Evolution of Emotional Communication: From Sounds in Nonhuman Mammals to Speech and Music in Man

April 28<sup>th</sup> – May 1<sup>st</sup>, 2010

Reisensburg

Günzburg, Germany
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University of Veterinary Medicine Hannover
Bünteweg 17
30559 Hannover
Germany
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Table of Contents

Welcome Note ...................................................................................................................... 5
Sponsors ............................................................................................................................... 6
Scientific Program ............................................................................................................... 7
Poster Presentations ........................................................................................................... 9
Abstracts of Talks ............................................................................................................... 10
Abstracts of Posters ............................................................................................................ 20
List of Participants ............................................................................................................ 28
General Information ......................................................................................................... 29
Notes ................................................................................................................................. 30
Map ................................................................................................................................. 36

Local organisers:
Sönke von den Berg, Dr. Michael Großbach, Ursula Seifert, Prof. Dr. Günter Ehret

Scientific committee:
Prof. Dr. Elke Zimmermann, Prof. Dr. Eckart Altenmüller

Technical support:
Sönke von den Berg, Dr. Michael Großbach
Welcome Note

Dear participants,

a hearty welcome to our interdisciplinary symposium on the Evolution of Emotional Communication.

This interdisciplinary symposium provides a framework for discussing ongoing research in the field of behavioural, cognitive and evolutionary neurosciences. It aims at deepening our understanding of shared and unique principles important to reconstruct evolutionary pathways for emotional communication in the acoustic domain.

We are looking forward to a stimulating conference and wish you all a pleasant stay at the Reisensburg.

Elke Zimmermann
Eckart Altenmüller
Sponsors
Scientific Program

Thursday, April 29th

08:00  Registration
08:45  Welcome address (G. Ehret, E. Zimmermann and E. Altenmüller)

**Evolution of emotional communication in the acoustic domain: comparative insights from different mammalian groups** (Chair: R. Kopiez and D. Wildgruber)

09:00  Emotional vocalizing and auditory perception in house mice (G. Ehret)
09:30  Vocalisations as indicators of emotional states in rats and cats (S.M. Brudzynski)
10:00  Emotional communication in bats (S. Schmidt)
10:30  Coffee/tea break
11:00  The vocal expression of emotional intensity and quality in African elephants (J. Soltis)
11:30  Toward the biological roots of affective prosody in human speech and music: universal affect cues in vocal communication across mammals (E. Zimmermann, L.M.C. Leliveld and S. Schehka)
12:00  Lunch

**Evolution of laughter** (Chair: G. Ehret)

14:00  Reconstructing the evolution of laughter in great apes and humans (M. Davila Ross, M.J. Owren and E. Zimmermann)
14:30  Evolution of smiling and laughter in apes, hominins, and humans (M.J. Owren)
15:00  Encoding and decoding of different types of laughter - evidence from acoustics, behaviour and fMRI' (D. Szameitat, K. Alter and D. Wildgruber)
15:30  Coffee/tea break and poster presentation

**Evening lecture** (Chair: S. Schmidt)

17:30  Is frog vocal communication emotional? (P.M. Narins)
19:00  Dinner
Friday, April 30th

Evolution of emotional speech processing (Chair: R. Dengler and S. Koelsch)

09:00  Non-verbal emotional vocalisations across cultures (D.A. Sauter)
09:30  Understanding social, cognitive, and neural dimensions of vocal emotion processing (M.D. Pell)
10:00  Reflections on an orbitofronto-striatal interface in emotion processing (S.A. Kotz)
10:30  Coffee/tea break
11:00  Emotional speech in basal ganglia disorders (C. Schröder, M. Wittfoth and R. Dengler)
12:00  Lunch

Evolution of music (Chair: S.A. Kotz and K. Alter)

14:00  The co-evolution of music, culture, and cooperation (S. Kirschner)
14:30  When meaning sounds: how environmental sounds and music affect conceptual word processing (M. Kiefer)
15:00  Music and Emotions: Is the chill-effect a useful research tool? (E. Altenmüller, R. Kopiez, O. Grewe, F. Nagel and H. Egermann)
15:30  Coffee/tea break
16:00  Neural correlates of music-evoked emotions (S. Koelsch)
16:30  Musical invasion of vocal emotion circuits of the brain (I. Peretz)
17:00  Concluding remarks (E. Altenmüller and E. Zimmermann)
19:00  Dinner
## Poster presentations

**Friday, April 30th**

1. **Anticipation of food reward and 50 kHz ultrasonic vocalisations in rats**  
   *J.C. Brenes and R.K.W. Schwarting*

2. **Strain and sex differences in rat motivation-related ultrasonic vocalizations**  
   *C. Natusch and R.K.W. Schwarting*

3. **Brain activation for maternal auditory perception of pup calls in virgin female mice: Auditory system**  
   *D.B. Geissler, C. Schmid and G. Ehret*

4. **Brain activation for maternal auditory perception of pup calls in virgin female mice: Limbic system**  
   *C. Schmid, D.B. Geissler and G. Ehret*

5. **Impact of immobilization stress on the behaviour and stress hormone level in the Short-tailed fruit bat, *Carollia perspicillata***  
   *S. Ammersdörfer and K.-H. Esser*

6. **The psychophysiology of listening to conspecifics? Insights from a bat model**  
   *M. Göpfert, S. Ammersdörfer and K.-H. Esser*

7. **Do bats evaluate the affective state, and individuality, in communication calls?**  
   *H. Kastein, A.K.V. Kumar, S. Kandula and S. Schmidt*

8. **Affect cues in communication calls of tree shrews.**  
   *J. Brunke, S. Schehka and E. Zimmermann*

9. **Acoustic recognition of familiarity linked to emotional state in a nocturnal primate**  
   *L.M.C. Leliveld and E. Zimmermann*

10. **Do phylogeny and/or familiarity influence cross-taxon perception of acoustically conveyed emotions in human listeners?**  
    *M. Scheumann, A. Hasting, S.A. Kotz and E. Zimmermann*

11. **The valence of emotional animal vocalisations modulates electrophysiological correlates of the human orienting response**  
    *A.S. Hasting, M. Scheumann, E. Zimmermann and S.A. Kotz*

12. **Emotional prosody perception in patients with lesions in the basal ganglia: Perceptual impairments can be linked to different processing stages**  
    *S. Paulmann, M.D. Pell and S.A. Kotz*
Abstracts of Talks

