more prevalent in the absence of anesthesia. Overall, our results demonstrate that the AC provides cues about the statistical context of sound to subcortical brain regions via direct feedback, regulating processing of both prediction and repetition.

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Signature Maria Geffen

Auditory Expectations, Learning and Plasticity

Precision in Predictive coding: The Role of Neuromodultion in Deviance Detection

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

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SUBMISSION DETAILS

Individual Abstract Behaviour becomes more efficient when we can predict a stimulus. This is the basis of the enormous flexibility underlying interactions with our physical and social environment. Filtering out non-relevant stimuli is an important but understudied aspect of cognition. Today, there is rather universal agreement in neuroscience, that a major function of the brain is to constantly predict the environment on multiple levels and time scales (Friston, 2005), For example, one anticipates how a word of a friend will sound, and when and how a sentence will end, even before it has ended. This proposal is based on the assumption that the brain's neuronal circuitry is organized as a highly predictive machine.

The ability of the brain to recognize which prediction errors carry reliable information is critical in the process of prediction error minimization. For example, if a sensor is malfunctioning because of an impairment (e.g., hearing loss or tinnitus) or because it is operating out of its appropriate physical range, the sensory input it provides is not adequately reporting on real changes in the environment, which may generate misinformative prediction errors. According to the predictive coding theory, this distinction between signal and noise is based on an important element, the so-called precision, which weights the driving power of prediction errors according to how reliable they are estimated to be (Friston, 2005).

Neuromodulatory inputs not only gate plasticity (Martins and Froemke, 2015), but also change the balance of top-down versus bottom-up influence and it well known that neuromodulation strongly impacts sensory processing, learning and memory. 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). Therefore, 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. We have used single neuron recordings and microiontophoresis manipulation of the cholinergic system in the rat brain to study how these neuromodulators shape the predictive responses in cortical and subcortical brain regions in the rat brain

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Auditory Expectations, Learning and Plasticity

Transformations of Auditory Sequences into Neural Expectancy Signals

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

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SUBMISSION DETAILS

Individual Abstract There is considerable interest in understanding the neural transformations that occur at every stage in the auditory system. These are no longer thought to be simply feedforward or unidirectional, but rather are better conceived of as bidirectional processes and interactions that occur at every stage in the auditory system and influence sensory processing and expectation. A prime example of a system that efficiently transforms auditory sequences into higher-order structures is the human language system. However, because this system in humans is often thought to be special, the aspects of it that have parallels with the neural systems of other animals remains an open question. In this presentation, we overview work in human and nonhuman primates involving the processing of auditory sequences using statistical learning tasks that generate auditory expectancies. There is now evidence from comparative neuroimaging work that a broad auditory cortical system is involved in processing auditory dependencies separated in time. We also present data from neurophysiological recordings in nonhuman primates and human neurosurgery patients identifying auditory cortical expectancy signals and those that only appear when expectations are not met. This comparative research has generated hypotheses on the key neural transformations and neuronal codes that bind sequentially distributed auditory dependencies in time. We conclude the presentation by showing that there are now closer nonhuman animal parallels to the human auditory and language system, which bodes well for understanding fundamental aspects of it with animal models and more directly informing research with patients that have auditory disorders.

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Signature Christopher Petkov

Auditory Expectations, Learning and Plasticity

Immediate Neural Network Impact and Compensation after the Loss of a Semantic Hub

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Zsuzsanna Kocsis

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SUBMISSION DETAILS

Individual Abstract The human brain extracts meaning from the world using an extensive neural system for semantic knowledge. Whether such broadly distributed systems crucially depend on or can compensate for the loss of one of their highly interconnected hubs is controversial. The strongest level of causal evidence for the role of a brain hub is to evaluate its acute network-level impact following disconnection and any rapid functional compensation that ensues. We report rare neurophysiological data from two patients who underwent awake intracranial recordings during a speech prediction task immediately before and after neurosurgical treatment that required disconnection of the left anterior temporal lobe (ATL), a crucial hub for semantic knowledge. Informed by a predictive coding framework, we tested three sets of hypotheses including diaschisis causing disruption in interconnected sites and incomplete or complete compensation by other language-critical and speech processing sites. Immediately after ATL disconnection, we observed highly specific neurophysiological alterations in the recorded fronto-temporal network, including abnormally magnified high gamma responses to the speech sounds in auditory cortex. We also observed evidence for rapid compensation, seen as focal increases in effective connectivity involving language-critical sites in the inferior frontal gyrus and speech processing sites in auditory cortex. However, compensation was incomplete, in part because after ATL disconnection speech prediction signals were depleted in auditory cortex. This study provides direct causal evidence for a semantic hub in the human brain and shows striking neural impact and a rapid attempt at compensation in a neural network after the loss of one of its hubs.

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Signature Zsuzsanna Kocsis

Auditory Expectations, Learning and Plasticity

Laminar and High Spatial Resolution fMRI of Human Auditory Predictive Processing.

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Federico De Martino

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SUBMISSION DETAILS

Individual Abstract To deal with dynamic changes in the soundscape and adjust our behaviour accordingly, a key function of our brain is to predict future states of the world. This has led to a transformative way of thinking about brain function. That is, what we perceive does not reflect the sensory stimulus itself, but rather a combination of the stimulus and an internal (generative) model of its causes. This idea has led to several theoretical advances some of which are capitalized by Predictive Coding (PC). PC assumes that generative models are formed through the exchange of prediction errors (feedforward) and predictions (feedback) across hierarchical processing stages. In addition, PC assumes that prediction errors are modulated by the precision of currently available predictions. Results from invasive animal and human electrophysiological studies support the relevance of predictions for neural processing at different hierarchical levels. Nevertheless, especially in humans the evidence grounding PC principles onto fundamental neurocomputational units (i.e. cortical layers, subdivisions of subcortical structures) is limited and this hampers our understanding of how PC supports the processing of sounds in context in the human brain. Ultra-high field fMRI at high spatial resolution offers a unique opportunity to investigate how computations are embedded in the mesoscopic (cortical) architecture of the human brain (in vivo and non-invasively). Laminar fMRI has already been used to investigate predictive processes in the human visual cortex. In this talk I will describe recent results from studies investigating how predictions and prediction errors are processed in auditory cortical layers. We combine ultra-high field fMRI with biophysical and computational approaches to gain further insights into the computations underlying these responses.

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Auditory Expectations, Learning and Plasticity

Category Learning and Dimension-Selective Attention in Auditory Cortex

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Lori Holt

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SUBMISSION DETAILS

Individual Abstract Human listeners possess rich category representations for speech sounds and words. Yet speech input exhibits complexity across multiple acoustic dimensions, and short-term speech input regularities may not match long-term norms (as in foreign accents). Theoretical accounts of speech perception often have appealed to selective attention as a means by which to balance these demands. However, we do not yet understand how – and whether - listeners learn to selectively attend to informative acoustic dimensions during category learning, how selective attention impacts cortical representations of relevant dimensions, and whether selective attention involves suppression of irrelevant dimensions as well as enhancement of relevant dimensions.

We are examining these questions using novel non-speech auditory categories. Participants complete five days of stimulus-response-feedback training during which they learn four nonspeech categories to criterion. The categories are structured to require listeners to learn acoustic patterns positioned in either a high- or low-frequency band, with simultaneous irrelevant acoustic patterns in the opposite band. Thus, category learning requires reliance on – and perhaps selective attention to – the category-diagnostic acoustic patterns. Control trials involve categorization across an orthogonal dimension, stimulus amplitude ('big' or 'small' Category A). In a single post-training MRI session, listeners categorize sounds in a 2AFC task with categories differentiated by information in either high or low spectral bands, or on relative amplitude. Combined with tonotopic mapping and "attention-o-tonotopic" mapping driven by overt endogenous attention to high and low frequency bands, we examine how dimension-selective attention driven by implicit demands of categorization impact cortical activation.

This work illuminates the cortical mechanisms supporting dimension-based auditory selective

attention, providing a bridge to compare explicitly directed attention (i.e., “listen high”) and selective attention that emerges with learning. Comparison with our control (amplitude) condition allows for assessment of a putative role for suppression. Finally, the study links human studies with non-human animal studies of frequency-selective auditory attention with non-speech stimuli.

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Signature Lori L Holt

Auditory Expectations, Learning and Plasticity

Neural Mechanisms for Tracking Uncertainty in Rapidly Unfolding Sound Sequences.

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Maria Chait

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SUBMISSION DETAILS

Individual Abstract The brain maintains a hierarchy of models to monitor the statistics of its surroundings and inform behaviour. Determining how such models are instantiated and updated is key to understanding the brain as a statistical learning machine.

The auditory system, supported by a network of auditory, hippocampal, and frontal sources, automatically discovers regularities in rapid tone sequences even when these are not behaviourally relevant. We have previously identified specific brain signatures of sequence structure tracking in humans. The transition from a random tone pattern to a structured pattern (RAN-REG) elicits a slow increase in tonic activity that is consistent with gradual evidence accumulation and instantiation of a new model. In contrast, the opposite transition (REG-RAN) evokes an ‘interrupt’ response’: a sharp drop in sustained activity, hypothesized to reflect immediate suppression of top-down prior expectations. The activity settles at a low sustained level, consistent with the weaker statistical constraints in the RAN pattern.

In this series of MEG experiments, we investigated how “model establishment” and “interrupt” responses are affected by information rate (by using sequences of identical statistical properties but halving tone-pip length; 25 vs 50 ms) and predictability of pattern transitions.

We examined responses to the following sequence transitions: REG1-REG2 (from one regular to a different regular pattern) REG-RAN (from a regular to a random pattern) REG1-RAN-REG1 (a regular pattern interrupted by a 500ms random pattern followed by the resuming of the original pattern). The probabilities of these transitions were varied to model a range of environmental volatilities. Naive participants performed a decoy task, while listening passively to the sounds.

We report the following key findings:
(1) The detailed dynamics of discovering, abandoning and learning new structure in sound sequences are observable in the MEG signal.
(2) The dynamics of “model establishment” roughly scaled with tone duration but with some evidence of increasing sluggishness with longer tones.
(3) In REG1-RAN-REG1 trials, post interruption model establishment occurred much faster than in REG1-REG2 trials, suggesting that a model of the original sequence was automatically preserved and re-activated.
(4) The “interrupt” response did not differ between high probably and low probability interruptions, suggesting an automatic process that (unlike what is expected from a Bayesian system) is not affected by volatility per se.

Ongoing EEG work comparing such brain responses in human and non-human primates explores how mnemonic systems may have evolved to support pattern sensitivity in humans.

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Signature Maria Chait

Auditory Expectations, Learning and Plasticity

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Christopher Petkov

Affiliation Newcastle University and University of Iowa

Participant(s) Christopher Petkov (Chair), Maria Geffen (Co-chair), Kerry Walker (Co-chair), Lori Holt (Presenter), Manuel Malmierca (Presenter), Zsuzsanna Kocsis (Presenter), Maria Chait (Presenter), Federico De Martino (Presenter), Maria Geffen (Presenter), Christopher Petkov (Presenter), Ryszard Auksztulewicz (Presenter)

SUBMISSION DETAILS

Session Description The auditory system constantly generates predictions about the sensory world based on prior experience, which creates expectations about upcoming future events. Auditory expectations powerfully shape sensation, perception and cognition, and a theoretical 'predictive coding' framework has advanced in large part from studies in the auditory domain. The expectancy process is thought to be mediated by neural interactions between feedforward and feedback processes all along the auditory pathway, using corticofugal projections from auditory cortex to the periphery, and back. However, until recently it had been unclear how different types of auditory expectations are detected and the role of different stages of the auditory pathway.

