Invertebrate Sound and Vibration 2013

Glasgow ~ Scotland

XIV International Conference on Invertebrate Sound and Vibration

ISV 2013

University of Strathclyde, Glasgow, United Kingdom
July 23-26 2013

Conference Chair:

Dr James Windmill

Co-organiser:

Dr Shira Gordon

Supported by:

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Contents

Conference Information

Special features:

- Civic Reception at the Glasgow City Chambers, hosted by the Lord Provost of Glasgow
- Society for Experimental Biology Scholarships – conference fee waivers (£195) for young researchers
- Prize giving: Certificates and financial incentives - Best presentation-£50 and Best posters-£50, £25, £25
- Discussion session on future ISV conferences

Networking:

- Poster-and-wine event on the evening of the 24th July. This includes a whisky tasting session hosted by David Morgan (Wine and Spirit Education Trust tutor), and a demonstration of the new PSV500 scanning laser vibrometer by Polytec Ltd.
- Lunch (60 minutes) and two (2) coffee breaks (20 minutes each) each day
- Conference dinner and ceilidh at the Òran Mór on the evening of the 26th July

Merchandise:

ISV2013 T-Shirts available for purchase from the on-line shop, see www.isv2013.org

Notes:

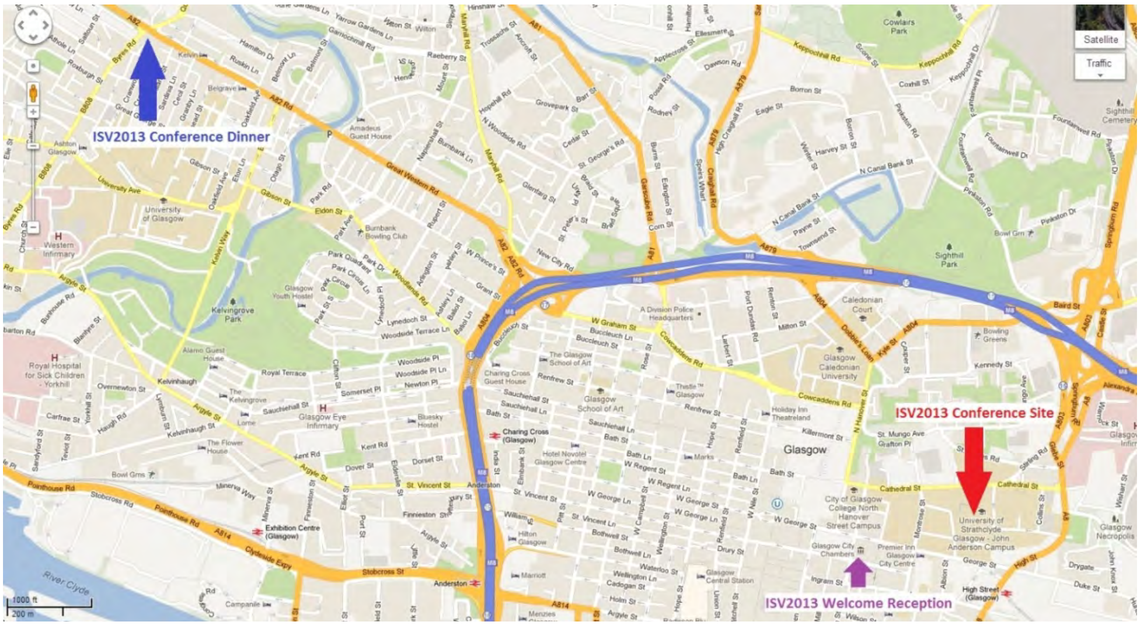
The civic reception is free to all, including partners. A guest registration (£85.00) is available allowing partners access to the conference, including the wine and poster evening, and the conference dinner.
Accommodation can be booked via the conference website.

For further information:

Email: info@isv2013.org
Web: www.isv2013.org
Tel: 0141 548 3221

Conference Site Map

Conference Venue: John Anderson Building (Talks, Posters, Coffee Breaks, Lunches)
Civic Reception: Glasgow City Chambers
Conference Dinner: Òran Mór (731-735 Great Western Road. Tel: 0141 357 6200)



Conference Plenary Talks

Daniel Robert
So many ears, so little time
School of Biological Sciences, University of Bristol, United Kingdom
9.40am, Tuesday 23rd July

Friedrich Barth
Airflows, Sensors, and a Spider's Jump to Catch a Fly
Department of Neurobiology, University of Vienna, Austria
4.40pm, Tuesday 23rd July

Andrew Mason
Complex signals: what do spiders have to say?
Integrative Behaviour and Neuroscience, University of Toronto Scarborough, Canada
12.00pm, Wednesday 24th July

Jayne Yack
Rap Battles and Screaming in Caterpillars: Let the youth have their say!
Department of Biology, Carleton University, Canada
9.20am, Thursday 25th July

Michael Greenfield
'Dagmar and Otto von Helversen Lecture'
Acoustic communication in the nocturnal Lepidoptera: revelations of a hidden world
Institut de Recherche sur la Biologie de l'Insecte, University of Tours, France
9.40am, Friday 26th July