Thursday, April 29th

Emotional vocalizing and auditory perception in house mice

G. Ehret
Institute of Neurobiology, University of Ulm, Ulm, Germany
Email: guenter.ehret@uni-ulm.de

The mouse vocal repertoire consists of 8 types of vocalisations with distinct properties in the spectral and temporal domain and in call intensity (Ehret, 2006, in Kanwal & Ehret, Behavior and Neurodynamics for Auditory Communication, OUP, 85-114). Among them are pure tonal ultrasounds of pups and adults, low-frequency sounds of pups (wriggling calls, smacking sounds) and broadband sounds of pups (distress call, birth cry) and adults (distress call, defensive call of females). The behavioural contexts of vocalizing lead to estimates of callers’ emotional backgrounds which are well represented by acoustic properties of the sounds: (1) Distress and hostility as negative emotions are expressed by loud, long, often noisy sounds with broad frequency spectra (many harmonics, noise) covering most of the mouse hearing range; (2) fear in young animals and confusion and submissiveness in adults is expressed by frequency-modulated tonal ultrasonic whistles; (3) comfort or comfort expectation is expressed by soft, harmonically structured low-frequency calls or series of low-frequency clicks. Call structures conform in part to Morton’s motivation-structural rules (Amer Nat 111, 855-869, 1977) complemented by August & Anderson (J Mammal 68, 1-9, 1987). They are not changed in mice heterozygous for a Foxp2 mutation leading to severe speech production deficits in humans (Gaub et al., GBB in press, 2010). The perception and classification of these calls by mechanisms of the auditory system happens in mice according to three basic (emotional) meanings – attraction, aversion, cohesion – which can be generalised to perception of communication calls in other mammals (Ehret, 2006, see above).

Vocalisations as indicators of emotional states in rats and cats

S.M. Brudzynski
Department of Psychology, Brock University, St.Catharines, Ontario, Canada
Email: sbrudzyn@brocku.ca

Two ascending mesolimbic tegmental systems are involved in the initiation and maintenance of two basic emotional states. The ascending cholinergic system can initiate a negative state with accompanying autonomic and somatic symptoms, and the ascending dopaminergic system can initiate a positive state also with characteristic physiological changes. These organismal states, including the relevant emotional states are signalled by vocalization to conspecifics. Emission of the state-characteristic vocalization has adaptive value for individuals living in social groups. As shown for cats and rats, negative, alarming/threatening vocalisations are initiated by release of acetylcholine in the medial cholinceptive vocalization strip. These vocalisations are characterised by a low and relatively constant sound frequency,
long duration of individual calls, and repeatable pattern of their emission. Positive, appetitive calls are initiated by release of dopamine in the shell of the nucleus accumbens, and at least in rats, are characterised by high sound frequency with modulated frequency and short duration of individual calls. They are usually emitted in high numbers and in rapid succession of one after another. A common neural substrate, congruent valence, and similarities in some general acoustic features of these vocalisations in cats and rats suggest a high degree of homology of these systems across species. Finally, high repeatability of relevant acoustic features of positive and negative vocalisations makes them useful as indices of animal emotional states.

**Emotion-related acoustic communication in bats**

*S. Schmidt*

Institute of Zoology, University of Veterinary Medicine Hannover, Hannover, Germany

Email: sabine.schmidt@tiho-hannover.de

Some features of emotional prosody in human speech may be rooted in mechanisms common to mammals.

We studied call production, and perception, during social interactions in bats, a highly vocal group evolutionarily remote from primates. The present paper focuses on acoustic communication during agonistic encounters in the Indian False Vampire bat. Three call types with distinct time-frequency contours occurred, aggression calls, whistles and response calls.

In a first experiment, agonistic approach situations were analyzed to assess the extent to which these call types reflected the specific part of the caller in the interaction, and the intensity of the agonistic display. A frame-by-frame video analysis followed by a sound analysis revealed that call type indicated the part of the respective caller while interaction intensity was encoded in similar parameter changes across call types. The systematic change of vocal parameters with affect intensity corresponded to prosodic changes in human speech. A series of playback experiments based on a habituation-dishabituation paradigm investigated how the bats categorized the vocalisations emitted during third-party interactions. Stimuli comprised vocalisations from agonistic versus affiliative interactions, the different call types used in agonistic interactions, and calls of a given type from different interaction intensities. The bats were able to discriminate between interaction types, call types and interaction intensities within a call type. However, they did not necessarily form categories corresponding to call type and interaction intensity within call type in reciprocal experiments, an evidence for a context-dependent evaluation of social calls.

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**The vocal expression of emotional intensity and quality in African elephants**

*J. Soltis*

Education and Science, Disney's Animal Kingdom, Bay Lake, Florida, USA

Email: Joseph.Soltis@disney.com

The vocal expression of emotion in mammals has been largely confined to primates and domesticated animals. Recently, however, the investigation of emotional expression in the voice has grown to include a broader array of mammals.
This report examines the vocal expression of emotion in the African elephant (*Loxodonta africana*), the largest terrestrial mammal. Despite its unique vocal production anatomy, including an external and flexible trunk, the African elephant vocal expression of emotion is similar to other mammals. In conditions of arousal or distress, African elephant “rumble” vocalisations exhibit increased and more variable fundamental frequencies, and increased amplitudes and durations, compared to periods of relative calm. It is unclear at this point, however, if such acoustic responses are due to changes in emotional intensity (low to high) or changes in emotional quality (positive to negative), or both. This presentation provides preliminary evidence related to the expression of positive emotion in the voiced sounds of elephants, highlighting the methodological issues surrounding the measurement of emotions in animal sounds.

**Toward the biological roots of affective prosody in human speech and music: universal affect cues in vocal communication across mammals**

E. Zimmermann, L.M.C. Leliveld and S. Schehka
Institute of Zoology, University of Veterinary Medicine Hannover, Hannover, Germany
Email: Elke.Zimmermann@tiho-hannover.de

For human acoustic communication, recent findings suggest that some basic emotions are universally expressed and recognised across different cultures. Shared acoustic cues in affective prosody were postulated to code for the respective quality and intensity of an emotion favouring the hypothesis that these universals may have derived from a prehuman basis.

In this talk, we will explore this “prehuman origin hypothesis of affective prosody” by a comparative approach on nonhuman mammals focusing on a specific component of affective prosody, the affect intensity. We assessed affect intensity in nonhuman mammals on the behavioural level. Based on our own work and an extensive literature review, we extracted four general contexts for which we compared empirical data on the expression of acoustically conveyed affect intensity/arousal states across studied taxonomic orders of mammals (Primates, Scandentia, Chiroptera, Rodentia, Carnivora, Artiodactyla, Proboscidea, Cetacea), diverging largely in size, ecological niches and social systems.