This symposium will provide a timely update to address:
• How do auditory expectations form, as an important basis for learning?
• What happens when expectations are not met and the system needs to adapt?
• In disorders that affect the auditory system how are expectancy signals affected?
• Is there plasticity that compensates for impact on the auditory system, and can auditory system impact be remediated?

The symposium will feature presentations from prominent early career and senior scientists, experts in the field of auditory expectancy, learning and plasticity. The presentations will cover a broad range of animal species, including murine models, nonhuman primates and humans. The speakers will showcase the latest neurophysiological approaches possible with each species, ranging from insights at the single neuron levels to mesoscopic and macroscopic studies of the auditory system in humans, including patients with auditory and communication impairments. The presentations will highlight cutting-edge approaches, including circuit-level optogenetic and pharmacological manipulations to identify causal elements involved in auditory expectancy and human intracranial recording and neuroimaging studies. The speakers will also provide insights on

how the auditory field is the leading modality helping to test and advance computational theories on predictive coding.

Presenter Diversity The symposium is gender balanced. The speakers represent five countries and a diversity of backgrounds. Six of the speakers are immigrants to the countries in which they are working.

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Signature Christopher Petkov

Auditory Expectations, Learning and Plasticity

Prediction, Attention, and Memory in the Auditory Cortex

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Ryszard Auksztulewicz

Affiliation European Neuroscience Institute Göttingen

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SUBMISSION DETAILS

Individual Abstract The brain is thought to generate internal predictions, based on the memory of past stimulation, to optimise behaviour. However, it is unclear to what extent these predictions are modulated by other top-down factors such as attention and task demands, and whether predictions of different sensory features are mediated by the same neural mechanisms. In this talk I will present results of studies combining human and rodent electrophysiology with computational modelling to identify the neural mechanisms of sensory predictions and their interactions with other cognitive factors. First, in non-invasive studies using MEG/EEG and direct recordings from humans using ECoG, analysis of behavioural and neural data showed that the effects of predictions are not automatic but are modulated by their contextual relevance. Second, computational modelling of the data suggested that these modulations could be linked to specific candidate mechanisms, including gain control in sensory regions. Finally, in a series of studies using invasive recordings in anaesthetised rodents, neural representations related to stimulus memory and predictions could be simultaneously decoded from auditory cortical activity, shedding light on the evolutionary conservation of predictive processing across species.

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Signature Ryszard Auksztulewicz

Auditory Expectations, Learning and Plasticity

Corticofugal Regulation of Predictive Coding

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Maria Geffen

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SUBMISSION DETAILS

Individual Abstract Sensory systems must account for both contextual factors and prior experience to adaptively engage with the dynamic external environment. In the central auditory system, neurons modulate their responses to sounds based on statistical context. These response modulations can be understood through a hierarchical predictive coding lens: responses to repeated stimuli are progressively decreased, in a process known as repetition suppression, whereas unexpected stimuli produce a prediction error signal. Prediction error incrementally increases along the auditory hierarchy from the inferior colliculus (IC) to the auditory cortex (AC), suggesting that these regions may engage in hierarchical predictive coding. A potential substrate for top-down predictive cues is the massive set of descending projections from the AC to subcortical structures, although the role of this system in predictive processing has never been directly assessed. We tested the effect of optogenetic inactivation of the auditory cortico-collicular feedback in awake mice on responses of IC neurons to stimuli designed to test prediction error and repetition suppression. Inactivation of the cortico-collicular pathway led to a decrease in prediction error in IC. Repetition suppression was unaffected by cortico-collicular inactivation, suggesting that this metric may reflect fatigue of bottom-up sensory inputs rather than predictive processing. We also discovered populations of IC units that exhibit repetition enhancement, a sequential increase in firing with stimulus repetition. Cortico-collicular inactivation led to a decrease in repetition enhancement in the central nucleus of IC, suggesting that it is a top-down phenomenon. Negative prediction error, a stronger response to a tone in a predictable rather than unpredictable sequence, was suppressed in shell IC units during cortico-collicular inactivation. These changes in predictive coding metrics arose from bidirectional modulations in the response to the standard and deviant contexts, such that the units in IC responded more similarly to each context in the absence of cortical input. We also investigated how these metrics compare between the anesthetized and awake states by recording from the same units under both conditions. We found that metrics of

predictive coding and deviance detection differ depending on the anesthetic state of the animal, with negative prediction error emerging in the central IC and repetition enhancement and prediction error being more prevalent in the absence of anesthesia. Overall, our results demonstrate that the AC provides cues about the statistical context of sound to subcortical brain regions via direct feedback, regulating processing of both prediction and repetition.

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Signature Maria Geffen

Auditory Expectations, Learning and Plasticity

Precision in Predictive coding: The Role of Neuromodultion in Deviance Detection

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Manuel Malmierca

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SUBMISSION DETAILS

Individual Abstract Behaviour becomes more efficient when we can predict a stimulus. This is the basis of the enormous flexibility underlying interactions with our physical and social environment. Filtering out non-relevant stimuli is an important but understudied aspect of cognition. Today, there is rather universal agreement in neuroscience, that a major function of the brain is to constantly predict the environment on multiple levels and time scales (Friston, 2005), For example, one anticipates how a word of a friend will sound, and when and how a sentence will end, even before it has ended. This proposal is based on the assumption that the brain's neuronal circuitry is organized as a highly predictive machine.

The ability of the brain to recognize which prediction errors carry reliable information is critical in the process of prediction error minimization. For example, if a sensor is malfunctioning because of an impairment (e.g., hearing loss or tinnitus) or because it is operating out of its appropriate physical range, the sensory input it provides is not adequately reporting on real changes in the environment, which may generate misinformative prediction errors. According to the predictive coding theory, this distinction between signal and noise is based on an important element, the so-called precision, which weights the driving power of prediction errors according to how reliable they are estimated to be (Friston, 2005).

Neuromodulatory inputs not only gate plasticity (Martins and Froemke, 2015), but also change the balance of top-down versus bottom-up influence and it well known that neuromodulation strongly impacts sensory processing, learning and memory. 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). Therefore, 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. We have used single neuron recordings and microiontophoresis manipulation of the cholinergic system in the rat brain to study how these neuromodulators shape the predictive responses in cortical and subcortical brain regions in the rat brain

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Auditory Expectations, Learning and Plasticity

Transformations of Auditory Sequences into Neural Expectancy Signals

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Christopher Petkov

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SUBMISSION DETAILS

Individual Abstract There is considerable interest in understanding the neural transformations that occur at every stage in the auditory system. These are no longer thought to be simply feedforward or unidirectional, but rather are better conceived of as bidirectional processes and interactions that occur at every stage in the auditory system and influence sensory processing and expectation. A prime example of a system that efficiently transforms auditory sequences into higher-order structures is the human language system. However, because this system in humans is often thought to be special, the aspects of it that have parallels with the neural systems of other animals remains an open question. In this presentation, we overview work in human and nonhuman primates involving the processing of auditory sequences using statistical learning tasks that generate auditory expectancies. There is now evidence from comparative neuroimaging work that a broad auditory cortical system is involved in processing auditory dependencies separated in time. We also present data from neurophysiological recordings in nonhuman primates and human neurosurgery patients identifying auditory cortical expectancy signals and those that only appear when expectations are not met. This comparative research has generated hypotheses on the key neural transformations and neuronal codes that bind sequentially distributed auditory dependencies in time. We conclude the presentation by showing that there are now closer nonhuman animal parallels to the human auditory and language system, which bodes well for understanding fundamental aspects of it with animal models and more directly informing research with patients that have auditory disorders.

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Signature Christopher Petkov

Auditory Expectations, Learning and Plasticity

Immediate Neural Network Impact and Compensation after the Loss of a Semantic Hub

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Zsuzsanna Kocsis

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SUBMISSION DETAILS

Individual Abstract The human brain extracts meaning from the world using an extensive neural system for semantic knowledge. Whether such broadly distributed systems crucially depend on or can compensate for the loss of one of their highly interconnected hubs is controversial. The strongest level of causal evidence for the role of a brain hub is to evaluate its acute network-level impact following disconnection and any rapid functional compensation that ensues. We report rare neurophysiological data from two patients who underwent awake intracranial recordings during a speech prediction task immediately before and after neurosurgical treatment that required disconnection of the left anterior temporal lobe (ATL), a crucial hub for semantic knowledge. Informed by a predictive coding framework, we tested three sets of hypotheses including diaschisis causing disruption in interconnected sites and incomplete or complete compensation by other language-critical and speech processing sites. Immediately after ATL disconnection, we observed highly specific neurophysiological alterations in the recorded fronto-temporal network, including abnormally magnified high gamma responses to the speech sounds in auditory cortex. We also observed evidence for rapid compensation, seen as focal increases in effective connectivity involving language-critical sites in the inferior frontal gyrus and speech processing sites in auditory cortex. However, compensation was incomplete, in part because after ATL disconnection speech prediction signals were depleted in auditory cortex. This study provides direct causal evidence for a semantic hub in the human brain and shows striking neural impact and a rapid attempt at compensation in a neural network after the loss of one of its hubs.

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Signature Zsuzsanna Kocsis

Auditory Expectations, Learning and Plasticity

Laminar and High Spatial Resolution fMRI of Human Auditory Predictive Processing.

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Federico De Martino

Affiliation Maastricht University

Participant(s) Christopher Petkov (Chair), Maria Geffen (Co-chair), Kerry Walker (Co-chair), Lori Holt (Presenter), Manuel Malmierca (Presenter), Zsuzsanna Kocsis (Presenter), Maria Chait (Presenter), Federico De Martino (Presenter), Maria Geffen (Presenter), Christopher Petkov (Presenter), Ryszard Auksztulewicz (Presenter)

SUBMISSION DETAILS

Individual Abstract To deal with dynamic changes in the soundscape and adjust our behaviour accordingly, a key function of our brain is to predict future states of the world. This has led to a transformative way of thinking about brain function. That is, what we perceive does not reflect the sensory stimulus itself, but rather a combination of the stimulus and an internal (generative) model of its causes. This idea has led to several theoretical advances some of which are capitalized by Predictive Coding (PC). PC assumes that generative models are formed through the exchange of prediction errors (feedforward) and predictions (feedback) across hierarchical processing stages. In addition, PC assumes that prediction errors are modulated by the precision of currently available predictions. Results from invasive animal and human electrophysiological studies support the relevance of predictions for neural processing at different hierarchical levels. Nevertheless, especially in humans the evidence grounding PC principles onto fundamental neurocomputational units (i.e. cortical layers, subdivisions of subcortical structures) is limited and this hampers our understanding of how PC supports the processing of sounds in context in the human brain.
Ultra-high field fMRI at high spatial resolution offers a unique opportunity to investigate how computations are embedded in the mesoscopic (cortical) architecture of the human brain (in vivo and non-invasively). Laminar fMRI has already been used to investigate predictive processes in the human visual cortex. In this talk I will describe recent results from studies investigating how predictions and prediction errors are processed in auditory cortical layers. We combine ultra-high field fMRI with biophysical and computational approaches to gain further insights into the computations underlying these responses.

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Signature Federico De Martino

Auditory Expectations, Learning and Plasticity

Category Learning and Dimension-Selective Attention in Auditory Cortex

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Lori Holt

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SUBMISSION DETAILS

Individual Abstract Human listeners possess rich category representations for speech sounds and words. Yet speech input exhibits complexity across multiple acoustic dimensions, and short-term speech input regularities may not match long-term norms (as in foreign accents). Theoretical accounts of speech perception often have appealed to selective attention as a means by which to balance these demands. However, we do not yet understand how – and whether - listeners learn to selectively attend to informative acoustic dimensions during category learning, how selective attention impacts cortical representations of relevant dimensions, and whether selective attention involves suppression of irrelevant dimensions as well as enhancement of relevant dimensions.