Complete Conference Program

Monday 22nd July

17:00	**REGISTRATION OPENS – 4th FLOOR JOHN ANDERSON BUILDING**			
19:00	**CIVIC RECEPTION AT THE GLASGOW CITY CHAMBERS, GEORGE SQUARE**			

Tuesday 23rd July

08:40	**REGISTRATION OPENS – 3rd FLOOR JOHN ANDERSON BUILDING**		
	COFFEE		
09:30	*Welcome*	**Professor Kenny Miller** Vice Principal, University of Strathclyde	
09:40	*Plenary (page 14)*	**Daniel Robert - *So many ears, so little time*** School of Biological Sciences, University of Bristol, United Kingdom	
10:40	**COFFEE**		
	Talk Session 1 - *Chair:* ***Joseph Jackson***		
11:00	*Page: 46*	**Manuela Nowotny** Frequency analysis in the bushcricket ear	J. W. Goethe-Universität, Germany
11:20	*34*	**David Mackie** Model Locust Tympanal System: understanding the link between biomechanics and neurophysiology	University of Strathclyde, UK
11:40	*56*	**John Stout** Males Influence Both the Phonotactic Responsiveness of Female *Gryllus bimaculatus* and Song Encoding by their ON1 and AN2 Neurons	Andrews University, USA
12:00	*38*	**Andrew Mikhail** What does a butterfly hear? Tuning and amplitude discrimination in the Blue Morpho butterfly	Carleton University, Canada
12:20	*50*	**Klaus Reinhold** Phenotypic plasticity in response to food quality and anthropogenic noise in the grasshopper *Chorthippus biguttulus*	Bielefeld University, Germany
12:40	*40*	**Fernando Montealegre-Z** Dynamics of pressure difference receiver tympanal membranes in a bushcricket ear (Tettigoniidae)	University of Lincoln, UK
13:00	**LUNCH**		
	Talk Session 2 - *Chair:* ***Damian Elias***		
14:00	*Page: 19*	**Taina Conrad** New insights into vibrations as species-specific signals in mason bees	University of Ulm, Germany
14:20	*23*	**Jeremy Gibson** Treehoppers follow an experimentally imposed amplitude gradient	University of Missouri, USA
14:40	*36*	**Valerio Mazzoni** Mating Disruption of Insect Pests with Vibrational Signals: from Theory to Practice	Fondazione Edmund Mach, Italy
15:00	*44*	**Roland Mühlethaler** Acoustic communication in Pear psyllids (*Cacospylla pyri* L.) and occurrence of stridulatory organs in the genus *Cacopsylla* (Hemiptera: Psylloidea)	Museum für Naturkunde, Germany
15:20	*47*	**Kirill Orci** Drumming call variation and female response specificity in a group of closely related species of stoneflies (Plecoptera)	MTA-ELTE-MTM Ecology Research Group, Hungary
15:40	*52*	**Conrado Rosi-Denadai** *Amphion floridensis* and the Backthroat Boys: How are these caterpillars producing sound?	Carleton University, Canada

16:00	*54*	**Sen Sivalinghem** Vibratory communication in a black widow spider (Araneae: Theridiidae): From signal production to reception	University of Toronto Scarborough, Canada
16:20		**COFFEE**	
16:40	*Plenary (page 11)*	**Friedrich Barth - *Airflows, Sensors, and a Spider's Jump to Catch a Fly*** Department of Neurobiology, University of Vienna, Austria	
17:40	***End of talks***		
18:00		**POSTER AND WINE EVENT – 3rd FLOOR JOHN ANDERSON BUILDING**	

Wednesday 24th July

09:00		**COFFEE**	
	Talk Session 3** - Chair: **Manuela Nowotny		
09:20	*Page: 49*	**Gerit Pfuhl** Mapping the auditory pathway in heliothine moth	Norwegian University of Science and Technology, Norway
09:40	*51*	**Bernd Ronacher** Grasshoppers use local but not global cues for acoustic pattern recognition	Humboldt Universität zu Berlin, Germany
10:00	*24*	**Shira Gordon** Hearing of Aging Locusts	University of Strathclyde, UK
10:20	*26*	**Matthias Hennig** How female crickets evaluate conspecific songs: a comparative view	Humboldt Universität zu Berlin, Germany
10:40	*27*	**Stefan Hirtenlehner** A comparison of cricket phonotaxis under outdoor and laboratory conditions	Karl-Franzens-Universität Graz, Austria
11:00	*33*	**Amanda Lindeman** What's the password? Female red turpentine beetles (*Dendroctonus valens* LeConte) grant access to their galleries based on an assessment of male signals	Carleton University, Canada
11:20	*30*	**Kostas Kostarakos** Calling song recognition in an insect brain	Karl-Franzens-Universität Graz, Austria
11:40		**COFFEE**	
12:00	*Plenary (page 13)*	**Andrew Mason - *Complex signals: what do spiders have to say?*** Integrative Behaviour and Neuroscience, University of Toronto Scarborough, Canada	
13:00	***End of talks***		
		SIGHTSEEING	