It was furthermore investigated whether the acoustically conveyed affect intensity is biologically relevant. Comparative data revealed that across contexts, affect intensity was coded in comparable acoustic features. For studied mammalian orders, acoustically conveyed affect/arousal states were of significant relevance for listeners. All in all cross-taxa findings on nonhuman mammals support the hypothesis that some acoustic features of the intensity component of affective prosody in human speech and music have deep-reaching phylogenetic roots, deriving from precursors already present and relevant in the vocal communication system of nonhuman mammals.
Reconstructing the evolution of laughter in great apes and humans

M. Davila Ross\textsuperscript{1}, M.J. Owren\textsuperscript{2} and E. Zimmermann\textsuperscript{3}
\textsuperscript{1}Psychology Department, University of Portsmouth, Portsmouth, UK
\textsuperscript{2}Department of Psychology, Georgia State University, Atlanta, Georgia, USA
\textsuperscript{3}Institute of Zoology, University of Veterinary Medicine Hannover, Hannover, Germany
Email: Marina.Davila-Ross@port.ac.uk

It has long been argued that human laughter has its origin in ancestral nonhuman primate displays.
The goal of the present work was to test this hypothesis by applying acoustic and phylogenetic methods based on acoustics of tickle-induced vocalisations from all four extant great apes and tickle-induced laughter of human infants. Acoustic outcomes revealed both important similarities and differences among the species, while the phylogenetic trees reconstructed from the acoustic data matched the well-established genetic topology of the Hominidae. In sum, the current study provides strong evidence that tickle-induced laughter is homologous in great apes and humans. Observations made on the use of laughter in great apes and humans further suggest a strong link between the form and function of laughter across the species. We predict that there were two main kinds of selection-driven evolutionary change in laughter within the past 10 to 16 million years, to a smaller degree, among the apes and, most distinctively, after the separation of hominins from the last common ancestor with chimpanzees and bonobos.

The evolution of smiling and laughter in apes, hominins, and humans

M.J. Owren
Department of Psychology, Georgia State University, Atlanta, Georgia, USA
Email: owren@gsu.edu

Human smiling and laughter is believed to have evolved from less elaborated emotional expressions present in ancestral nonhuman primates. However, much remains to be learned about how and why these signals emerged. One important clue is that smiling and laughter each occur in both emotion-dependent and emotion-independent versions. Furthermore, these two forms are traceable to subcortical versus cortical neural pathways, respectively.
The current work presents a evolutionary model of smiling and laughter to explain these and other critical characteristics of these signals. Smiling is proposed to have evolved first, initially appearing in a spontaneous, emotion-dependent form that functioned to facilitate emotional bonds and concomitant cooperative behaviour among genetically unrelated individuals. However, the very success of this reliable version inherently created an advantage for signalers who could smile in a strategic, emotion-independent fashion, thereby producing selection pressure for increased volitional and cortically based control over facial musculature. Devaluation of smiling as a reliable indicator of signaler affect in turn set the stage for elaboration of emotion-dependent laughter, when then created selection pressure for a volitional, emotion-independent version. The result was increased volitional control over the larynx, which created unprecedented, new opportunities for hominin vocal signaling and fundamentally changing the course of human evolution. While speculative, this model is consistent with key evidence from physiological, developmental, functional, and phylogenetic levels of analysis, as well as with basic principles of evolution and communication.
Encoding and decoding of different types of laughter – evidence from acoustics, behaviour and fMRI

D. Szameitat¹, K. Alter² and D. Wildgruber¹
¹Department of Psychiatry, University of Tübingen, Tübingen, Germany
²Institute of Neuroscience, Newcastle University, Newcastle, UK
Email: dirk.wildgruber@med.uni-tuebingen.de

Laughter is highly relevant for social interaction. In humans as well as in non-human primates laughter can be induced by tickling. Human laughter, however, has diversified and encompasses emotional laughter types with various communicative functions, e.g. joy and taunt.

We investigated if listeners are able to decode the sender’s emotional state from auditory presented laughter samples without contextual knowledge. Discrimination of laughter type (joy, taunt, tickling, Schadenfreude) and judgement along three emotional dimensions (arousal, valence, dominance) was evaluated. Furthermore, it was analysed if distinct laughter types can be differentiated by their acoustical properties. The results showed that laughter can be differentiated at behavioural level and at the level of acoustic properties.

Moreover, it was unravelled how the diversification of ecological functions is associated with distinct cerebral responses underlying laughter perception. Functional MRI revealed a double-dissociation of cerebral responses during perception of tickling laughter and emotional laughter (joy and taunt) with higher activations in the anterior rostral medial frontal cortex (arMFC) when emotional laughter was perceived, and stronger responses in the right superior temporal gyrus (STG) during appreciation of tickling laughter. Responses within the arMFC presumably reflect increasing demands on social cognition induced by the greater social salience of the emotional laughter types. Enhanced activation of the STG for tickling laughter may be linked to its higher acoustic complexity. These findings support the postulated diversification of human laughter in the course of evolution from an unequivocal play signal to laughter with distinct emotional contents subserving complex social functions.

Is frog vocal communication emotional?

P.M. Narins
Departments of Physiological Science, and Ecology & Evolutionary Biology, UCLA, Los Angeles, California, USA
Email: pnarins@ucla.edu

Animal vocal communication occurs when a sound signal generated by one individual is transmitted through an appropriate channel and results in a behavioural change in a second individual.

In this lecture, I will review two studies that may involve emotional communication in frogs, including: (1) Cross-modal integration as the basis for understanding agonistic behaviour in territorial dart-poison frogs, *Allobates femoralis*. We used an electromechanical model frog to present territorial males with visual and auditory cues separated by experimentally-introduced temporal delays or spatial disparities to probe temporal and spatial integration in this animal. Aggressive (and presumably emotional) behaviour was evoked only with the confluence of auditory and visual cues in this animal. Our results demonstrate that temporal and spatial integration may be reliably estimated in a freely-behaving frog; and (2) Generation of vocal
nonlinearities may be individual specific, and may signal emotional content of the sender. We have provided the first evidence in amphibians of ultrasonic (US) communication coupled with vocalisations containing highly nonlinear phenomena (NLP), including subharmonics, biphonation, fast frequency transitions, chaotic regimes, etc. This extraordinary upward extension into the ultrasonic range of both the advertisement calls and the frog’s hearing sensitivity has likely coevolved in response to the intense ambient noise from local streams. Vocalisations containing NLP are highly variable from one utterance to the next, and therefore may serve as a substrate for individual recognition as well as an adaption against habituation. Examples from several amphibian species will be discussed. Supported by NIH, UCLA and the Veneklasen Foundation.

Friday, April 30th

Non-verbal emotional vocalizations across cultures

D.A. Sauter$^{1,2}$

$^1$Department of Psychology, University College London, London, UK

$^2$Max Planck Institute for Psycholinguistics, Nijmegen, The Netherlands

Email: disa.sauter@mpi.nl

Despite differences in language, culture, and ecology, some human characteristics are similar in people all over the world, while other features vary from one group to the next. These similarities and differences can inform arguments about what aspects of the human mind are part of our shared biological heritage and which are predominantly products of culture and language.