We are examining these questions using novel non-speech auditory categories. Participants complete five days of stimulus-response-feedback training during which they learn four nonspeech categories to criterion. The categories are structured to require listeners to learn acoustic patterns positioned in either a high- or low-frequency band, with simultaneous irrelevant acoustic patterns in the opposite band. Thus, category learning requires reliance on – and perhaps selective attention to – the category-diagnostic acoustic patterns. Control trials involve categorization across an orthogonal dimension, stimulus amplitude ('big' or 'small' Category A). In a single post-training MRI session, listeners categorize sounds in a 2AFC task with categories differentiated by information in either high or low spectral bands, or on relative amplitude. Combined with tonotopic mapping and "attention-o-tonotopic" mapping driven by overt endogenous attention to high and low frequency bands, we examine how dimension-selective attention driven by implicit demands of categorization impact cortical activation.

This work illuminates the cortical mechanisms supporting dimension-based auditory selective

attention, providing a bridge to compare explicitly directed attention (i.e., “listen high”) and selective attention that emerges with learning. Comparison with our control (amplitude) condition allows for assessment of a putative role for suppression. Finally, the study links human studies with non-human animal studies of frequency-selective auditory attention with non-speech stimuli.

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Signature Lori L Holt

Auditory Expectations, Learning and Plasticity

Neural Mechanisms for Tracking Uncertainty in Rapidly Unfolding Sound Sequences.

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Maria Chait

Affiliation UCL Ear Institute

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SUBMISSION DETAILS

Individual Abstract The brain maintains a hierarchy of models to monitor the statistics of its surroundings and inform behaviour. Determining how such models are instantiated and updated is key to understanding the brain as a statistical learning machine.

The auditory system, supported by a network of auditory, hippocampal, and frontal sources, automatically discovers regularities in rapid tone sequences even when these are not behaviourally relevant. We have previously identified specific brain signatures of sequence structure tracking in humans. The transition from a random tone pattern to a structured pattern (RAN-REG) elicits a slow increase in tonic activity that is consistent with gradual evidence accumulation and instantiation of a new model. In contrast, the opposite transition (REG-RAN) evokes an 'interrupt' response': a sharp drop in sustained activity, hypothesized to reflect immediate suppression of top-down prior expectations. The activity settles at a low sustained level, consistent with the weaker statistical constraints in the RAN pattern.

In this series of MEG experiments, we investigated how "model establishment" and "interrupt" responses are affected by information rate (by using sequences of identical statistical properties but halving tone-pip length; 25 vs 50 ms) and predictability of pattern transitions.

We examined responses to the following sequence transitions: REG1-REG2 (from one regular to a different regular pattern) REG-RAN (from a regular to a random pattern) REG1-RAN-REG1 (a regular pattern interrupted by a 500ms random pattern followed by the resuming of the original pattern). The probabilities of these transitions were varied to model a range of environmental volatilities. Naive participants performed a decoy task, while listening passively to the sounds.

We report the following key findings:
(1) The detailed dynamics of discovering, abandoning and learning new structure in sound sequences are observable in the MEG signal.
(2) The dynamics of “model establishment” roughly scaled with tone duration but with some evidence of increasing sluggishness with longer tones.
(3) In REG1-RAN-REG1 trials, post interruption model establishment occurred much faster than in REG1-REG2 trials, suggesting that a model of the original sequence was automatically preserved and re-activated.
(4) The “interrupt” response did not differ between high probably and low probability interruptions, suggesting an automatic process that (unlike what is expected from a Bayesian system) is not affected by volatility per se.

Ongoing EEG work comparing such brain responses in human and non-human primates explores how mnemonic systems may have evolved to support pattern sensitivity in humans.

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Signature Maria Chait

Auditory Expectations, Learning and Plasticity

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Christopher Petkov

Affiliation Newcastle University and University of Iowa

Participant(s) Christopher Petkov (Chair), Maria Geffen (Co-chair), Kerry Walker (Co-chair), Lori Holt (Presenter), Manuel Malmierca (Presenter), Zsuzsanna Kocsis (Presenter), Maria Chait (Presenter), Federico De Martino (Presenter), Maria Geffen (Presenter), Christopher Petkov (Presenter), Ryszard Auksztulewicz (Presenter)

SUBMISSION DETAILS

Session Description The auditory system constantly generates predictions about the sensory world based on prior experience, which creates expectations about upcoming future events. Auditory expectations powerfully shape sensation, perception and cognition, and a theoretical ‘predictive coding’ framework has advanced in large part from studies in the auditory domain. The expectancy process is thought to be mediated by neural interactions between feedforward and feedback processes all along the auditory pathway, using corticofugal projections from auditory cortex to the periphery, and back. However, until recently it had been unclear how different types of auditory expectations are detected and the role of different stages of the auditory pathway.

This symposium will provide a timely update to address:
• How do auditory expectations form, as an important basis for learning?
• What happens when expectations are not met and the system needs to adapt?
• In disorders that affect the auditory system how are expectancy signals affected?
• Is there plasticity that compensates for impact on the auditory system, and can auditory system impact be remediated?

The symposium will feature presentations from prominent early career and senior scientists, experts in the field of auditory expectancy, learning and plasticity. The presentations will cover a broad range of animal species, including murine models, nonhuman primates and humans. The speakers will showcase the latest neurophysiological approaches possible with each species, ranging from insights at the single neuron levels to mesoscopic and macroscopic studies of the auditory system in humans, including patients with auditory and communication impairments. The presentations will highlight cutting-edge approaches, including circuit-level optogenetic and pharmacological manipulations to identify causal elements involved in auditory expectancy and human intracranial recording and neuroimaging studies. The speakers will also provide insights on

how the auditory field is the leading modality helping to test and advance computational theories on predictive coding.

Presenter Diversity The symposium is gender balanced. The speakers represent five countries and a diversity of backgrounds. Six of the speakers are immigrants to the countries in which they are working.

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Signature Christopher Petkov

Auditory Expectations, Learning and Plasticity

Prediction, Attention, and Memory in the Auditory Cortex

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Ryszard Auksztulewicz

Affiliation European Neuroscience Institute Göttingen

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SUBMISSION DETAILS

Individual Abstract The brain is thought to generate internal predictions, based on the memory of past stimulation, to optimise behaviour. However, it is unclear to what extent these predictions are modulated by other top-down factors such as attention and task demands, and whether predictions of different sensory features are mediated by the same neural mechanisms. In this talk I will present results of studies combining human and rodent electrophysiology with computational modelling to identify the neural mechanisms of sensory predictions and their interactions with other cognitive factors. First, in non-invasive studies using MEG/EEG and direct recordings from humans using ECoG, analysis of behavioural and neural data showed that the effects of predictions are not automatic but are modulated by their contextual relevance. Second, computational modelling of the data suggested that these modulations could be linked to specific candidate mechanisms, including gain control in sensory regions. Finally, in a series of studies using invasive recordings in anaesthetised rodents, neural representations related to stimulus memory and predictions could be simultaneously decoded from auditory cortical activity, shedding light on the evolutionary conservation of predictive processing across species.

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Signature Ryszard Auksztulewicz

Auditory Expectations, Learning and Plasticity

Corticofugal Regulation of Predictive Coding

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Maria Geffen

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SUBMISSION DETAILS

Individual Abstract Sensory systems must account for both contextual factors and prior experience to adaptively engage with the dynamic external environment. In the central auditory system, neurons modulate their responses to sounds based on statistical context. These response modulations can be understood through a hierarchical predictive coding lens: responses to repeated stimuli are progressively decreased, in a process known as repetition suppression, whereas unexpected stimuli produce a prediction error signal. Prediction error incrementally increases along the auditory hierarchy from the inferior colliculus (IC) to the auditory cortex (AC), suggesting that these regions may engage in hierarchical predictive coding. A potential substrate for top-down predictive cues is the massive set of descending projections from the AC to subcortical structures, although the role of this system in predictive processing has never been directly assessed. We tested the effect of optogenetic inactivation of the auditory cortico-collicular feedback in awake mice on responses of IC neurons to stimuli designed to test prediction error and repetition suppression. Inactivation of the cortico-collicular pathway led to a decrease in prediction error in IC. Repetition suppression was unaffected by cortico-collicular inactivation, suggesting that this metric may reflect fatigue of bottom-up sensory inputs rather than predictive processing. We also discovered populations of IC units that exhibit repetition enhancement, a sequential increase in firing with stimulus repetition. Cortico-collicular inactivation led to a decrease in repetition enhancement in the central nucleus of IC, suggesting that it is a top-down phenomenon. Negative prediction error, a stronger response to a tone in a predictable rather than unpredictable sequence, was suppressed in shell IC units during cortico-collicular inactivation. These changes in predictive coding metrics arose from bidirectional modulations in the response to the standard and deviant contexts, such that the units in IC responded more similarly to each context in the absence of cortical input. We also investigated how these metrics compare between the anesthetized and awake states by recording from the same units under both conditions. We found that metrics of

predictive coding and deviance detection differ depending on the anesthetic state of the animal, with negative prediction error emerging in the central IC and repetition enhancement and prediction error being more prevalent in the absence of anesthesia. Overall, our results demonstrate that the AC provides cues about the statistical context of sound to subcortical brain regions via direct feedback, regulating processing of both prediction and repetition.

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Signature Maria Geffen

Auditory Expectations, Learning and Plasticity

Precision in Predictive coding: The Role of Neuromodultion in Deviance Detection

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Manuel Malmierca

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SUBMISSION DETAILS

Individual Abstract Behaviour becomes more efficient when we can predict a stimulus. This is the basis of the enormous flexibility underlying interactions with our physical and social environment. Filtering out non-relevant stimuli is an important but understudied aspect of cognition. Today, there is rather universal agreement in neuroscience, that a major function of the brain is to constantly predict the environment on multiple levels and time scales (Friston, 2005), For example, one anticipates how a word of a friend will sound, and when and how a sentence will end, even before it has ended. This proposal is based on the assumption that the brain's neuronal circuitry is organized as a highly predictive machine.

The ability of the brain to recognize which prediction errors carry reliable information is critical in the process of prediction error minimization. For example, if a sensor is malfunctioning because of an impairment (e.g., hearing loss or tinnitus) or because it is operating out of its appropriate physical range, the sensory input it provides is not adequately reporting on real changes in the environment, which may generate misinformative prediction errors. According to the predictive coding theory, this distinction between signal and noise is based on an important element, the so-called precision, which weights the driving power of prediction errors according to how reliable they are estimated to be (Friston, 2005).