Thursday 25th July

09:00		**COFFEE**	
09:20	*Plenary (page 15)*	**Jayne Yack** ***Rap Battles and Screaming in Caterpillars: Let the youth have their say!*** Department of Biology, Carleton University, Canada	
10:20		**COFFEE**	
	Talk Session 4** - Chair: **Fernando Montealegre-Z		
10:40	*Page: 28*	**Joseph Jackson** The effects of two similar acoustic signals on an active ear	University of Strathclyde, UK
11:00	*35*	**Robert Malkin** The Locust Ear: A General Mechanism for Tonotopy and Energy Localisation	University of Bristol, UK
11:20	*45*	**Ryo Nakano** Male Courtship Song Disrupts Orientation Flight in the Yellow Peach Moth, *Conogethes punctiferalis*	National Institute of Fruit Tree Science, Japan

11:40	*39*	**Doreen Möckel** Mechanical basis of self-generated sound in the locust ear	J. W. Goethe-Universität, Germany
12:00	*42*	**Glenn Morris** *Tympanotriba vittata*, another katydid with strange stridulatory acoustic adaptations	University of Toronto at Mississauga, Canada
12:20	*25*	**Manfred Hartbauer** Mechanisms driving the evolution towards chorus synchrony - a case study on *Mecopoda elongata* (Orthoptera: Tettigoniidae)	Karl-Franzens-Universität Graz, Austria
12:40		**LUNCH**	
	Talk Session 5 *- Chair:* ***Manfred Hartbauer***		
13:40	*Page: 18*	**Benedict Chivers** A comparative analysis of the stridulatory file across katydid species (Orthoptera: Tettigoniidae)	University of Lincoln, UK
14:00	*37*	**Natasha Mhatre** Two to tango: how tree cricket song changes with temperature and auditory tuning keeps up	University of Bristol, UK
14:20	*32*	**Reinhard Lakes-Harlan** Sound production of *Mecopoda elongata*: circadian rhythm and maturation	Justus-Liebig University Giessen, Germany
14:40	*29*	**Thorin Jonsson** Complex acoustic networks in the cricket wings	University of Bristol, UK
15:00	*22*	**Andrew French** Calcium ions modulate transduction, and are strongly buffered in spider mechanosensory neurons	Dalhousie University, Canada
15:20	*57*	**Alexander Sweger** Airborne and vibratory signal production in the purring wolf spider, *Gladicosa gulosa*	University of Cincinnati, USA
15:40		**COFFEE**	
	Talk Session 6 *- Chair:* ***Roland Mühlethaler***		
16:00	*59*	**Matthew Wale** Crabs unquiet in noisy seas	University of Bristol, UK
16:20	*43*	**Beth Mortimer** Sonic properties of silks	University of Oxford, UK
16:40	*58*	**Paivi Torkkeli** Several Octopamine Receptor Subtypes are Involved in Modulation of Spider Mechanosensory Neurons	Dalhousie University, Canada
17:00	*21*	**Damian Elias** Anthropogenic effects on vibratory environments and orb-web spider foraging behavior	University of California, Berkeley, USA
17:20	*55*	**Ales Škorjanc** Sensory hair motion in oscillating air-flow is matched by neuronal filter properties of filiform sensilla	University of Ljubljana, Slovenia
17:40	***End of talks***		
18:30		**BUS LEAVES FOR CONFERENCE DINNER ROTTENROW EAST/COLLINS STREET**	
19:00		**CONFERENCE DINNER – ORAN MOR, GREAT WESTERN ROAD, GLASGOW**	
23:30		**BUS LEAVES FOR UNIVERSITY**	

Friday 26th July

09:20	**COFFEE**		
09:40	*Plenary (page 12)*	**Michael Greenfield - Dagmar and Otto von Helversen Lecture** ***Acoustic communication in the nocturnal Lepidoptera: revelations of a hidden world*** Institut de Recherche sur la Biologie de l'Insecte, University of Tours, France	
10:40	**COFFEE**		
	Talk Session 7** - Chair: **Natasha Mhatre		
11:00	*Page: 20*	**Monika Eberhard** Intrinsic variability and temperature effects in locust auditory neurons	Humboldt-Universität zu Berlin, Germany
11:20	*31*	**Anka Kuhelj** Insight into intraspecific interactions in the leafhopper *Aphrodes makarovi* (Hemiptera: Cicadellidae)	National Institute of Biology, Slovenia
11:40	*41*	**Erica Morley** The proxemics and acoustic geometry of courtship in Drosophila melanogaster	University of Toronto Scarborough, Canada
12:00	*48*	**Krisztina Petróczki** Are calling song characteristics affected by anthropogenic noise in the tree cricket, *Oecanthus pellucens*?	University of Debrecen, Hungary
12:20	*53*	**Johannes Schul** The evolutionary history of the diversity of Neoconocephalus acoustic communication	University of Missouri, USA
12:40	**LUNCH**		
13:30	*General Meeting*	**Discussion of Future ISV** **Closing Remarks**	
14:00	**Conference Ends.**		