I will present data from a cross-cultural project investigating the recognition of non-verbal vocalizations of emotions, such as screams and laughs, across two highly different cultural groups. English participants were compared to individuals from remote, culturally isolated Namibian villages. Vocalizations communicating the so-called “basic emotions” (anger, disgust, fear, joy, sadness, and surprise) were bidirectionally recognised. In contrast, a set of additional positive emotions was only recognised within, but not across, cultural boundaries. These results indicate that a number of primarily negative emotions are associated with vocalizations that can be recognised across cultures, while at least some positive emotions are communicated with culture-specific signals. I will discuss these findings in the context of accounts of emotions at differing levels of analysis, with an emphasis on the often-neglected positive emotions.
Understanding social, cognitive, and neural dimensions of vocal emotion processing

M.D. Pell
School of Communication Sciences and Disorders, McGill University, Montreal, Quebec, Canada
Email: marc.pell@mcgill.ca

Significant gains have been made in how we describe the neuro-cognitive apparatus for recognizing vocal emotion expressions in speech. But how do we characterise the mental representations activated by vocal emotion cues, and what do we know about the time course of these processes? Our knowledge in these areas is still rudimentary, although describing the cognitive processing structure of vocal emotion recognition more clearly would facilitate descriptions of the neural architecture involved. Here, I will discuss new studies that look at how and when underlying meanings of vocal emotion expressions are “recognised” (both implicitly and explicitly), with implications for how acoustic information in speech is represented in emotional memory. Based on implicit processing tasks (priming, ERPs, eyetracking), results demonstrate that vocal emotion meanings are activated automatically and in an emotion-specific manner; converging data suggest that discrete emotional meanings in the voice are implicitly registered and differentiated in the 300-400 ms time window. When explicit emotion processing tasks are presented (forced-choice paradigm), findings again argue that vocal emotions are processed according to their discrete meanings. However, the time course for conscious recognition varies significantly by emotional expression type; following a gating study, we observed that fear, sadness, and anger were recognised most quickly (500-700 ms), whereas happiness and disgust were recognised much slower (1000-1500 ms).

Together, our research suggests that vocal expressions of basic emotion quickly and automatically activate emotion-specific concepts in memory, although the ability to consciously retrieve and evaluate this information varies significantly by emotion type.

Reflections on an orbitofronto-striatal interface in emotion processing

S.A. Kotz
IRG Neurocognition of Rhythm in Communication, Max Plank Institute for Human Cognitive and Brain Sciences, Leipzig, Germany
Email: kotz@cbs.mpg.de

Both the orbito-frontal cortex (OFC) and the basal ganglia (BG) have been implicated in the processing of vocal emotion expressions. We suggest that the two structures may interface during the integration of verbal and non-verbal vocal emotion expressions during late, cognitive processing stages as evidenced by recent event-related brain potential (ERP) and behavioural patient evidence. In accordance with our recent network model on emotional speech processing (Schirmer and Kotz, 2006), we propose that the BG and the OFC are involved in the integration and evaluation of vocal emotion expressions. However, I will discuss recent evidence that the OFC is functionally differentiated and may thus respond to emotion expressions during early automatic and late controlled, evaluative processing stages. Which processing stages the OFC responds to may critically hinge on the nature of stimulus and task type. In a similar fashion, the role of the BG will be discussed.
Evolution of Emotional Communication: From Sounds in Nonhuman Mammals to Speech and Music in Man

Emotional speech in basal ganglia disorders

C. Schröder, M. Wittfoth and R. Dengler
Department of Neurology, Medical School Hannover, Hannover, Germany
Email: Schroeder.Christine@mh-hannover.de

Even though the mesocortical dopamine system is known to play an important role in affect control and reward related behaviour, only little is known about the impact of basal ganglia disorders on emotional communication. The ability to perceive and express emotions via speech plays an essential role in everyday social life. Here, studies investigating perception and production of emotional prosody in basal ganglia disorders like Parkinson’s disease and primary focal dystonia will be reviewed and own results will be presented. Evidence will be provided that patients with basal ganglia disorders may have changes of emotional prosody processing and show alterations of emotional speech production. Together, these studies highlight the importance of the basal ganglia and their connections for emotional communication.

The co-evolution of music, culture, and cooperation

S. Kirschner
Department of Developmental and Comparative Psychology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany
Email: kirschner@eva.mpg.de

Humans are the only primates that make music, often causing strong emotional reactions in performers and listeners. Although gorillas and chimpanzees also use vocalizations and drumming gestures to express their emotional state, there are several unique aspects of human music, the origins of which require explanation. Given that in traditional cultures music making and dancing are often collective actions, integrated in important group ceremonies such as initiation rites, weddings, or preparations for battle, one hypothesis is that our human ancestors invented music as a tool for supporting group cohesion and ultimately increasing prosocial in-group behaviour.

During my talk I will first illustrate why this hypothesis is well suited to explain the strong connection between music and emotions in modern humans, before presenting a series of empirical studies that tested different predictions derived from this group cohesion scenario. In the first study we showed that preschool children spontaneously synchronise their body movements to an external beat at earlier ages and with higher accuracy if the stimulus is presented in the social context of joint drumming. The second study was designed as a follow-up to compare the influence of German and Brazilian culture on the early development of such synchronization skills. In the third study we showed that joint music making promotes subsequent cooperative and helpful behaviour among four-year-old children. Finally, if there is time left, I will mention some ongoing comparative research on rhythmic synchronization in dolphins and on the cohesive effects of music vs. religion.
When meaning sounds: how environmental sounds and music affect conceptual word processing

M. Kiefer
Department of Psychiatry, University of Ulm, Ulm, Germany
Email: markus.kiefer@uni-ulm.de

Recent models of embodied cognition propose that interactions with the environment form their conceptual memory traces in distributed modality-specific brain areas, which typically process sensory or action-related information. In support of this embodiment view, neuroimaging studies have demonstrated that conceptual word or picture processing engages brain areas typically involved in perception and action.

In generalizing the view of embodied concepts, we demonstrated close links between conceptual representations of sound information and the auditory perceptual system: Conceptual processing of words referring to objects, for which sound information is highly relevant (e.g., bell or telephone), activated auditory brain areas (pSTG/MTG), which were also activated by listening to real sounds. Importantly, activity within this area increased selectively as a function of the relevance of acoustic object information. This shows that access to conceptual sound information involves a partial reinstatement of brain activity during the perception of objects. The links between conceptual and auditory brain systems strongly depend on concrete sensory sound experience. The intensive experience of musicians was used to locate neuroplastic changes in conceptual representations of musical instruments. Visual recognition of musical instruments during a picture-word matching task automatically activated auditory areas only in professional musicians, but not in musical laypersons. These areas in auditory association cortex were also recruited by auditory perception of real sounds. This evidence demonstrates that experience-driven neuroplasticity in professional musicians is not confined to the alteration of perceptual and motor maps, but even affects the higher-level functional reorganization of semantic maps embodied in auditory cortex.

Music and emotions: is the chill-effect a useful research tool?

E. Altenmüller¹, R. Kopiez², O. Grewe¹, F. Nagel¹ and H. Egermann¹
¹Institute of Music Physiology andMusicians’ Medicine (IMMM)
²Institute of Research in Music Education (IfMPF)/Hanover Music Lab (HML)
University of Music and Drama, Hannover, Germany
Email: altenmueller@hmt-hannover.de

Although music is generally acknowledged as a powerful tool for eliciting emotions, little is known concerning the neurobiological basis of these emotions. We investigated the psychological and neurobiological basis of strong emotional responses to music (SEM), leading to shivers down the spine.