Neuromodulatory inputs not only gate plasticity (Martins and Froemke, 2015), but also change the balance of top-down versus bottom-up influence and it well known that neuromodulation strongly impacts sensory processing, learning and memory. 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). Therefore, 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. We have used single neuron recordings and microiontophoresis manipulation of the cholinergic system in the rat brain to study how these neuromodulators shape the predictive responses in cortical and subcortical brain regions in the rat brain

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Auditory Expectations, Learning and Plasticity

Transformations of Auditory Sequences into Neural Expectancy Signals

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Christopher Petkov

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SUBMISSION DETAILS

Individual Abstract There is considerable interest in understanding the neural transformations that occur at every stage in the auditory system. These are no longer thought to be simply feedforward or unidirectional, but rather are better conceived of as bidirectional processes and interactions that occur at every stage in the auditory system and influence sensory processing and expectation. A prime example of a system that efficiently transforms auditory sequences into higher-order structures is the human language system. However, because this system in humans is often thought to be special, the aspects of it that have parallels with the neural systems of other animals remains an open question. In this presentation, we overview work in human and nonhuman primates involving the processing of auditory sequences using statistical learning tasks that generate auditory expectancies. There is now evidence from comparative neuroimaging work that a broad auditory cortical system is involved in processing auditory dependencies separated in time. We also present data from neurophysiological recordings in nonhuman primates and human neurosurgery patients identifying auditory cortical expectancy signals and those that only appear when expectations are not met. This comparative research has generated hypotheses on the key neural transformations and neuronal codes that bind sequentially distributed auditory dependencies in time. We conclude the presentation by showing that there are now closer nonhuman animal parallels to the human auditory and language system, which bodes well for understanding fundamental aspects of it with animal models and more directly informing research with patients that have auditory disorders.

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Signature Christopher Petkov

Auditory Expectations, Learning and Plasticity

Immediate Neural Network Impact and Compensation after the Loss of a Semantic Hub

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Zsuzsanna Kocsis

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SUBMISSION DETAILS

Individual Abstract The human brain extracts meaning from the world using an extensive neural system for semantic knowledge. Whether such broadly distributed systems crucially depend on or can compensate for the loss of one of their highly interconnected hubs is controversial. The strongest level of causal evidence for the role of a brain hub is to evaluate its acute network-level impact following disconnection and any rapid functional compensation that ensues. We report rare neurophysiological data from two patients who underwent awake intracranial recordings during a speech prediction task immediately before and after neurosurgical treatment that required disconnection of the left anterior temporal lobe (ATL), a crucial hub for semantic knowledge. Informed by a predictive coding framework, we tested three sets of hypotheses including diaschisis causing disruption in interconnected sites and incomplete or complete compensation by other language-critical and speech processing sites. Immediately after ATL disconnection, we observed highly specific neurophysiological alterations in the recorded fronto-temporal network, including abnormally magnified high gamma responses to the speech sounds in auditory cortex. We also observed evidence for rapid compensation, seen as focal increases in effective connectivity involving language-critical sites in the inferior frontal gyrus and speech processing sites in auditory cortex. However, compensation was incomplete, in part because after ATL disconnection speech prediction signals were depleted in auditory cortex. This study provides direct causal evidence for a semantic hub in the human brain and shows striking neural impact and a rapid attempt at compensation in a neural network after the loss of one of its hubs.

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Signature Zsuzsanna Kocsis

Auditory Expectations, Learning and Plasticity

Laminar and High Spatial Resolution fMRI of Human Auditory Predictive Processing.

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Federico De Martino

Affiliation Maastricht University

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SUBMISSION DETAILS

Individual Abstract To deal with dynamic changes in the soundscape and adjust our behaviour accordingly, a key function of our brain is to predict future states of the world. This has led to a transformative way of thinking about brain function. That is, what we perceive does not reflect the sensory stimulus itself, but rather a combination of the stimulus and an internal (generative) model of its causes. This idea has led to several theoretical advances some of which are capitalized by Predictive Coding (PC). PC assumes that generative models are formed through the exchange of prediction errors (feedforward) and predictions (feedback) across hierarchical processing stages. In addition, PC assumes that prediction errors are modulated by the precision of currently available predictions. Results from invasive animal and human electrophysiological studies support the relevance of predictions for neural processing at different hierarchical levels. Nevertheless, especially in humans the evidence grounding PC principles onto fundamental neurocomputational units (i.e. cortical layers, subdivisions of subcortical structures) is limited and this hampers our understanding of how PC supports the processing of sounds in context in the human brain. Ultra-high field fMRI at high spatial resolution offers a unique opportunity to investigate how computations are embedded in the mesoscopic (cortical) architecture of the human brain (in vivo and non-invasively). Laminar fMRI has already been used to investigate predictive processes in the human visual cortex. In this talk I will describe recent results from studies investigating how predictions and prediction errors are processed in auditory cortical layers. We combine ultra-high field fMRI with biophysical and computational approaches to gain further insights into the computations underlying these responses.

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Mahdi	Enan	Maastricht University
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Essa	Yacoub	University of Minnesota

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Signature Federico De Martino

Auditory Expectations, Learning and Plasticity

Category Learning and Dimension-Selective Attention in Auditory Cortex

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Lori Holt

Affiliation Carnegie Mellon University

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SUBMISSION DETAILS

Individual Abstract Human listeners possess rich category representations for speech sounds and words. Yet speech input exhibits complexity across multiple acoustic dimensions, and short-term speech input regularities may not match long-term norms (as in foreign accents). Theoretical accounts of speech perception often have appealed to selective attention as a means by which to balance these demands. However, we do not yet understand how – and whether - listeners learn to selectively attend to informative acoustic dimensions during category learning, how selective attention impacts cortical representations of relevant dimensions, and whether selective attention involves suppression of irrelevant dimensions as well as enhancement of relevant dimensions.

We are examining these questions using novel non-speech auditory categories. Participants complete five days of stimulus-response-feedback training during which they learn four nonspeech categories to criterion. The categories are structured to require listeners to learn acoustic patterns positioned in either a high- or low-frequency band, with simultaneous irrelevant acoustic patterns in the opposite band. Thus, category learning requires reliance on – and perhaps selective attention to – the category-diagnostic acoustic patterns. Control trials involve categorization across an orthogonal dimension, stimulus amplitude ('big' or 'small' Category A). In a single post-training MRI session, listeners categorize sounds in a 2AFC task with categories differentiated by information in either high or low spectral bands, or on relative amplitude. Combined with tonotopic mapping and "attention-o-tonotopic" mapping driven by overt endogenous attention to high and low frequency bands, we examine how dimension-selective attention driven by implicit demands of categorization impact cortical activation.

This work illuminates the cortical mechanisms supporting dimension-based auditory selective

attention, providing a bridge to compare explicitly directed attention (i.e., “listen high”) and selective attention that emerges with learning. Comparison with our control (amplitude) condition allows for assessment of a putative role for suppression. Finally, the study links human studies with non-human animal studies of frequency-selective auditory attention with non-speech stimuli.

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Frederic	Dick	University College London

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Signature Lori L Holt

Auditory Expectations, Learning and Plasticity

Neural Mechanisms for Tracking Uncertainty in Rapidly Unfolding Sound Sequences.

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Maria Chait

Affiliation UCL Ear Institute

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SUBMISSION DETAILS

Individual Abstract The brain maintains a hierarchy of models to monitor the statistics of its surroundings and inform behaviour. Determining how such models are instantiated and updated is key to understanding the brain as a statistical learning machine.

The auditory system, supported by a network of auditory, hippocampal, and frontal sources, automatically discovers regularities in rapid tone sequences even when these are not behaviourally relevant. We have previously identified specific brain signatures of sequence structure tracking in humans. The transition from a random tone pattern to a structured pattern (RAN-REG) elicits a slow increase in tonic activity that is consistent with gradual evidence accumulation and instantiation of a new model. In contrast, the opposite transition (REG-RAN) evokes an 'interrupt' response': a sharp drop in sustained activity, hypothesized to reflect immediate suppression of top-down prior expectations. The activity settles at a low sustained level, consistent with the weaker statistical constraints in the RAN pattern.

In this series of MEG experiments, we investigated how "model establishment" and "interrupt" responses are affected by information rate (by using sequences of identical statistical properties but halving tone-pip length; 25 vs 50 ms) and predictability of pattern transitions.

We examined responses to the following sequence transitions: REG1-REG2 (from one regular to a different regular pattern) REG-RAN (from a regular to a random pattern) REG1-RAN-REG1 (a regular pattern interrupted by a 500ms random pattern followed by the resuming of the original pattern). The probabilities of these transitions were varied to model a range of environmental volatilities. Naive participants performed a decoy task, while listening passively to the sounds.

We report the following key findings:
(1) The detailed dynamics of discovering, abandoning and learning new structure in sound sequences are observable in the MEG signal.
(2) The dynamics of “model establishment” roughly scaled with tone duration but with some evidence of increasing sluggishness with longer tones.
(3) In REG1-RAN-REG1 trials, post interruption model establishment occurred much faster than in REG1-REG2 trials, suggesting that a model of the original sequence was automatically preserved and re-activated.
(4) The “interrupt” response did not differ between high probably and low probability interruptions, suggesting an automatic process that (unlike what is expected from a Bayesian system) is not affected by volatility per se.

Ongoing EEG work comparing such brain responses in human and non-human primates explores how mnemonic systems may have evolved to support pattern sensitivity in humans.

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Signature Maria Chait

Auditory Expectations, Learning and Plasticity

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Christopher Petkov

Affiliation Newcastle University and University of Iowa

Participant(s) Christopher Petkov (Chair), Maria Geffen (Co-chair), Kerry Walker (Co-chair), Lori Holt (Presenter), Manuel Malmierca (Presenter), Zsuzsanna Kocsis (Presenter), Maria Chait (Presenter), Federico De Martino (Presenter), Maria Geffen (Presenter), Christopher Petkov (Presenter), Ryszard Auksztulewicz (Presenter)

SUBMISSION DETAILS

Session Description The auditory system constantly generates predictions about the sensory world based on prior experience, which creates expectations about upcoming future events. Auditory expectations powerfully shape sensation, perception and cognition, and a theoretical 'predictive coding' framework has advanced in large part from studies in the auditory domain. The expectancy process is thought to be mediated by neural interactions between feedforward and feedback processes all along the auditory pathway, using corticofugal projections from auditory cortex to the periphery, and back. However, until recently it had been unclear how different types of auditory expectations are detected and the role of different stages of the auditory pathway.

This symposium will provide a timely update to address:
• How do auditory expectations form, as an important basis for learning?
• What happens when expectations are not met and the system needs to adapt?
• In disorders that affect the auditory system how are expectancy signals affected?
• Is there plasticity that compensates for impact on the auditory system, and can auditory system impact be remediated?

The symposium will feature presentations from prominent early career and senior scientists, experts in the field of auditory expectancy, learning and plasticity. The presentations will cover a broad range of animal species, including murine models, nonhuman primates and humans. The speakers will showcase the latest neurophysiological approaches possible with each species, ranging from insights at the single neuron levels to mesoscopic and macroscopic studies of the auditory system in humans, including patients with auditory and communication impairments. The presentations will highlight cutting-edge approaches, including circuit-level optogenetic and pharmacological manipulations to identify causal elements involved in auditory expectancy and human intracranial recording and neuroimaging studies. The speakers will also provide insights on

how the auditory field is the leading modality helping to test and advance computational theories on predictive coding.

Presenter Diversity The symposium is gender balanced. The speakers represent five countries and a diversity of backgrounds. Six of the speakers are immigrants to the countries in which they are working.

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Signature Christopher Petkov

Auditory Expectations, Learning and Plasticity

Prediction, Attention, and Memory in the Auditory Cortex

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Ryszard Auksztulewicz

Affiliation European Neuroscience Institute Göttingen

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SUBMISSION DETAILS

Individual Abstract The brain is thought to generate internal predictions, based on the memory of past stimulation, to optimise behaviour. However, it is unclear to what extent these predictions are modulated by other top-down factors such as attention and task demands, and whether predictions of different sensory features are mediated by the same neural mechanisms. In this talk I will present results of studies combining human and rodent electrophysiology with computational modelling to identify the neural mechanisms of sensory predictions and their interactions with other cognitive factors. First, in non-invasive studies using MEG/EEG and direct recordings from humans using ECoG, analysis of behavioural and neural data showed that the effects of predictions are not automatic but are modulated by their contextual relevance. Second, computational modelling of the data suggested that these modulations could be linked to specific candidate mechanisms, including gain control in sensory regions. Finally, in a series of studies using invasive recordings in anaesthetised rodents, neural representations related to stimulus memory and predictions could be simultaneously decoded from auditory cortical activity, shedding light on the evolutionary conservation of predictive processing across species.