List of Posters

19	79	**Caitlin Preston** Morphological Diversity and the Evolutionary Origins of Vogel's Organs in Nymphalidae Butterflies	Carleton University, Canada
20	80	**Michael Reichert** Directional Hearing in Masking Noise in the Grasshopper *Chorthippus biguttulus*	Humboldt-Universität zu Berlin, Germany
21	81	**Andrew Reid** Microscale Acoustic Systems – Bio-inspired Micro-Electro-Mechanical Systems	University of Strathclyde, UK
22	82	**Doris Reineke** When to Kick? Cues Triggering Collective Mechanical Defence in *Aphis nerii* (family: Aphididae)	Karl-Franzens-Universität Graz, Austria
23	83	**Heiner Römer** Asymmetry in the song of crickets: Preferences of females and proximate mechanism of discrimination.	Karl-Franzens-Universität Graz, Austria
24	84	**Conrado Rosi-Denadai** Vibratory Communication and Putative Vibration Receptors in the Masked Birch Caterpillar *Drepana arcuata* (Drepanoidea)	Carleton University, Canada
25	85	**Stefan Schöneich** Neuronal coupling of ventilatory and chirp rhythm in singing field crickets	University of Cambridge, UK
26	86	**Lev Shestakov** Courtship songs in a new hybrid zone between *Chorthippus albomarginatus* and *Ch. karelini* (Acrididae: Gomphocerinae) in Russia	Russian Academy of Sciences, Russia
27	87	**Lev Shestakov** Stable and variable parameters in vibrational songs of sympatric pentatomid bug species (Heteroptera, Pentatomidae)	Russian Academy of Sciences, Russia
28	88	**Lev Shestakov** The role of different courtship song elements in mate recognition of *Gryllus bimaculatus*	Russian Academy of Sciences, Russia
29	89	**Alexander Sweger** Singing in the Rain: Spiders Signaling on Sodden Substrates.	University of Cincinnati, USA
30	90	**Takuma Takanashi** Substrate vibrations mediate startle behavior via femoral chordotonal organ in a cerambycid beetle	Forestry and Forest Products Research Institute, Japan
31	91	**Yansheng Zhang** A novel bio-mimetic MEMS microphone with better directional sensitivity performance in the low frequency range	University of Strathclyde, UK
32	92	**Mikhail Zhemchuzhnikov** Do cave crickets Phaeophilacris bredoides Kalt. perceive sound signals?	Russian Academy of Sciences, Russia
33	93	**Mikhail Zhemchuzhnikov** From the tympanum to the brain: projection pattern of auditory cells in the moth *Heliothis Virescens* (Noctuidae)	Russian Academy of Sciences, Russia

Plenary Talk Abstracts

Airflows, Sensors, and a Spider's Jump to Catch a Fly

Friedrich G. Barth
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In recent years the biological significance of *medium flows* has received considerable attention, which is mainly due to an advanced understanding of the underlying physics. Likewise, the *perception* of air and water flows has increasingly been recognized as a sensory capacity of its own, different from hearing air- or waterborne sound and from sensing substrate vibrations. The present lecture will focus on airflow sensing by terrestrial arthropods, but its messages relate to the sensing of water flows as well.

Thanks to a combination of experimental work and *physical-mathematical modeling* the principles underlying the workings of arthropod airflow sensors are known in some detail. So far, the sensors mainly studied have been insect filiform hairs and spider trichobothria, both as individual sensors and sensor arrays. Beyond this, however, there is a fascinating *diversity of airflow sensors* (regarding their numbers, innervation, and specific topography) in much neglected other animal taxa. There is indeed a large and promising mine of research awaiting exploitation by comparative physiological and neuroethological studies.

Another, and maybe harder to open treasure chest, is the detailed analysis of the *complex flow patterns* representing the biologically relevant stimuli and their relation to ecology, behavior, and the physiology and specific arrangement of the sensors.

After having pointed out some fundamental properties of cuticular hairs sensing airflows, the *fine-tuned jump of a hungry spider when catching a freely flying fly* will serve to illustrate the challenges and rewards of a study aiming at an understanding of the relation between a particular airflow pattern and a specific behavior.

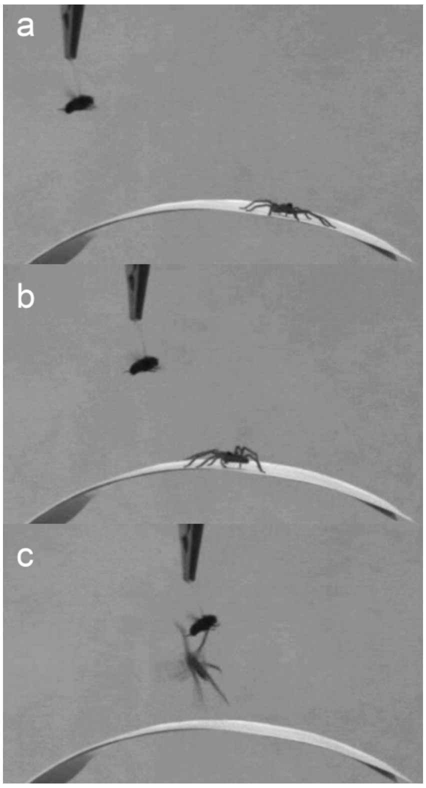

Fig.1: A blindfolded wandering spider *(Cupiennius salei)* catching a humming fly approaching from the left. Note that the spider has already turned towards the fly in *b* (*from Barth FG 2013: The slightest whiff of air: Airflow sensing in arthropods. In: Bleckmann H, Mogdans J, Coombs S (eds). Flow sensing in air and water: Behavioral, neural and engineering principles of operation.Springer, Heidelberg; in press).* Video by C.Klopsch, CF Schaber and FG Barth.