In order to observe distinct acoustical and music-structural elements related to chill reactions, in a series of experiments, on-line emotional self-report was obtained while participants were listening to music inducing strong emotions. During the experiment psychophysiological measures were taken and after each piece of music, subjects filled in personality scales and questionnaires regarding their knowledge and recalls connected to the music.

Despite of highly individual emotional reactions towards music, some inter-individually constant characteristics of music eliciting chill responses could be found. Chills were much more frequent in previously known music and in familiar music styles. Furthermore, distinct musical events frequently caused strong emotional responses, especially when violating
expectancies. Interestingly, when listening in a group setting, chill responses were less frequent than when listening alone. These results demonstrate that strong emotional responses are not only related to the psychoacoustic properties of the respective pieces of music, but furthermore to biographical memories, personality traits and social environments. Therefore, a simple stimulus-response type of reaction cannot be assumed and strong emotional responses seem to be primarily linked to the individual’s listening biography and evocation of its associative networks and memory traces. The regular and measurable occurrence of a simple physiological phenomenon (chills) during complex individual emotional episodes could be used as an objective indicator, and thus be one approach for a deeper understanding of human emotions.

**Neural correlates of music-evoked emotions**

*S. Koelsch*
Cluster of Excellence "Languages of Emotion", Freie Universität Berlin, Berlin, Germany
Email: koelsch@cbs.mpg.de

Music is capable of evoking exceptionally strong emotions and of reliably affecting the mood of individuals. This talk reviews functional neuroimaging and lesion studies showing that music-evoked emotions involve virtually all limbic and paralimbic brain structures. These structures are crucially involved in the initiation, generation, detection, maintenance, regulation, and termination of emotions that have survival value for the individual and the species. Therefore, at least some music-evoked emotions involve the very core of evolutionarily adaptive neuro-affective mechanisms. Because dysfunctions in these structures are related to emotional disorders, a better understanding of music-evoked emotions and their neural correlates can lead to a more systematic and effective use of music in therapy.

**Musical invasion of vocal emotion circuitries of the brain**

*I. Peretz*
BRAMS, Psychology, University of Montreal, Quebec, Canada
Email: Isabelle.Peretz@umontreal.ca

Musical emotions resemble other important classes of emotions in being universal, immediate and consistent from an early age. One possibility is that music is particularly suited (or designed) to invade or co-opt emotion circuits that have evolved for biologically important sounds. One likely emotional system for neural invasion (or “neural recycling”, to adopt the terminology of Dehaene & Cohen, Neuron, 2007) is the system dealing with emotional vocalisations, such as laughs, screams and prosody. Communication among humans (and animals) is often carried out using acoustical signals, whose affective value might be genetically transmitted and supported by specialized brain emotion circuits. Musical emotions might invade these evolved circuits for vocal emotions and adjust them for its particularities. If so, the study of musical emotions might benefit from what has been learned about these other emotions. Brain organisation for vocal emotions could constrain brain organisation for musical emotions. I will review and present new evidence in support of common brain organisation for vocal and musical emotions.
Impact of immobilization stress on the behaviour and stress hormone level in the Short-tailed fruit bat, *Carollia perspicillata*

S. Ammersdörfer\(^1,2\), and K.-H. Esser\(^1,2\)
\(^1\)Institute of Zoology, University of Veterinary Medicine Hannover, Hannover, Germany
\(^2\)Center for Systems Neuroscience, Hannover, Germany
Email: sandra.ammersdoerfer@tiho-hannover.de

The present project sets out to study the effects of aversive experience (i.e. immobilization stress) on the behaviour and stress hormone level in the Short-tailed fruit bat, *Carollia perspicillata*. Phyllostomid bats show a complex social organisation and behaviour (including human-like abilities such as individual recognition by voice and vocal learning) and have a highly developed limbic system, as compared to rodents. Therefore, these bats appear predestined for modelling emotion-relevant functions of the human nervous system (e.g. stress responses). Behaviourally, stressed animals and controls were observed in a custom-made 3D-plus maze for bats. This experimental design consists of four arms (two open and two enclosed ones) and serves as a test for anxiety, which is supposed to correlate with the stress level of the animal. To validate the applicability of this otherwise (i.e. in rodents) well-established behavioural test in bats, stress hormone levels of the animals were determined. Stress hormones, like cortisol, are released in response to stressful situations. Fecal cortisol sampling was chosen to avoid the necessity of handling of the animals, which can produce a stressful situation itself. Another advantage of fecal sampling is that each individual can be used as its own control (pre vs. post stress), which excludes the impact of inter-individual variations in both behaviour and hormone level. The results of this study show that aversive experience leads to both, stress-induced behavioural alterations, as well as an increase in the cortisol concentrations of the animals faeces.

The psychophysiology of listening to conspecifics – insights from a bat model

M. Göpfert\(^1\), S. Ammersdörfer\(^1,2\), and K.-H. Esser\(^1,2\)
\(^1\)Institute of Zoology, University of Veterinary Medicine Hannover, Hannover, Germany;
\(^2\)Center for Systems Neuroscience, Hannover, Germany
Email: sandra.ammersdoerfer@tiho-hannover.de

In previous studies, *Phyllostomus discolor* has been used successfully for modelling different aspects of human speech, e.g., vocal learning and dialects, individual recognition by voice, and the necessity of real-time auditory feedback (review: Esser, K.-H. 2003: Speech communication 41, 179-188). Further, for the majority of about 20 different types of species-specific communication calls, the context of call emission (e.g., threat, attack, isolation,
roosting in physical contact) could be deciphered by behavioural monitoring and sound recordings. Accordingly, calls were either classified as agonistic (negative emotional valence) or affiliative (positive valence).

Our present approach addresses the question whether or not psychophysiological responses (e.g., changes in heart and/or respiration rate) can be used to discriminate objectively between sociopositive and -negative sound stimuli. For obtaining the electrocardiogram (via silver-wire electrodes) and for registration of thoracic movements (via laser) the trunk of an awake bat was positioned in a padded holder. Threat, attack, isolation and contact calls were played back from a digital call library at natural sound pressure levels. A significant increase in instantaneous heart rate was confined to stimuli with a negative valence (= all except contact call) whereas a sound-induced increase in respiration rate was found throughout. In the latter case, responses to socionegative stimuli were significantly stronger as compared to contact-call stimuli.

**Anticipation of food reward and 50 kHz ultrasonic vocalizations in rats**

_J.C. Brenes and R.K.W. Schwarting_

Experimental and Physiological Psychology, Philipps-University, Marburg, Germany

Email: brenes@staff.uni-marburg.de

Rats can emit 50 kHz ultrasonic vocalizations, which are thought to represent their subjective affective stimuli such as sex, food, drug of abuse, electrical brain stimulation, play, and tickling. Although 50 kHz calls could gauge an appetitive motivational state, the role of these calls in incentive motivation tasks has not been systematically investigated. This study, therefore, sought to determine whether anticipation of food reward could elicit 50 kHz calls.