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Signature Ryszard Auksztulewicz

Auditory Expectations, Learning and Plasticity

Corticofugal Regulation of Predictive Coding

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Maria Geffen

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SUBMISSION DETAILS

Individual Abstract Sensory systems must account for both contextual factors and prior experience to adaptively engage with the dynamic external environment. In the central auditory system, neurons modulate their responses to sounds based on statistical context. These response modulations can be understood through a hierarchical predictive coding lens: responses to repeated stimuli are progressively decreased, in a process known as repetition suppression, whereas unexpected stimuli produce a prediction error signal. Prediction error incrementally increases along the auditory hierarchy from the inferior colliculus (IC) to the auditory cortex (AC), suggesting that these regions may engage in hierarchical predictive coding. A potential substrate for top-down predictive cues is the massive set of descending projections from the AC to subcortical structures, although the role of this system in predictive processing has never been directly assessed. We tested the effect of optogenetic inactivation of the auditory cortico-collicular feedback in awake mice on responses of IC neurons to stimuli designed to test prediction error and repetition suppression. Inactivation of the cortico-collicular pathway led to a decrease in prediction error in IC. Repetition suppression was unaffected by cortico-collicular inactivation, suggesting that this metric may reflect fatigue of bottom-up sensory inputs rather than predictive processing. We also discovered populations of IC units that exhibit repetition enhancement, a sequential increase in firing with stimulus repetition. Cortico-collicular inactivation led to a decrease in repetition enhancement in the central nucleus of IC, suggesting that it is a top-down phenomenon. Negative prediction error, a stronger response to a tone in a predictable rather than unpredictable sequence, was suppressed in shell IC units during cortico-collicular inactivation. These changes in predictive coding metrics arose from bidirectional modulations in the response to the standard and deviant contexts, such that the units in IC responded more similarly to each context in the absence of cortical input. We also investigated how these metrics compare between the anesthetized and awake states by recording from the same units under both conditions. We found that metrics of

predictive coding and deviance detection differ depending on the anesthetic state of the animal, with negative prediction error emerging in the central IC and repetition enhancement and prediction error being more prevalent in the absence of anesthesia. Overall, our results demonstrate that the AC provides cues about the statistical context of sound to subcortical brain regions via direct feedback, regulating processing of both prediction and repetition.

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Signature Maria Geffen

Auditory Expectations, Learning and Plasticity

Precision in Predictive coding: The Role of Neuromodultion in Deviance Detection

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Manuel Malmierca

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SUBMISSION DETAILS

Individual Abstract Behaviour becomes more efficient when we can predict a stimulus. This is the basis of the enormous flexibility underlying interactions with our physical and social environment. Filtering out non-relevant stimuli is an important but understudied aspect of cognition. Today, there is rather universal agreement in neuroscience, that a major function of the brain is to constantly predict the environment on multiple levels and time scales (Friston, 2005), For example, one anticipates how a word of a friend will sound, and when and how a sentence will end, even before it has ended. This proposal is based on the assumption that the brain's neuronal circuitry is organized as a highly predictive machine.

The ability of the brain to recognize which prediction errors carry reliable information is critical in the process of prediction error minimization. For example, if a sensor is malfunctioning because of an impairment (e.g., hearing loss or tinnitus) or because it is operating out of its appropriate physical range, the sensory input it provides is not adequately reporting on real changes in the environment, which may generate misinformative prediction errors. According to the predictive coding theory, this distinction between signal and noise is based on an important element, the so-called precision, which weights the driving power of prediction errors according to how reliable they are estimated to be (Friston, 2005).

Neuromodulatory inputs not only gate plasticity (Martins and Froemke, 2015), but also change the balance of top-down versus bottom-up influence and it well known that neuromodulation strongly impacts sensory processing, learning and memory. 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). Therefore, 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. We have used single neuron recordings and microiontophoresis manipulation of the cholinergic system in the rat brain to study how these neuromodulators shape the predictive responses in cortical and subcortical brain regions in the rat brain

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Auditory Expectations, Learning and Plasticity

Transformations of Auditory Sequences into Neural Expectancy Signals

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Christopher Petkov

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SUBMISSION DETAILS

Individual Abstract There is considerable interest in understanding the neural transformations that occur at every stage in the auditory system. These are no longer thought to be simply feedforward or unidirectional, but rather are better conceived of as bidirectional processes and interactions that occur at every stage in the auditory system and influence sensory processing and expectation. A prime example of a system that efficiently transforms auditory sequences into higher-order structures is the human language system. However, because this system in humans is often thought to be special, the aspects of it that have parallels with the neural systems of other animals remains an open question. In this presentation, we overview work in human and nonhuman primates involving the processing of auditory sequences using statistical learning tasks that generate auditory expectancies. There is now evidence from comparative neuroimaging work that a broad auditory cortical system is involved in processing auditory dependencies separated in time. We also present data from neurophysiological recordings in nonhuman primates and human neurosurgery patients identifying auditory cortical expectancy signals and those that only appear when expectations are not met. This comparative research has generated hypotheses on the key neural transformations and neuronal codes that bind sequentially distributed auditory dependencies in time. We conclude the presentation by showing that there are now closer nonhuman animal parallels to the human auditory and language system, which bodes well for understanding fundamental aspects of it with animal models and more directly informing research with patients that have auditory disorders.

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Signature Christopher Petkov

Auditory Expectations, Learning and Plasticity

Immediate Neural Network Impact and Compensation after the Loss of a Semantic Hub

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Zsuzsanna Kocsis

Affiliation University of Iowa

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SUBMISSION DETAILS

Individual Abstract The human brain extracts meaning from the world using an extensive neural system for semantic knowledge. Whether such broadly distributed systems crucially depend on or can compensate for the loss of one of their highly interconnected hubs is controversial. The strongest level of causal evidence for the role of a brain hub is to evaluate its acute network-level impact following disconnection and any rapid functional compensation that ensues. We report rare neurophysiological data from two patients who underwent awake intracranial recordings during a speech prediction task immediately before and after neurosurgical treatment that required disconnection of the left anterior temporal lobe (ATL), a crucial hub for semantic knowledge. Informed by a predictive coding framework, we tested three sets of hypotheses including diaschisis causing disruption in interconnected sites and incomplete or complete compensation by other language-critical and speech processing sites. Immediately after ATL disconnection, we observed highly specific neurophysiological alterations in the recorded fronto-temporal network, including abnormally magnified high gamma responses to the speech sounds in auditory cortex. We also observed evidence for rapid compensation, seen as focal increases in effective connectivity involving language-critical sites in the inferior frontal gyrus and speech processing sites in auditory cortex. However, compensation was incomplete, in part because after ATL disconnection speech prediction signals were depleted in auditory cortex. This study provides direct causal evidence for a semantic hub in the human brain and shows striking neural impact and a rapid attempt at compensation in a neural network after the loss of one of its hubs.

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Signature Zsuzsanna Kocsis

Auditory Expectations, Learning and Plasticity

Laminar and High Spatial Resolution fMRI of Human Auditory Predictive Processing.

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Federico De Martino

Affiliation Maastricht University

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SUBMISSION DETAILS

Individual Abstract To deal with dynamic changes in the soundscape and adjust our behaviour accordingly, a key function of our brain is to predict future states of the world. This has led to a transformative way of thinking about brain function. That is, what we perceive does not reflect the sensory stimulus itself, but rather a combination of the stimulus and an internal (generative) model of its causes. This idea has led to several theoretical advances some of which are capitalized by Predictive Coding (PC). PC assumes that generative models are formed through the exchange of prediction errors (feedforward) and predictions (feedback) across hierarchical processing stages. In addition, PC assumes that prediction errors are modulated by the precision of currently available predictions. Results from invasive animal and human electrophysiological studies support the relevance of predictions for neural processing at different hierarchical levels. Nevertheless, especially in humans the evidence grounding PC principles onto fundamental neurocomputational units (i.e. cortical layers, subdivisions of subcortical structures) is limited and this hampers our understanding of how PC supports the processing of sounds in context in the human brain.
Ultra-high field fMRI at high spatial resolution offers a unique opportunity to investigate how computations are embedded in the mesoscopic (cortical) architecture of the human brain (in vivo and non-invasively). Laminar fMRI has already been used to investigate predictive processes in the human visual cortex. In this talk I will describe recent results from studies investigating how predictions and prediction errors are processed in auditory cortical layers. We combine ultra-high field fMRI with biophysical and computational approaches to gain further insights into the computations underlying these responses.

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Signature Federico De Martino

Auditory Expectations, Learning and Plasticity

Category Learning and Dimension-Selective Attention in Auditory Cortex

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Lori Holt

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SUBMISSION DETAILS

Individual Abstract Human listeners possess rich category representations for speech sounds and words. Yet speech input exhibits complexity across multiple acoustic dimensions, and short-term speech input regularities may not match long-term norms (as in foreign accents). Theoretical accounts of speech perception often have appealed to selective attention as a means by which to balance these demands. However, we do not yet understand how – and whether - listeners learn to selectively attend to informative acoustic dimensions during category learning, how selective attention impacts cortical representations of relevant dimensions, and whether selective attention involves suppression of irrelevant dimensions as well as enhancement of relevant dimensions.

We are examining these questions using novel non-speech auditory categories. Participants complete five days of stimulus-response-feedback training during which they learn four nonspeech categories to criterion. The categories are structured to require listeners to learn acoustic patterns positioned in either a high- or low-frequency band, with simultaneous irrelevant acoustic patterns in the opposite band. Thus, category learning requires reliance on – and perhaps selective attention to – the category-diagnostic acoustic patterns. Control trials involve categorization across an orthogonal dimension, stimulus amplitude (‘big’ or ‘small’ Category A). In a single post-training MRI session, listeners categorize sounds in a 2AFC task with categories differentiated by information in either high or low spectral bands, or on relative amplitude. Combined with tonotopic mapping and “attention-o-tonotopic” mapping driven by overt endogenous attention to high and low frequency bands, we examine how dimension-selective attention driven by implicit demands of categorization impact cortical activation.

This work illuminates the cortical mechanisms supporting dimension-based auditory selective

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Signature Lori L Holt

Auditory Expectations, Learning and Plasticity

Neural Mechanisms for Tracking Uncertainty in Rapidly Unfolding Sound Sequences.

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Maria Chait

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SUBMISSION DETAILS

Individual Abstract The brain maintains a hierarchy of models to monitor the statistics of its surroundings and inform behaviour. Determining how such models are instantiated and updated is key to understanding the brain as a statistical learning machine.

The auditory system, supported by a network of auditory, hippocampal, and frontal sources, automatically discovers regularities in rapid tone sequences even when these are not behaviourally relevant. We have previously identified specific brain signatures of sequence structure tracking in humans. The transition from a random tone pattern to a structured pattern (RAN-REG) elicits a slow increase in tonic activity that is consistent with gradual evidence accumulation and instantiation of a new model. In contrast, the opposite transition (REG-RAN) evokes an 'interrupt' response': a sharp drop in sustained activity, hypothesized to reflect immediate suppression of top-down prior expectations. The activity settles at a low sustained level, consistent with the weaker statistical constraints in the RAN pattern.