Our work was generously supported by the DARPA BIOSenSE program grant FA9550-05-1-0459 to FGB. The contributions of my Ph.D. students as well as the expertise in fluid mechanics and micromechanics shared by the late JAC Humphrey and by VV Tsukruk are much appreciated.

Acoustic communication in the nocturnal Lepidoptera: revelations of a hidden world

Michael Greenfield
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University of Tours, France
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Whereas the vast majority of pair formation in moths is accomplished via long-range advertisement pheromones emitted by females and short-range courtship pheromones presented by males, a small but critical percentage of species among the Pyraloidea and Noctuoidea use sound in mating communication. These mating communications are generally ultrasound, broadcast by males, and function in courtship, but long-range advertisement songs are also known in some moth species. Behavioral analyses of these advertisements show a high degree of convergence with communication in other acoustic species such as orthopterans and anurans.

Tympanal hearing with a particular sensitivity to ultrasound in the context of defensive behavior for avoiding insectivorous bats is widespread in the Lepidoptera, and phylogenetic inference indicates that this perceptual trait preceded the evolution of song. This evolutionary sequence suggests that male song originated via the sensory bias mechanism, but the trajectory by which ancestral defensive behavior in females – negative responses to bat echolocation signals – may have evolved toward positive responses to male song remains unclear. Analyses of various acoustic moth species offer some insight to this improbable transition, and to the general process by which signals may evolve via the sensory bias mechanism.

Complex signals: what do spiders have to say?

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Courtship signals vary in complexity, but are often more elaborate than long-range advertisement signals, having multiple signal components sometimes produced in different sensory modalities. The interaction between components within complex signals and the contribution of individual components to overall signal function are poorly understood. I will compare courtship displays in three spider groups that span a range of complexity in signal structure: jumping spiders; wolf spiders; and widow spiders. Jumping spiders of the genus *Habronattus* show highly elaborate male courtship displays that comprise multiple signal elements in at least two sensory modalities (visual and vibratory). In this group, prolonged, multimodal courtship displays are highly structured (with a regular, species-specific progression of signal elements throughout the display), and show a pattern of diversification across the genus that is consistent with selection for suites of multimodal traits driven by female preferences for displays of higher complexity.

In contrast, Australian redback spiders (*Latrodectus hasselti*) prolonged male courtship displays are relatively unstructured. Evidence in this system suggests that courtship signals, consisting primarily of web-borne vibration, are a simple broadcast of vibrational energy that is integrated by females to arrive at a mate-acceptance threshold. Wolf spiders (genus *Schizocosa*) represent an intermediate between these two. Males produce complex vibrational displays comprising multiple elements that are produced by independent mechanisms and that are correlated with distinct aspects of male quality (developmental history vs current condition). I speculate that these differences in complexity and information content of male signals critically depend on effects of variable substrates on signal transmission and constraints of female sensory capacities (largely a function of hunting ecology).

Too many ears, too little time

Frequency analysis in a bushcricket

Daniel Robert
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Often taking no more space than a cubic millimeter, insect ears present remarkable sophistication. Far from being simple, insect ears carry on many of the elementary tasks of acoustic detection known from vertebrates and mammals [1]. One of these challenging tasks is to detect and analyse pressure waves in terms of their spectral composition. Bush cricket ears have been known for some time to perform frequency analysis, yet only recently have the key biophysical mechanisms been revealed in some detail [2, 3]. Across auditory animals tympanal membranes are invariably heterogeneous, presenting a complicated histoarchitecture that for a large part determines their mechanical response. This acousto-mechanical conversion constitutes the first step in the process of hearing. In locusts, vibrational travelling waves were first shown to transit across the membrane; a response that enables the mechanical processing of incoming sounds into some of their frequency components. In effect, the travelling wave's topographical destination varies with frequency, therefore specifying the decomposition of waveforms into different frequencies, a crude form of tonotopy. For the bushcricket *Copiphora gorgonensis*, no such tonotopic decomposition takes place at the tympanal membrane. Such effect arises only in the mechanical response of the anatomical structures supporting and surrounding the mechanoreceptor organ (3). In *Copiphora,* the crucial auditory processing stage of impedance conversion arises from the functional histoarchitecture a cuticular element linking the tympanal membrane to the frequency-dispersive analyser (3). Taken step by step, the auditory biophysics of *Copiphora* constitutes a surprising case of high-level evolutionary convergence whereby the bushcricket's auditory system is endowed with all key steps of auditory processing of vertebrates, just constructed many times smaller.