To this aim, male Wistar rats were tested in a home cage where they learned to associate the 1.5-h daily feeding session with a preceding tone-cue. Food-paired rats rapidly showed conditioned anticipatory activity and short latencies to eat, but not a substantial increase in 50 kHz calling throughout the days. Indeed, these animals showed progressively less 50 kHz calls compared to food-unpaired controls (never fed in the testing cage), especially during the first minutes of the task. Conversely, a remarkable reduction in anticipatory activity and food intake, and a huge increase in 50 kHz calling during all test phases were detected as soon as the food-paired rats were sated. In general, 50 kHz calls increased when the appetitive properties of that reward were temporally devalued, but not when animals were initially engaged in appetitive and consummatory behaviours towards a high-valued reward. Our data somewhat support the assumption that 50 kHz calls can index an appetitive motivational state in the rat; however this effect became noticeable just when certain homeostatic and testing conditions were given.
Affect cues in communication calls of tree shrews

J. Brunke, S. Schehka and E. Zimmermann
Institute of Zoology, University of Veterinary Medicine Hannover, Hannover, Germany
Email: jennifer.brunke@tiho-hannover.de

Comparative studies on affective prosody in human speech revealed remarkable cross-cultural similarities suggesting that affective prosody may have originated from a prehuman basis. To explore this hypothesis, the acoustic variation in communication calls and its perception in tree shrews were examined.

Tree shrews are small diurnal mammals, genetically closely related to primates, living in dispersed pairs in the dense tropical forests of south-east Asia. Calls were induced experimentally in a social encounter, and a disturbance paradigm, respectively, and related to two behaviourally defined arousal states within specific behavioural contexts. Context and arousal state of the caller reliably predicted spectral and temporal variations in call structure. Whereas context is closely associated with the frequency-time contour of calls (call type), arousal is expressed in shifts of fundamental frequency and the rate of call production. In a habituation-dishabituation paradigm, testing the effect of arousal-related variation within the same call type, tree shrews were able to discriminate acoustically between two arousal states. All in all, these findings document the relevance of affect cues in the vocal communication system of a non-primate mammal, the tree shrew, and support that mechanisms involved in the acoustical expression and perception of emotions are deeply rooted in mammals. [Work supported by DFG FOR 499.]

Brain activation for maternal auditory perception of pup calls in virgin female mice: auditory cortex

D.B. Geissler, C. Schmid and G. Ehret
Institute of Neurobiology, University of Ulm, Ulm, Germany
Email: diana.geissler@uni-ulm.de

Maternal emotion/motivation for pup-caring behaviour is present in mothers right after delivery. Virgin females show pup-caring behaviour after a few minutes contact with pups. Pup-caring behaviour in the nest is released in mothers and virgin females by low-frequency harmonically structured wriggling calls of the pups. Responses of virgin females to wriggling-call models depend on their estrous phase (Ehret & Schmid, Physiol Behav 96, 2009, 428-433). Pups isolated outside the nest emit tonal ultrasounds releasing phonotaxic behaviour in mothers and in virgin females with 5 days but not with one day of pup-caring experience (Ehret & Buckenmäier, J Physiol 88, 1994,315-329). Here, we ask how differences in maternal emotion/motivation between virgin females of little (1 day) or much (5 days) pup-caring experience in various estrous phases is reflected in the neural activation in primary and high-order fields of the auditory cortex when the animals listen and respond to models of wriggling calls or ultrasounds. Neuronal activation was quantified via c-Fos immunocytochemistry by counting Fos-positive cells in the primary auditory cortical fields AI, AAF, UF (primary, anterior, ultrasonic field) and the higher-order fields AII (secondary field) and DP (dorsoposterior field).

Call models activated primary fields independent of their perceptual quality and the emotional/motivational states of the animals. Activation of AII and DP reflected perceptual
differences of call models according to emotional/motivational differences due to duration of pup-caring experience (ultrasounds) or estrous phase (wriggling calls). In DP a left-hemisphere advantage of activation occurred for recognised wriggling calls, most clearly only in diestrus.

The valence of emotional animal vocalizations modulates electrophysiological correlates of the human orienting response

A.S. Hasting¹, M. Scheumann², E. Zimmermann² and S.A. Kotz¹
¹IRG Neurocognition of Rhythm in Communication, Max Plank Institute for Human Cognitive and Brain Sciences, Leipzig, Germany
²Institute of Zoology, University of Veterinary Medicine, Hannover, Germany
Email: hasting@cbs.mpg.de

Since Darwin (1892) it is postulated that emotional expressions contain universals that are retained across species by evolutionary mechanisms. In the auditory modality, behavioural studies gathered evidence that humans are able to distinguish the emotional valence of vocalizations of dogs, cats or macaques above chance level. Furthermore, a recent fMRI study showed that emotional animal vocalizations activate the same neuronal network as human emotional vocalizations. However, it is to date unclear whether such cross-specific perception of emotion is actually based on phylogenetic relation, or whether it is rather effected by the familiarity of the acoustic signals.

To investigate the relative contribution of these factors, we presented affiliative and agonistic vocalizations as novels in a three-stimulus oddball paradigm. 24 vocalizations per category were recorded from four species varying in the degree of phylogenetic relation and familiarity with respect to the human recipient. Participants engaged in a target detection task on a tone deviating in frequency from the standard tone and were uninformed about the occurrence of the novels. Event-related potentials to the novels showed the typical pattern of an orienting response comprising N1, MMN, P3a and P3b components, whose characteristics varied depending on species and emotional context. For closely related species, emotion effects were observed in the time frame of the MMN, whereas P3a and P3b showed effects for unfamiliar species only. Correlational analyses confirmed that emotional measures related to early, automatic processing stages (MMN), whereas measures of familiarity related to later, attentive processing stages (P3a/P3b).
Do bats evaluate the affective state, and individuality, in communication calls?

H. Kastein¹, A.K. V. Kumar², S. Kandula² and S. Schmidt¹
¹Institute of Zoology, University of Veterinary Medicine Hannover, Hannover, Germany
²School of Biological Sciences, Madurai Kamaraj University, India
Email: Hanna.Kastein@tiho-hannover.de

In a number of mammalian species, including bats, vocal cues corresponding to prosodic cues in humans can be correlated with an affective state, as well as the individuality, of the caller. The present study addresses the question to which extent the respective acoustic cues in aggression and response calls of the Indian False Vampire bat (*Megaderma lyra*) are evaluated by conspecific receivers. In a first experiment, we tested spontaneous reactions to aggression and response call stimuli, typical for agonistic interactions of different intensities, or for different individuals. Then we conducted a habituation-dishabituation experiment to test the ability to categorize different affective states, or individuality, within a given call type. A frame by frame analysis of the parameters duration to maximum deflection, holding time, and duration of the return movement revealed that spontaneous reactions for both call types, and different intensities of agonistic interactions, were similar. Significant differences were only found for the duration to maximum deflection in aggression calls emitted during interactions of different intensities. First results of the habituation-dishabituation experiment suggest that the bats may evaluate different affect intensities within call types, and distinguish between different individuals. Supported by the DFG SCHM 879/6-3

Acoustic recognition of familiarity linked to emotional state in a nocturnal primate.