In this series of MEG experiments, we investigated how "model establishment" and "interrupt" responses are affected by information rate (by using sequences of identical statistical properties but halving tone-pip length; 25 vs 50 ms) and predictability of pattern transitions.

We examined responses to the following sequence transitions: REG1-REG2 (from one regular to a different regular pattern) REG-RAN (from a regular to a random pattern) REG1-RAN-REG1 (a regular pattern interrupted by a 500ms random pattern followed by the resuming of the original pattern). The probabilities of these transitions were varied to model a range of environmental volatilities. Naive participants performed a decoy task, while listening passively to the sounds.

We report the following key findings:
(1) The detailed dynamics of discovering, abandoning and learning new structure in sound sequences are observable in the MEG signal.
(2) The dynamics of “model establishment” roughly scaled with tone duration but with some evidence of increasing sluggishness with longer tones.
(3) In REG1-RAN-REG1 trials, post interruption model establishment occurred much faster than in REG1-REG2 trials, suggesting that a model of the original sequence was automatically preserved and re-activated.
(4) The “interrupt” response did not differ between high probably and low probability interruptions, suggesting an automatic process that (unlike what is expected from a Bayesian system) is not affected by volatility per se.

Ongoing EEG work comparing such brain responses in human and non-human primates explores how mnemonic systems may have evolved to support pattern sensitivity in humans.

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Signature Maria Chait

Auditory Expectations, Learning and Plasticity

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Christopher Petkov

Affiliation Newcastle University and University of Iowa

Participant(s) Christopher Petkov (Chair), Maria Geffen (Co-chair), Kerry Walker (Co-chair), Lori Holt (Presenter), Manuel Malmierca (Presenter), Zsuzsanna Kocsis (Presenter), Maria Chait (Presenter), Federico De Martino (Presenter), Maria Geffen (Presenter), Christopher Petkov (Presenter), Ryszard Auksztulewicz (Presenter)

SUBMISSION DETAILS

Session Description The auditory system constantly generates predictions about the sensory world based on prior experience, which creates expectations about upcoming future events. Auditory expectations powerfully shape sensation, perception and cognition, and a theoretical ‘predictive coding’ framework has advanced in large part from studies in the auditory domain. The expectancy process is thought to be mediated by neural interactions between feedforward and feedback processes all along the auditory pathway, using corticofugal projections from auditory cortex to the periphery, and back. However, until recently it had been unclear how different types of auditory expectations are detected and the role of different stages of the auditory pathway.

This symposium will provide a timely update to address:
• How do auditory expectations form, as an important basis for learning?
• What happens when expectations are not met and the system needs to adapt?
• In disorders that affect the auditory system how are expectancy signals affected?
• Is there plasticity that compensates for impact on the auditory system, and can auditory system impact be remediated?

The symposium will feature presentations from prominent early career and senior scientists, experts in the field of auditory expectancy, learning and plasticity. The presentations will cover a broad range of animal species, including murine models, nonhuman primates and humans. The speakers will showcase the latest neurophysiological approaches possible with each species, ranging from insights at the single neuron levels to mesoscopic and macroscopic studies of the auditory system in humans, including patients with auditory and communication impairments. The presentations will highlight cutting-edge approaches, including circuit-level optogenetic and pharmacological manipulations to identify causal elements involved in auditory expectancy and human intracranial recording and neuroimaging studies. The speakers will also provide insights on

how the auditory field is the leading modality helping to test and advance computational theories on predictive coding.

Presenter Diversity The symposium is gender balanced. The speakers represent five countries and a diversity of backgrounds. Six of the speakers are immigrants to the countries in which they are working.

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Signature Christopher Petkov

Auditory Expectations, Learning and Plasticity

Prediction, Attention, and Memory in the Auditory Cortex

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Ryszard Auksztulewicz

Affiliation European Neuroscience Institute Göttingen

Participant(s) Christopher Petkov (Chair), Maria Geffen (Co-chair), Kerry Walker (Co-chair), Lori Holt (Presenter), Manuel Malmierca (Presenter), Zsuzsanna Kocsis (Presenter), Maria Chait (Presenter), Federico De Martino (Presenter), Maria Geffen (Presenter), Christopher Petkov (Presenter), Ryszard Auksztulewicz (Presenter)

SUBMISSION DETAILS

Individual Abstract The brain is thought to generate internal predictions, based on the memory of past stimulation, to optimise behaviour. However, it is unclear to what extent these predictions are modulated by other top-down factors such as attention and task demands, and whether predictions of different sensory features are mediated by the same neural mechanisms. In this talk I will present results of studies combining human and rodent electrophysiology with computational modelling to identify the neural mechanisms of sensory predictions and their interactions with other cognitive factors. First, in non-invasive studies using MEG/EEG and direct recordings from humans using ECoG, analysis of behavioural and neural data showed that the effects of predictions are not automatic but are modulated by their contextual relevance. Second, computational modelling of the data suggested that these modulations could be linked to specific candidate mechanisms, including gain control in sensory regions. Finally, in a series of studies using invasive recordings in anaesthetised rodents, neural representations related to stimulus memory and predictions could be simultaneously decoded from auditory cortical activity, shedding light on the evolutionary conservation of predictive processing across species.

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Signature Ryszard Auksztulewicz

Auditory Expectations, Learning and Plasticity

Corticofugal Regulation of Predictive Coding

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Maria Geffen

Affiliation University of Pennsylvania School of Medicine

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SUBMISSION DETAILS

Individual Abstract Sensory systems must account for both contextual factors and prior experience to adaptively engage with the dynamic external environment. In the central auditory system, neurons modulate their responses to sounds based on statistical context. These response modulations can be understood through a hierarchical predictive coding lens: responses to repeated stimuli are progressively decreased, in a process known as repetition suppression, whereas unexpected stimuli produce a prediction error signal. Prediction error incrementally increases along the auditory hierarchy from the inferior colliculus (IC) to the auditory cortex (AC), suggesting that these regions may engage in hierarchical predictive coding. A potential substrate for top-down predictive cues is the massive set of descending projections from the AC to subcortical structures, although the role of this system in predictive processing has never been directly assessed. We tested the effect of optogenetic inactivation of the auditory cortico-collicular feedback in awake mice on responses of IC neurons to stimuli designed to test prediction error and repetition suppression. Inactivation of the cortico-collicular pathway led to a decrease in prediction error in IC. Repetition suppression was unaffected by cortico-collicular inactivation, suggesting that this metric may reflect fatigue of bottom-up sensory inputs rather than predictive processing. We also discovered populations of IC units that exhibit repetition enhancement, a sequential increase in firing with stimulus repetition. Cortico-collicular inactivation led to a decrease in repetition enhancement in the central nucleus of IC, suggesting that it is a top-down phenomenon. Negative prediction error, a stronger response to a tone in a predictable rather than unpredictable sequence, was suppressed in shell IC units during cortico-collicular inactivation. These changes in predictive coding metrics arose from bidirectional modulations in the response to the standard and deviant contexts, such that the units in IC responded more similarly to each context in the absence of cortical input. We also investigated how these metrics compare between the anesthetized and awake states by recording from the same units under both conditions. We found that metrics of

predictive coding and deviance detection differ depending on the anesthetic state of the animal, with negative prediction error emerging in the central IC and repetition enhancement and prediction error being more prevalent in the absence of anesthesia. Overall, our results demonstrate that the AC provides cues about the statistical context of sound to subcortical brain regions via direct feedback, regulating processing of both prediction and repetition.

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Signature Maria Geffen

Auditory Expectations, Learning and Plasticity

Precision in Predictive coding: The Role of Neuromodultion in Deviance Detection

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Manuel Malmierca

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SUBMISSION DETAILS

Individual Abstract Behaviour becomes more efficient when we can predict a stimulus. This is the basis of the enormous flexibility underlying interactions with our physical and social environment. Filtering out non-relevant stimuli is an important but understudied aspect of cognition. Today, there is rather universal agreement in neuroscience, that a major function of the brain is to constantly predict the environment on multiple levels and time scales (Friston, 2005), For example, one anticipates how a word of a friend will sound, and when and how a sentence will end, even before it has ended. This proposal is based on the assumption that the brain's neuronal circuitry is organized as a highly predictive machine.

The ability of the brain to recognize which prediction errors carry reliable information is critical in the process of prediction error minimization. For example, if a sensor is malfunctioning because of an impairment (e.g., hearing loss or tinnitus) or because it is operating out of its appropriate physical range, the sensory input it provides is not adequately reporting on real changes in the environment, which may generate misinformative prediction errors. According to the predictive coding theory, this distinction between signal and noise is based on an important element, the so-called precision, which weights the driving power of prediction errors according to how reliable they are estimated to be (Friston, 2005).

Neuromodulatory inputs not only gate plasticity (Martins and Froemke, 2015), but also change the balance of top-down versus bottom-up influence and it well known that neuromodulation strongly impacts sensory processing, learning and memory. 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). Therefore, 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. We have used single neuron recordings and microiontophoresis manipulation of the cholinergic system in the rat brain to study how these neuromodulators shape the predictive responses in cortical and subcortical brain regions in the rat brain

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Auditory Expectations, Learning and Plasticity

Transformations of Auditory Sequences into Neural Expectancy Signals

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Christopher Petkov

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SUBMISSION DETAILS

Individual Abstract There is considerable interest in understanding the neural transformations that occur at every stage in the auditory system. These are no longer thought to be simply feedforward or unidirectional, but rather are better conceived of as bidirectional processes and interactions that occur at every stage in the auditory system and influence sensory processing and expectation. A prime example of a system that efficiently transforms auditory sequences into higher-order structures is the human language system. However, because this system in humans is often thought to be special, the aspects of it that have parallels with the neural systems of other animals remains an open question. In this presentation, we overview work in human and nonhuman primates involving the processing of auditory sequences using statistical learning tasks that generate auditory expectancies. There is now evidence from comparative neuroimaging work that a broad auditory cortical system is involved in processing auditory dependencies separated in time. We also present data from neurophysiological recordings in nonhuman primates and human neurosurgery patients identifying auditory cortical expectancy signals and those that only appear when expectations are not met. This comparative research has generated hypotheses on the key neural transformations and neuronal codes that bind sequentially distributed auditory dependencies in time. We conclude the presentation by showing that there are now closer nonhuman animal parallels to the human auditory and language system, which bodes well for understanding fundamental aspects of it with animal models and more directly informing research with patients that have auditory disorders.

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Signature Christopher Petkov

Auditory Expectations, Learning and Plasticity

Immediate Neural Network Impact and Compensation after the Loss of a Semantic Hub

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Zsuzsanna Kocsis

Affiliation University of Iowa

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SUBMISSION DETAILS

Individual Abstract The human brain extracts meaning from the world using an extensive neural system for semantic knowledge. Whether such broadly distributed systems crucially depend on or can compensate for the loss of one of their highly interconnected hubs is controversial. The strongest level of causal evidence for the role of a brain hub is to evaluate its acute network-level impact following disconnection and any rapid functional compensation that ensues. We report rare neurophysiological data from two patients who underwent awake intracranial recordings during a speech prediction task immediately before and after neurosurgical treatment that required disconnection of the left anterior temporal lobe (ATL), a crucial hub for semantic knowledge. Informed by a predictive coding framework, we tested three sets of hypotheses including diaschisis causing disruption in interconnected sites and incomplete or complete compensation by other language-critical and speech processing sites. Immediately after ATL disconnection, we observed highly specific neurophysiological alterations in the recorded fronto-temporal network, including abnormally magnified high gamma responses to the speech sounds in auditory cortex. We also observed evidence for rapid compensation, seen as focal increases in effective connectivity involving language-critical sites in the inferior frontal gyrus and speech processing sites in auditory cortex. However, compensation was incomplete, in part because after ATL disconnection speech prediction signals were depleted in auditory cortex. This study provides direct causal evidence for a semantic hub in the human brain and shows striking neural impact and a rapid attempt at compensation in a neural network after the loss of one of its hubs.