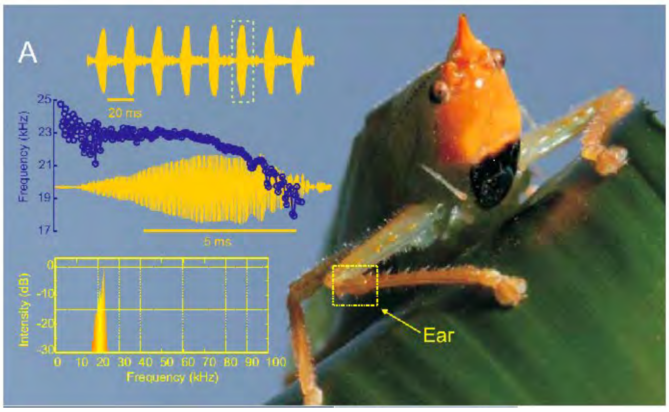

Fig. A. The bushcricket *Copiphora gorgonensis* , its tibial ear, and the acoustic features of its song. Each pulse within a trill (top panel) includes a notable frequency modulation (middle panel) within an otherwise relatively pure spectral composition (bottom panel).

1. Robert D, RR Hoy 2007 Auditory systems in insects. In: Invertebrate Neurobiology. Greenspan R & North G Eds. Cold Spring Harbour Laboratory Press
2. Palghat Udayashankar A, Kössl M, Nowotny M (2012) Tonotopically arranged traveling waves in the miniature hearing organ of bushcrickets. PLoS ONE 7(2): e31008.
3. Montealegre-Z F, Jonsson T, Robson-Brown KA, Postles M, Robert D 2012 Convergent evolution between insect and mammalian audition. Science 338:968-971

This work was supported by the Royal Society of London, the UK-India Research Initiative, the UK Biotechnology and Biological Sciences Research Council and the Human Frontier Science Program

Rap Battles and Screaming in Caterpillars: Let the youth have their say!

Jayne E. Yack
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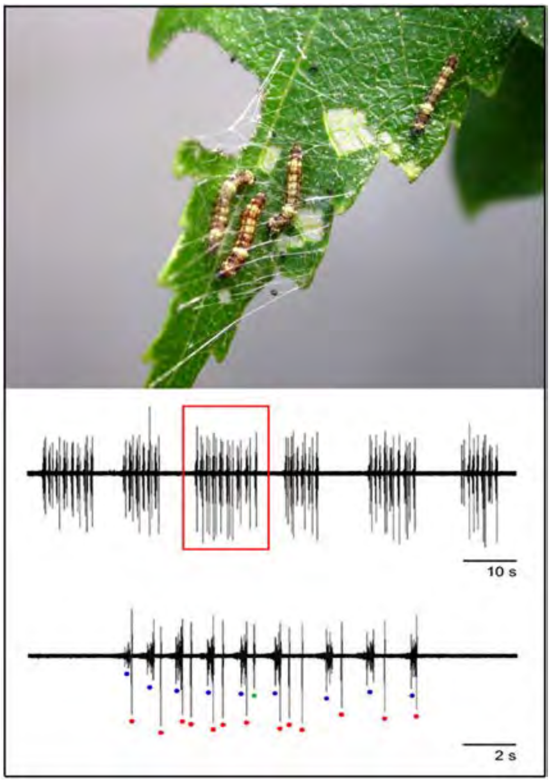
Over the past 60 years the subject of acoustic communication in various arthropods, including insects and spiders, has been reviewed in over 100 review articles, books, and book chapters. Acoustic communication systems are remarkably diverse, with organs of 'sound' production and reception occurring on almost every part of the body. The production or reception of air-, water- and solid-borne vibrations functions in a variety of contexts, including defense, host location, mating, and other social interactions. Despite extensive research on the topic, the vast majority of reports focus on adults. Given that a large portion of the life cycle is spent as an immature in many species, the dearth of information on acoustic communication in non-adults is rather surprising. There are two explanations for the under-representation of larvae and nymphs in the literature on arthropod acoustics: (a) they just don't use this form of communication and therefore reports are rare; or, (b) they do employ acoustic signals, but scientists have not noticed. My presentation will address the prevalence (or lack thereof) of acoustic communication in larval insects by focusing primarily on two model systems developed in my laboratory over the past several years: Defense sounds in Bombycoidea caterpillars, and vibratory territorial displays in Drepanoidea caterpillars.