L.M.C. Leliveld and E. Zimmermann
Institute of Zoology, University of Veterinary Medicine Hannover, Hannover, Germany
Email: Lisette.Maria.Charlotte.Leliveld@tiho-hannover.de

For primates living in cohesive social systems the acoustic recognition of familiarity depends on the social context of communication calls, and as a consequence possibly on the emotional state of the listener.

To explore to which extent these findings can be generalised to primates living in a dispersed social system, we performed playback experiments in a nocturnal primate, the gray mouse lemur. We compared the ability of gray mouse lemurs to acoustically discriminate familiarity, based on either an affiliative call, the trill, used during affiliative interactions, or an agonistic call, the tsak, used during agonistic encounters. 17 captive gray mouse lemurs were tested individually in a sound attenuated chamber, in which they were presented with playbacks of both trills and tsaks from a familiar and an unfamiliar sender, respectively. Playback stimuli were standardised in duration and sound pressure level. Based on behavioural responses to playbacks (e.g. latency to turn the head), we found that the subjects recognised familiarity based on one (trill), but not the other call type (tsak). These findings suggest that the acoustic recognition of familiar conspecifics is of biological importance even for nocturnal primates living in a dispersed social system, such as the gray mouse lemur. Furthermore the asymmetric behavioural response towards the two call types implies that the acoustically conveyed social context and thereby the induced emotional state of a listener may affect its behavioural responses specifically.
Strain and sex differences in rat motivation-related ultrasonic vocalizations

C. Natusch and R.K.W. Schwarting
Department of Psychology, Philipps-University of Marburg, Marburg, Germany
Email: natusch@staff.uni-marburg.de

Rats emit three types of ultrasonic vocalizations (USV’s), which can be assigned to different motivationally relevant situations. The 40-kHz-distress calls of rat pups occur in isolation from the mother and the nest. They help the mother to localise the pups in order to carry them back to the nest. The 50 kHz calls emitted by adult animals often appear in appetitive situations, but also when rats are separated from their cage mates and placed in a fresh cage (housing cage test, for details see Schwarting et al. Behav Brain Res 2007). In an aversive environment adult rats emit 22 kHz calls. Panksepp and co-workers suggested that these three types of vocalizations might serve as an index of the animal’s subjective state (Panksepp Science 2005 and Knutson et al. Psychol Bull 2002). For research on ultrasonic calls, different rat strains are used in various labs. Due to this variability it is difficult to compare results between labs, although similar tests are used.

To discover which strain would be the ideal model for a particular experiment and to provide a basis for comparison we recorded all three types of USV’s that occur in rats. We tested male and female rats of the three outbred strains which are most common for ultrasonic experiments, namely Long Evans, Sprague Dawley and Wistar Unilever. Results of these comparative experiments are going to be presented. They will address both quantitative and qualitative features of ultrasonic vocalizations.

Emotional prosody perception in patients with lesions in the basal ganglia: Perceptual impairments can be linked to different processing stages

S. Paulmann¹, M.D. Pell² and S.A. Kotz³
¹Psychology Department, University of Essex, Essex, UK
²School of Communication Sciences and Disorders, McGill University, Montreal, Quebec, Canada
³IRG Neurocognition of Rhythm in Communication, Max Plank Institute for Human Cognitive and Brain Sciences, Leipzig, Germany
Email: paulmann@essex.ac.uk

Based on observations that report recognition deficits for emotional prosody in patients with basal ganglia (BG) dysfunction, this study aimed to explore the underlying mechanisms substantiating the deficit.

We investigated three different processing stages of emotional prosody processing in an on-line ERP-experiment as well as an off-line behavioural task. We tested emotional prosody perception in BG-lesion patients using vocal expressions (with and without lexical content) of anger, fear, disgust and happiness compared to a neutral baseline. In addition, deviance detection of both emotional prosodic information alone and combined emotional prosodic and semantic information was investigated by means of a cross-splicing method. Results show that early in emotional prosody processing, the different emotions, except for fear, elicit similar differentiation in the ERP in both BG-patients and healthy controls reflected in P200 amplitude differences. Moreover, deviance of prosodic expectancy elicits a right lateraliised positive ERP component in healthy controls and patients. However, at later processing stages
healthy listeners show a negativity in response to combined emotional prosodic and semantic expectancy violations irrespective of emotion, whereas BG-patients show this negativity only for the emotions “happiness” and “anger”, but not “fear” or “disgust”. Finally, behavioural emotional prosody recognition rates revealed that patients are significantly impaired in explicit recognition of emotional prosody when compared to healthy controls. The combined data serve as preliminary evidence that focal lesions in left BG primarily affect executive processes (integration, evaluation, recognition) related to emotional prosody processing but are not necessarily implied in early more implicit emotional prosodic processing stages.

Do phylogeny and/or familiarity influence cross-taxa perception of acoustically conveyed emotions in human listeners?

M. Scheumann1, A. Hasting2, S.A. Kotz2 and E. Zimmermann1

1Institute of Zoology, University of Veterinary Medicine Hanover, Hanover, Germany
2IRG Neurocognition of Rhythm in Communication, Max Plank Institute for Human Cognitive and Brain Sciences, Leipzig, Germany
Email: marina.scheumann@tiho-hannover.de

Since Darwin (1872) it is suggested that vocal emotional communication follows similar rules in humans and animals. To explore this hypothesis we investigated whether humans can classify the emotional content of calls of human infants and animals. The latter vary in phylogenetic distance and in familiarity compared to humans. Twenty-eight male participants listened to 192 calls of 4 different species (human infant, chimpanzee, dog and tree shrew). All calls were recorded either in an affiliative context (= positive emotion) or in an agonistic context (= negative emotion). Participants were asked to describe the emotional content of the calls based on a 5-point scale ranging from very negative to very positive. To investigate familiarity, we asked the participant “What is this sound?” and they labelled them spontaneously. Participants classified and labelled the human infant calls correctly as negative or positive calls. In comparison, the three animal taxa lead to mixed results. The classification accuracy of the emotional content of the animal calls varied according to the recognition of the animal species and the context in which the calls were recorded. All in all, participants showed highest classification accuracy for calls of their own species, while classification of animal calls was dependent on familiarity with the respective vocalization.