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Signature Zsuzsanna Kocsis

Auditory Expectations, Learning and Plasticity

Laminar and High Spatial Resolution fMRI of Human Auditory Predictive Processing.

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Federico De Martino

Affiliation Maastricht University

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SUBMISSION DETAILS

Individual Abstract To deal with dynamic changes in the soundscape and adjust our behaviour accordingly, a key function of our brain is to predict future states of the world. This has led to a transformative way of thinking about brain function. That is, what we perceive does not reflect the sensory stimulus itself, but rather a combination of the stimulus and an internal (generative) model of its causes. This idea has led to several theoretical advances some of which are capitalized by Predictive Coding (PC). PC assumes that generative models are formed through the exchange of prediction errors (feedforward) and predictions (feedback) across hierarchical processing stages. In addition, PC assumes that prediction errors are modulated by the precision of currently available predictions. Results from invasive animal and human electrophysiological studies support the relevance of predictions for neural processing at different hierarchical levels. Nevertheless, especially in humans the evidence grounding PC principles onto fundamental neurocomputational units (i.e. cortical layers, subdivisions of subcortical structures) is limited and this hampers our understanding of how PC supports the processing of sounds in context in the human brain. Ultra-high field fMRI at high spatial resolution offers a unique opportunity to investigate how computations are embedded in the mesoscopic (cortical) architecture of the human brain (in vivo and non-invasively). Laminar fMRI has already been used to investigate predictive processes in the human visual cortex. In this talk I will describe recent results from studies investigating how predictions and prediction errors are processed in auditory cortical layers. We combine ultra-high field fMRI with biophysical and computational approaches to gain further insights into the computations underlying these responses.

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Signature Federico De Martino

Auditory Expectations, Learning and Plasticity

Category Learning and Dimension-Selective Attention in Auditory Cortex

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Lori Holt

Affiliation Carnegie Mellon University

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SUBMISSION DETAILS

Individual Abstract Human listeners possess rich category representations for speech sounds and words. Yet speech input exhibits complexity across multiple acoustic dimensions, and short-term speech input regularities may not match long-term norms (as in foreign accents). Theoretical accounts of speech perception often have appealed to selective attention as a means by which to balance these demands. However, we do not yet understand how – and whether - listeners learn to selectively attend to informative acoustic dimensions during category learning, how selective attention impacts cortical representations of relevant dimensions, and whether selective attention involves suppression of irrelevant dimensions as well as enhancement of relevant dimensions.

We are examining these questions using novel non-speech auditory categories. Participants complete five days of stimulus-response-feedback training during which they learn four nonspeech categories to criterion. The categories are structured to require listeners to learn acoustic patterns positioned in either a high- or low-frequency band, with simultaneous irrelevant acoustic patterns in the opposite band. Thus, category learning requires reliance on – and perhaps selective attention to – the category-diagnostic acoustic patterns. Control trials involve categorization across an orthogonal dimension, stimulus amplitude ('big' or 'small' Category A). In a single post-training MRI session, listeners categorize sounds in a 2AFC task with categories differentiated by information in either high or low spectral bands, or on relative amplitude. Combined with tonotopic mapping and "attention-o-tonotopic" mapping driven by overt endogenous attention to high and low frequency bands, we examine how dimension-selective attention driven by implicit demands of categorization impact cortical activation.

This work illuminates the cortical mechanisms supporting dimension-based auditory selective

attention, providing a bridge to compare explicitly directed attention (i.e., “listen high”) and selective attention that emerges with learning. Comparison with our control (amplitude) condition allows for assessment of a putative role for suppression. Finally, the study links human studies with non-human animal studies of frequency-selective auditory attention with non-speech stimuli.

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Signature Lori L Holt

Auditory Expectations, Learning and Plasticity

Neural Mechanisms for Tracking Uncertainty in Rapidly Unfolding Sound Sequences.

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Maria Chait

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SUBMISSION DETAILS

Individual Abstract The brain maintains a hierarchy of models to monitor the statistics of its surroundings and inform behaviour. Determining how such models are instantiated and updated is key to understanding the brain as a statistical learning machine.

The auditory system, supported by a network of auditory, hippocampal, and frontal sources, automatically discovers regularities in rapid tone sequences even when these are not behaviourally relevant. We have previously identified specific brain signatures of sequence structure tracking in humans. The transition from a random tone pattern to a structured pattern (RAN-REG) elicits a slow increase in tonic activity that is consistent with gradual evidence accumulation and instantiation of a new model. In contrast, the opposite transition (REG-RAN) evokes an ‘interrupt’ response’: a sharp drop in sustained activity, hypothesized to reflect immediate suppression of top-down prior expectations. The activity settles at a low sustained level, consistent with the weaker statistical constraints in the RAN pattern.

In this series of MEG experiments, we investigated how “model establishment” and “interrupt” responses are affected by information rate (by using sequences of identical statistical properties but halving tone-pip length; 25 vs 50 ms) and predictability of pattern transitions.

We examined responses to the following sequence transitions: REG1-REG2 (from one regular to a different regular pattern) REG-RAN (from a regular to a random pattern) REG1-RAN-REG1 (a regular pattern interrupted by a 500ms random pattern followed by the resuming of the original pattern). The probabilities of these transitions were varied to model a range of environmental volatilities. Naive participants performed a decoy task, while listening passively to the sounds.

We report the following key findings:
(1) The detailed dynamics of discovering, abandoning and learning new structure in sound sequences are observable in the MEG signal.
(2) The dynamics of “model establishment” roughly scaled with tone duration but with some evidence of increasing sluggishness with longer tones.
(3) In REG1-RAN-REG1 trials, post interruption model establishment occurred much faster than in REG1-REG2 trials, suggesting that a model of the original sequence was automatically preserved and re-activated.
(4) The “interrupt” response did not differ between high probably and low probability interruptions, suggesting an automatic process that (unlike what is expected from a Bayesian system) is not affected by volatility per se.

Ongoing EEG work comparing such brain responses in human and non-human primates explores how mnemonic systems may have evolved to support pattern sensitivity in humans.

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Signature Maria Chait

Auditory Expectations, Learning and Plasticity

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Topic Auditory Cortex and Thalamus: Structure & Function

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SUBMISSION DETAILS

Session Description The auditory system constantly generates predictions about the sensory world based on prior experience, which creates expectations about upcoming future events. Auditory expectations powerfully shape sensation, perception and cognition, and a theoretical 'predictive coding' framework has advanced in large part from studies in the auditory domain. The expectancy process is thought to be mediated by neural interactions between feedforward and feedback processes all along the auditory pathway, using corticofugal projections from auditory cortex to the periphery, and back. However, until recently it had been unclear how different types of auditory expectations are detected and the role of different stages of the auditory pathway.

This symposium will provide a timely update to address:
• How do auditory expectations form, as an important basis for learning?
• What happens when expectations are not met and the system needs to adapt?
• In disorders that affect the auditory system how are expectancy signals affected?
• Is there plasticity that compensates for impact on the auditory system, and can auditory system impact be remediated?

The symposium will feature presentations from prominent early career and senior scientists, experts in the field of auditory expectancy, learning and plasticity. The presentations will cover a broad range of animal species, including murine models, nonhuman primates and humans. The speakers will showcase the latest neurophysiological approaches possible with each species, ranging from insights at the single neuron levels to mesoscopic and macroscopic studies of the auditory system in humans, including patients with auditory and communication impairments. The presentations will highlight cutting-edge approaches, including circuit-level optogenetic and pharmacological manipulations to identify causal elements involved in auditory expectancy and human intracranial recording and neuroimaging studies. The speakers will also provide insights on

how the auditory field is the leading modality helping to test and advance computational theories on predictive coding.

Presenter Diversity The symposium is gender balanced. The speakers represent five countries and a diversity of backgrounds. Six of the speakers are immigrants to the countries in which they are working.

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Signature Christopher Petkov

Auditory Expectations, Learning and Plasticity

Prediction, Attention, and Memory in the Auditory Cortex

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Ryszard Auksztulewicz

Affiliation European Neuroscience Institute Göttingen

Participant(s) Christopher Petkov (Chair), Maria Geffen (Co-chair), Kerry Walker (Co-chair), Lori Holt (Presenter), Manuel Malmierca (Presenter), Zsuzsanna Kocsis (Presenter), Maria Chait (Presenter), Federico De Martino (Presenter), Maria Geffen (Presenter), Christopher Petkov (Presenter), Ryszard Auksztulewicz (Presenter)

SUBMISSION DETAILS

Individual Abstract The brain is thought to generate internal predictions, based on the memory of past stimulation, to optimise behaviour. However, it is unclear to what extent these predictions are modulated by other top-down factors such as attention and task demands, and whether predictions of different sensory features are mediated by the same neural mechanisms. In this talk I will present results of studies combining human and rodent electrophysiology with computational modelling to identify the neural mechanisms of sensory predictions and their interactions with other cognitive factors. First, in non-invasive studies using MEG/EEG and direct recordings from humans using ECoG, analysis of behavioural and neural data showed that the effects of predictions are not automatic but are modulated by their contextual relevance. Second, computational modelling of the data suggested that these modulations could be linked to specific candidate mechanisms, including gain control in sensory regions. Finally, in a series of studies using invasive recordings in anaesthetised rodents, neural representations related to stimulus memory and predictions could be simultaneously decoded from auditory cortical activity, shedding light on the evolutionary conservation of predictive processing across species.

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Signature Ryszard Auksztulewicz

Auditory Expectations, Learning and Plasticity

Corticofugal Regulation of Predictive Coding

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Maria Geffen

Affiliation University of Pennsylvania School of Medicine

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SUBMISSION DETAILS

Individual Abstract Sensory systems must account for both contextual factors and prior experience to adaptively engage with the dynamic external environment. In the central auditory system, neurons modulate their responses to sounds based on statistical context. These response modulations can be understood through a hierarchical predictive coding lens: responses to repeated stimuli are progressively decreased, in a process known as repetition suppression, whereas unexpected stimuli produce a prediction error signal. Prediction error incrementally increases along the auditory hierarchy from the inferior colliculus (IC) to the auditory cortex (AC), suggesting that these regions may engage in hierarchical predictive coding. A potential substrate for top-down predictive cues is the massive set of descending projections from the AC to subcortical structures, although the role of this system in predictive processing has never been directly assessed. We tested the effect of optogenetic inactivation of the auditory cortico-collicular feedback in awake mice on responses of IC neurons to stimuli designed to test prediction error and repetition suppression. Inactivation of the cortico-collicular pathway led to a decrease in prediction error in IC. Repetition suppression was unaffected by cortico-collicular inactivation, suggesting that this metric may reflect fatigue of bottom-up sensory inputs rather than predictive processing. We also discovered populations of IC units that exhibit repetition enhancement, a sequential increase in firing with stimulus repetition. Cortico-collicular inactivation led to a decrease in repetition enhancement in the central nucleus of IC, suggesting that it is a top-down phenomenon. Negative prediction error, a stronger response to a tone in a predictable rather than unpredictable sequence, was suppressed in shell IC units during cortico-collicular inactivation. These changes in predictive coding metrics arose from bidirectional modulations in the response to the standard and deviant contexts, such that the units in IC responded more similarly to each context in the absence of cortical input. We also investigated how these metrics compare between the anesthetized and awake states by recording from the same units under both conditions. We found that metrics of

predictive coding and deviance detection differ depending on the anesthetic state of the animal, with negative prediction error emerging in the central IC and repetition enhancement and prediction error being more prevalent in the absence of anesthesia. Overall, our results demonstrate that the AC provides cues about the statistical context of sound to subcortical brain regions via direct feedback, regulating processing of both prediction and repetition.