The lepidopteran superfamily Bombycoidea is a large group of ~3,500 species that includes the well-known silk and hawk moths. During the past several years we have documented defensive sound production in a few North American species (e.g. Bura *et al.* 2011, 2012). To determine how prevalent sound production is in this group, we tested Bombycoidea caterpillars representing 8 subfamilies across North America, Europe, and Costa Rica for their ability to produce airborne sounds (Bura *et al.*, in prep). To our surprise, our results showed that not only is sound production fairly common, but also diverse with respect to the sound producing mechanisms and functions. We report 4 different mechanisms of sound production that occur in 38% of the species tested. Moreover, the behaviours associated with sound production suggest that they function in aposematism, deimatic displays, and possibly mimicry. Thus, the diversity of sound producing mechanisms and function of defense signals in Bombycoidea caterpillars rivals that of the well-studied defense signals in adult Lepidoptera such as the tiger moths (Arctiidae). Moreover, some of these Bombycoidea caterpillar species tested (e.g. *Manduca sexta, Saturnia pyri*) have already been studied for their defensive behaviours. Yet, acoustic defenses have not been noted in these reports. I will discuss why these sounds have gone undetected, for the most part, until recently, and why some larvae might use sound over other forms of defense to communicate with their attackers.

Another group of 'acoustic' caterpillars that we have been studying is the Drepanoidea. This is a large superfamily comprising ~800 species, including the hooktip moths. Our research has focused primarily on the masked birch caterpillar, *Drepana arcuata* (Drepanidae: Drepaninae) that communicates ownership of its leaf shelter using complex vibratory displays. Resident late instar caterpillars defend solitary silken leaf shelters from roaming conspecifics. Caterpillars perform a repetitive vibratory display involving three signal components: anal scraping, mandible drumming and mandible scraping. Consistent with other territorial displays in animals, these signals are generated primarily by the resident; they escalate as the encounter proceeds, and typically cause the intruder to leave the territory (Yack *et al*. 2001). Recent studies suggest that these signals provide information about size (signaling resource holding potential) and motivation (signaling value assessment) of the contestants (Yack et al. in prep). Comparative studies of species representing the 3 main subfamilies (Thyatirinae, Drepaninae and Cyclidiinae) showed that at least 50 % of species use vibratory communication. Mapping behaviours and morphological structures onto a phylogeny provides support for the hypothesis that these signals derive from vibratory cues produced by movements associated with physical aggression (Scott *et al.* 2011; Scott & Yack, in prep). Territorial signaling is correlated with silk investment in late instar larvae that occupy solitary leaf shelters. More recent work has shown that earlier instars (1-2) living in groups produce even more complex signaling (with up to 4 signal types) when they are interacting with one another (see figure at left), and in these cases, signaling is associated with feeding, movement patterns and shelter building.



Within the Bombycoidea and Drepanoidea we see that acoustic communication is not only fairly common, but also diverse with respect to function and mechanisms of signal production. But these are only two superfamilies of Lepidoptera- hardly representative of other insects and spiders. The remainder of my talk will consider acoustic communication in the immature stages of other insects, and will discuss where we should be focusing our research efforts to better understand the role of acoustics in the young ones!

Bura VL, Hnain AK, Hick JN, Yack JE (2012) Defensive sound production in the tobacco hornworm, *Manduca sexta* (Bombycoidea: Sphingidae) *J. Insect Behav.* 25:114-126

Bura VL, Rower VG, Martin PR, Yack JE (2011) Whistling in caterpillars (*Amorpha juglandis*, Bombycoidea): Sound-producing mechanism and function. *J. Exp. Biol.* 214:30-37

Scott JL, Kawahara AY, Skevington JH, Yen S, Sami A, Smith ML, Yack JE (2010) The evolutionary origins of ritualized acoustic signals in caterpillars. *Nature Commun.* 1:4

Yack, JE, Smith, ML, Weatherhead, PJ (2001) Caterpillar Talk: Acoustically mediated territoriality in larval Lepidoptera. *P.N.A.S.* 98:11371-11375.

Contributed Talk Abstracts

A comparative analysis of the stridulatory file across katydid species (Orthoptera: Tettigoniidae)

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Sexual selection promotes the evolution of male signals that enhance access to females, while natural selection favours signal expressions that enhance fitness by reducing mortality risk. Acoustic insects like katydids offer excellent models to investigate this theory. Katydid songs are produced in a two-step process: the first step, termed stridulation, is a mechanism of frequency multiplication that allows the slow muscle contractions (7–30 Hz) to generate a higher frequency of vibrations. In this step, the plectrum on one wing is rubbed against the teeth of a file on the opposite wing (Fig. 1). The second step is amplification by the wing radiating cells. Katydids can hear and communicate over large distances, especially in habitats with little vegetation. But in habitats dominated by vegetation, the transmission of sound causes interference and so the spatial position of the sender and receiver is crucial in determining the maximum hearing distances and broadcast ranges. Therefore, traits employed to broadcast or detect signals are directly targeted by multivariate selection. In katydids, the call quality varies across species from pure tone (musical) to broadband (noisier signal). Both reflect adaptations for different environmental demands. For instance, musical calls particularly enhance communication in noisy environments, while favouring directional hearing, and a species-specific communication channel. Conversely, broadband signals seem less vulnerable to amplitude fluctuations, and might be considered adaptations for reliable long-range transfer of information.