Brain Activation for maternal auditory perception of pup calls in virgin female mice: Limbic system

C. Schmid, D.B. Geissler and G. Ehret
Institute of Neurobiology, University of Ulm, Ulm, Germany
Email: christina.schmid@uni-ulm.de

Pup-caring behaviour (licking, changing the nursing/warming position, nest building) in the nest is released in virgin females by low-frequency harmonically structured wriggling calls of the pups. Responses to wriggling-call models depend on the estrous phase of the females (Ehret & Schmid, Physiol Behav 96, 2009, 428-433). Pups isolated outside the nest emit tonal
ultrasounds releasing phonotaxic behaviour in virgin females with 5 days but not with one day of pup-caring experience (Ehret & Buckenmaier, J Physiol 88, 1994, 315-329).

Here, we ask how differences in maternal emotion/motivation between virgin females of little (1 day) or much (5 days) pup-caring experience in various estrous phases is reflected in the neural activation in centres of the limbic brain system that are involved in the control and release of maternal behaviour by pup stimuli. Neuronal activation was quantified via c-Fos immunocytochemistry by counting Fos-positive cells in the lateral septum (LS), medial preoptic area (MPOA), bed nucleus of the stria terminalis (BST), ventromedial nucleus of the hypothalamus (VMH), amygdala (AM), cortical amygdale (CAM), piriform cortex (PIR) and entorhinal cortex (ENT). Low activation levels correlated with listening to low-quality wriggling calls (LS) or low-quality ultrasounds (LS, MPOA, BST, PIR, ENT) and with low emotional/motivational levels due to little pup-experience (LS, MPOA, PIR, VMH, AM, CAM) or metestrus phase (LS, MPOA, PIR, ENT). Thus, neural activation in centers of the limbic system reflects levels of maternal motivation/emotion by pup-experience and the phase of the estrous cycle, and the acoustic quality of the stimuli releasing maternal behaviour.
List of participants

Ackermann Hermann hermann.ackermann@uni-tuebingen.de
Altenmüller Eckart altenmueller@hmt-hannover.de
Alter Kai kai.alter@ncl.ac.uk
Ammersdörfer Sandra sandra.ammersdoerfer@tiho-hannover.de
von den Berg Sönke svdberg@tiho-hannover.de
Brenes Juan Carlos brenes@staff.uni-marburg.de
Brudzynski Stefan sbrudzyn@brocku.ca
Brunke Jennifer jennifer.brunke@tiho-hannover.de
Cheimaris Andreas andreasc@seznam.cz
Davila Ross Marina marina.davila-ross@port.ac.uk
Dengler Reinhard dengler.reinhard@MH-Hannover.de
Ehret Günter guenter.ehret@uni-ulm.de
Geissler Diana diana.geissler@uni-ulm.de
Großbach Michael michael.grossbach@hmt-hannover.de
Haßfurther Birgit birgit.hassfurther@tiho-hannover.de
Hasting Anna hasting@cbs.mpg.de
Hoffmann Klaus-Peter kph@neurobiologie.rub.de
Ioannou Christos ioannou.ch@gmail.com
Janßen Simone sjjanssen@gmx.net
Kastein Hanna hanna.kastein@tiho-hannover.de
Kiefer Markus markus.kiefer@uni-ulm.de
Kirschner Sebastian kirschner@eva.mpg.de
Koelsch Stefan s.koelsch@fu-berlin.de
Kopiez Reinhard kopiez@hmt-hannover.de
Kotz Sonja kotz@cbs.mpg.de
Leliveld Lisette lisette_leliveld@hotmail.com
Narins Peter pnarins@ucla.edu
Natusch Claudia natusch@staff.uni-marburg.de
Owren Michael owren@gsu.edu
Paulmann Silke paulmann@essex.ac.uk
Pell Marc marc.pell@mcgill.ca
Peretz Isabelle isabelle.peretz@umontreal.ca
Sauter Disa disa.sauter@mpi.nl
Scheumann Marina marina.scheumann@tiho-hannover.de
Schmid Christina christina.schmid@uni-ulm.de
Schmidt Sabine sabine.schmidt@tiho-hannover.de
Schnitzler Hans-Ulrich hans-ulrich.schnitzler@uni-tuebingen.de
Schröder Christine markus.kiefer@uni-ulm.de
Soltis Joseph joseph.soltis@disney.com
Wildgruber Dirk dirk.wildgruber@med.uni-tuebingen.de
Zimmermann Elke elke.zimmermann@tiho-hannover.de
Zouvani Theodosia christos_ioannou_1@hotmail.com
General Information

Registration/Information Desk
Registration is possible during the dinner on Wednesday, 28th. On Thursday, 29th the registration/information desk will be open at the entrance to the Red Room (“Roter Saal”) from 8:00 to 8:45. The information desk will answer your questions.

Travel Reimbursement
For invited speakers the travel reimbursement will be taken care of on Friday in the coffee break between 10.30 and 11.00 at the information desk.

Talks
Talks will be held in the Red Room (“Roter Saal”). Please contact Sönke von den Berg or Dr. Michael Großbach in time with your presentation or laptop at hand so that we can arrange a smooth progress of events and keep the schedule.

Poster Presentation
The poster session will take place on Thursday between 15:30 and 17:30 next to the Red Room. Posters should be put up either on Thursday in the course of the day before the session starts. Please contact the organisers for help and information.

Coffee & Tea Breaks
Coffee, tea and mineral water are available free of charge to registered conference participants.

Lunch and Dinner
Lunch and dinner will be served on all conference days free of charge to registered conference participants in the dining room (“Speisesaal”).

Reisensburg Guests
For those staying at the Reisensburg breakfast will be served in the dining room (“Speisesaal”). Depending on your reservation dinner and breakfast will be served also on Saturday, 1st and Sunday, 2nd, respectively.

Parking
Parking space is available free of charge directly at the Reisensburg.

Taxi
Taxis can be ordered at the information desk or by calling 08221/5584 (Taxi Essenwanger).

Schedule for the Excursion to “Hohle Fels” on Saturday
For those who have registered to participate at the excursion on Saturday a bus will be waiting in front of the Reisensburg. Please be on time as we have a fixed reservations.

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<thead>
<tr>
<th>Time</th>
<th>Event</th>
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<tbody>
<tr>
<td>08:30</td>
<td>Departure at the Reisensburg by bus</td>
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<tr>
<td>10:00</td>
<td>Arrival at “Hohle Fels”, guided tour</td>
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<tr>
<td>11:00</td>
<td>Flute concert</td>
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<tr>
<td>11:30</td>
<td>Departure to the Geißenklösterle</td>
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<tr>
<td>11:45</td>
<td>Arrival at Geißenklösterle, guided tour</td>
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<tr>
<td>13:00</td>
<td>Lunch</td>
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<td>15:00</td>
<td>Guided tour through the Museum for Primeval History</td>
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<tr>
<td>16:00</td>
<td>End of excursion and departure</td>
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<tr>
<td>17:30</td>
<td>Arrival at the Reisensburg</td>
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If you have any questions feel free to ask the organisers.
We will try our best to ensure a pleasant and stimulating stay.