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Signature Maria Geffen

Auditory Expectations, Learning and Plasticity

Precision in Predictive coding: The Role of Neuromodultion in Deviance Detection

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Manuel Malmierca

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SUBMISSION DETAILS

Individual Abstract Behaviour becomes more efficient when we can predict a stimulus. This is the basis of the enormous flexibility underlying interactions with our physical and social environment. Filtering out non-relevant stimuli is an important but understudied aspect of cognition. Today, there is rather universal agreement in neuroscience, that a major function of the brain is to constantly predict the environment on multiple levels and time scales (Friston, 2005), For example, one anticipates how a word of a friend will sound, and when and how a sentence will end, even before it has ended. This proposal is based on the assumption that the brain's neuronal circuitry is organized as a highly predictive machine.

The ability of the brain to recognize which prediction errors carry reliable information is critical in the process of prediction error minimization. For example, if a sensor is malfunctioning because of an impairment (e.g., hearing loss or tinnitus) or because it is operating out of its appropriate physical range, the sensory input it provides is not adequately reporting on real changes in the environment, which may generate misinformative prediction errors. According to the predictive coding theory, this distinction between signal and noise is based on an important element, the so-called precision, which weights the driving power of prediction errors according to how reliable they are estimated to be (Friston, 2005).

Neuromodulatory inputs not only gate plasticity (Martins and Froemke, 2015), but also change the balance of top-down versus bottom-up influence and it well known that neuromodulation strongly impacts sensory processing, learning and memory. 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). Therefore, 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. We have used single neuron recordings and microiontophoresis manipulation of the cholinergic system in the rat brain to study how these neuromodulators shape the predictive responses in cortical and subcortical brain regions in the rat brain

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Auditory Expectations, Learning and Plasticity

Transformations of Auditory Sequences into Neural Expectancy Signals

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Christopher Petkov

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SUBMISSION DETAILS

Individual Abstract There is considerable interest in understanding the neural transformations that occur at every stage in the auditory system. These are no longer thought to be simply feedforward or unidirectional, but rather are better conceived of as bidirectional processes and interactions that occur at every stage in the auditory system and influence sensory processing and expectation. A prime example of a system that efficiently transforms auditory sequences into higher-order structures is the human language system. However, because this system in humans is often thought to be special, the aspects of it that have parallels with the neural systems of other animals remains an open question. In this presentation, we overview work in human and nonhuman primates involving the processing of auditory sequences using statistical learning tasks that generate auditory expectancies. There is now evidence from comparative neuroimaging work that a broad auditory cortical system is involved in processing auditory dependencies separated in time. We also present data from neurophysiological recordings in nonhuman primates and human neurosurgery patients identifying auditory cortical expectancy signals and those that only appear when expectations are not met. This comparative research has generated hypotheses on the key neural transformations and neuronal codes that bind sequentially distributed auditory dependencies in time. We conclude the presentation by showing that there are now closer nonhuman animal parallels to the human auditory and language system, which bodes well for understanding fundamental aspects of it with animal models and more directly informing research with patients that have auditory disorders.

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Signature Christopher Petkov

Auditory Expectations, Learning and Plasticity

Immediate Neural Network Impact and Compensation after the Loss of a Semantic Hub

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Zsuzsanna Kocsis

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SUBMISSION DETAILS

Individual Abstract The human brain extracts meaning from the world using an extensive neural system for semantic knowledge. Whether such broadly distributed systems crucially depend on or can compensate for the loss of one of their highly interconnected hubs is controversial. The strongest level of causal evidence for the role of a brain hub is to evaluate its acute network-level impact following disconnection and any rapid functional compensation that ensues. We report rare neurophysiological data from two patients who underwent awake intracranial recordings during a speech prediction task immediately before and after neurosurgical treatment that required disconnection of the left anterior temporal lobe (ATL), a crucial hub for semantic knowledge. Informed by a predictive coding framework, we tested three sets of hypotheses including diaschisis causing disruption in interconnected sites and incomplete or complete compensation by other language-critical and speech processing sites. Immediately after ATL disconnection, we observed highly specific neurophysiological alterations in the recorded fronto-temporal network, including abnormally magnified high gamma responses to the speech sounds in auditory cortex. We also observed evidence for rapid compensation, seen as focal increases in effective connectivity involving language-critical sites in the inferior frontal gyrus and speech processing sites in auditory cortex. However, compensation was incomplete, in part because after ATL disconnection speech prediction signals were depleted in auditory cortex. This study provides direct causal evidence for a semantic hub in the human brain and shows striking neural impact and a rapid attempt at compensation in a neural network after the loss of one of its hubs.

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Signature Zsuzsanna Kocsis

Auditory Expectations, Learning and Plasticity

Laminar and High Spatial Resolution fMRI of Human Auditory Predictive Processing.

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Federico De Martino

Affiliation Maastricht University

Participant(s) Christopher Petkov (Chair), Maria Geffen (Co-chair), Kerry Walker (Co-chair), Lori Holt (Presenter), Manuel Malmierca (Presenter), Zsuzsanna Kocsis (Presenter), Maria Chait (Presenter), Federico De Martino (Presenter), Maria Geffen (Presenter), Christopher Petkov (Presenter), Ryszard Auksztulewicz (Presenter)

SUBMISSION DETAILS

Individual Abstract To deal with dynamic changes in the soundscape and adjust our behaviour accordingly, a key function of our brain is to predict future states of the world. This has led to a transformative way of thinking about brain function. That is, what we perceive does not reflect the sensory stimulus itself, but rather a combination of the stimulus and an internal (generative) model of its causes. This idea has led to several theoretical advances some of which are capitalized by Predictive Coding (PC). PC assumes that generative models are formed through the exchange of prediction errors (feedforward) and predictions (feedback) across hierarchical processing stages. In addition, PC assumes that prediction errors are modulated by the precision of currently available predictions. Results from invasive animal and human electrophysiological studies support the relevance of predictions for neural processing at different hierarchical levels. Nevertheless, especially in humans the evidence grounding PC principles onto fundamental neurocomputational units (i.e. cortical layers, subdivisions of subcortical structures) is limited and this hampers our understanding of how PC supports the processing of sounds in context in the human brain. Ultra-high field fMRI at high spatial resolution offers a unique opportunity to investigate how computations are embedded in the mesoscopic (cortical) architecture of the human brain (in vivo and non-invasively). Laminar fMRI has already been used to investigate predictive processes in the human visual cortex. In this talk I will describe recent results from studies investigating how predictions and prediction errors are processed in auditory cortical layers. We combine ultra-high field fMRI with biophysical and computational approaches to gain further insights into the computations underlying these responses.

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Signature Federico De Martino

Auditory Expectations, Learning and Plasticity

Category Learning and Dimension-Selective Attention in Auditory Cortex

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Lori Holt

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SUBMISSION DETAILS

Individual Abstract Human listeners possess rich category representations for speech sounds and words. Yet speech input exhibits complexity across multiple acoustic dimensions, and short-term speech input regularities may not match long-term norms (as in foreign accents). Theoretical accounts of speech perception often have appealed to selective attention as a means by which to balance these demands. However, we do not yet understand how – and whether - listeners learn to selectively attend to informative acoustic dimensions during category learning, how selective attention impacts cortical representations of relevant dimensions, and whether selective attention involves suppression of irrelevant dimensions as well as enhancement of relevant dimensions.

We are examining these questions using novel non-speech auditory categories. Participants complete five days of stimulus-response-feedback training during which they learn four nonspeech categories to criterion. The categories are structured to require listeners to learn acoustic patterns positioned in either a high- or low-frequency band, with simultaneous irrelevant acoustic patterns in the opposite band. Thus, category learning requires reliance on – and perhaps selective attention to – the category-diagnostic acoustic patterns. Control trials involve categorization across an orthogonal dimension, stimulus amplitude ('big' or 'small' Category A). In a single post-training MRI session, listeners categorize sounds in a 2AFC task with categories differentiated by information in either high or low spectral bands, or on relative amplitude. Combined with tonotopic mapping and "attention-o-tonotopic" mapping driven by overt endogenous attention to high and low frequency bands, we examine how dimension-selective attention driven by implicit demands of categorization impact cortical activation.

This work illuminates the cortical mechanisms supporting dimension-based auditory selective

attention, providing a bridge to compare explicitly directed attention (i.e., “listen high”) and selective attention that emerges with learning. Comparison with our control (amplitude) condition allows for assessment of a putative role for suppression. Finally, the study links human studies with non-human animal studies of frequency-selective auditory attention with non-speech stimuli.

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Signature Lori L Holt

Auditory Expectations, Learning and Plasticity

Neural Mechanisms for Tracking Uncertainty in Rapidly Unfolding Sound Sequences.

Submission ID 3003150

Submission Type Symposia

Topic Auditory Cortex and Thalamus: Structure & Function

Status Submitted

Submitter Maria Chait

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SUBMISSION DETAILS

Individual Abstract The brain maintains a hierarchy of models to monitor the statistics of its surroundings and inform behaviour. Determining how such models are instantiated and updated is key to understanding the brain as a statistical learning machine.

The auditory system, supported by a network of auditory, hippocampal, and frontal sources, automatically discovers regularities in rapid tone sequences even when these are not behaviourally relevant. We have previously identified specific brain signatures of sequence structure tracking in humans. The transition from a random tone pattern to a structured pattern (RAN-REG) elicits a slow increase in tonic activity that is consistent with gradual evidence accumulation and instantiation of a new model. In contrast, the opposite transition (REG-RAN) evokes an ‘interrupt’ response’: a sharp drop in sustained activity, hypothesized to reflect immediate suppression of top-down prior expectations. The activity settles at a low sustained level, consistent with the weaker statistical constraints in the RAN pattern.

In this series of MEG experiments, we investigated how “model establishment” and “interrupt” responses are affected by information rate (by using sequences of identical statistical properties but halving tone-pip length; 25 vs 50 ms) and predictability of pattern transitions.

We examined responses to the following sequence transitions: REG1-REG2 (from one regular to a different regular pattern) REG-RAN (from a regular to a random pattern) REG1-RAN-REG1 (a regular pattern interrupted by a 500ms random pattern followed by the resuming of the original pattern). The probabilities of these transitions were varied to model a range of environmental volatilities. Naive participants performed a decoy task, while listening passively to the sounds.

We report the following key findings:
(1) The detailed dynamics of discovering, abandoning and learning new structure in sound sequences are observable in the MEG signal.
(2) The dynamics of “model establishment” roughly scaled with tone duration but with some evidence of increasing sluggishness with longer tones.
(3) In REG1-RAN-REG1 trials, post interruption model establishment occurred much faster than in REG1-REG2 trials, suggesting that a model of the original sequence was automatically preserved and re-activated.
(4) The “interrupt” response did not differ between high probably and low probability interruptions, suggesting an automatic process that (unlike what is expected from a Bayesian system) is not affected by volatility per se.

Ongoing EEG work comparing such brain responses in human and non-human primates explores how mnemonic systems may have evolved to support pattern sensitivity in humans.

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