Since stridulation begins with the interaction file-plectrum, pure-tone calls should therefore require an accurate design of the stridulatory structures: file and wing resonators. An untested theory predicts that file teeth spatial distribution should exhibit lower variance in musical species compared to those employing broadband calls. Using 46 katydid species which express broadband or pure-tone signals, measuring inter-tooth spacing in their files, and controlling for phylogenetic dependence, we strongly support this prediction empirically.

Our evidence highlights the asymmetric demands imposed on the adaptive design of signalling phenotypes by selection arising from environmental components involving both sexual and ecological effects on fitness.

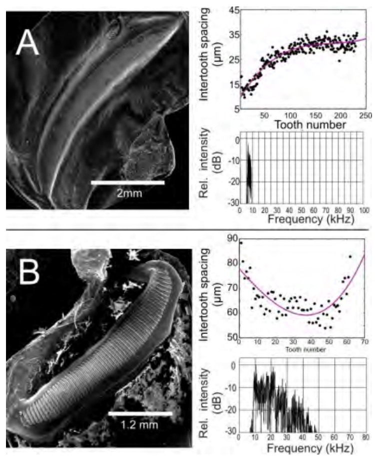

Fig. 1. File tooth organization in two different species using: A: Pure tones (*Panacanthus pallicornis*, Conoceph.), and B: Broadband signals (*Panoploscelis specularis*, Pseudop.)

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New insights into vibrations as species-specific signals in mason bees

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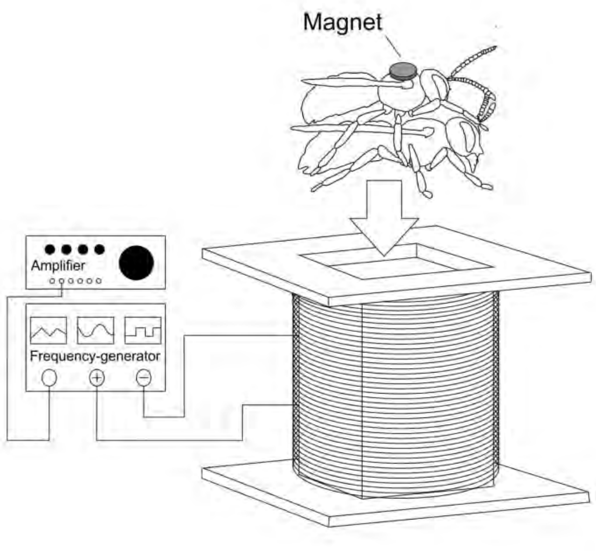
Vibrational signals are used by various animal species when communicating and commonly play an important role in mating. Even though many bee species are known to emit vibrational signals during mating, there are almost no studies on the function of these vibrations. Vibrational signals are produced by bees through vibrations of the thorax, as is the case in the precopulatory mating behavior of the red mason bee *Osmia bicornis*. A previous study has already shown that a female might use these thorax vibrations to choose a suitable mate. We could show that male vibration burst length was significantly longer in accepted than in rejected males (Conrad et al. 2010). Vibrations may therefore indicate vigor and assure that the males selected by females are in fact the healthier ones.

Sexual selection can be a prominent force in species divergence, and if the bees' vibrational signals are species-specific, they can also play a role in species divergence. In order to investigate the role in species divergence we analyzed vibrations of *O. bicornis* from England, Germany and Denmark and of the sister species *O. cornuta*.

Our results showed significant differences in the frequency and modulation of vibrational signals between *O. bicornis* and *O. cornuta* and between the subspecies of *O. bicornis,* supporting our hypothesis that they might have an additional function to showing an individuals' strength. Based on these results we conducted bioassays to further investigate if and how the differences in vibrational signals are actually used by the bees. In order to change males' vibrations we invented an interesting new technique involving magnets and an inductor to experimentally change the bees' vibrations. With this technique we were able to change a German male's vibrations into an English one's, and vice versa. This consequently led to a difference in female choice. In order to finally prove the function of vibrational signals for species recognition and as an isolation barrier we are presently performing further behavioral experiments.



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Intrinsic Variability and Temperature Effects in Locust Auditory Neurons

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Recognition of acoustic communication signals is crucial for many insects. Various factors can prevent accurate signal recognition, e.g. shifts in environmental temperature, extrinsic noise and intrinsic neuronal noise. The latter is determined as the trial-to-trial variability of the neuron's responses to identical sounds. Basic properties of neurons such as spike rate, conduction velocity, and spike amplitude are influenced by temperature shifts; for acoustically communicating insects this means that both the production and perception of sound are strongly temperature dependent. Here we focus on how temperature affects intrinsic noise and thus the coding efficiency of auditory neurons.

In grasshoppers, processing of auditory input starts within the metathoracic ganglion. The first three processing stages comprise receptor neurons, local and ascending interneurons, which are part of a feedforward network. Here, the first stages of song pattern recognition and analysis of sound direction are accomplished.

To investigate the responses of auditory neurons in grasshoppers to changing temperatures, we recorded intracellularly from identified neurons at two different temperatures (first at 28°, then at 20°C). Short acoustic broad-band stimuli (100 ms, 1 – 40 kHz) were delivered five times each at intensities rising from 32 to 88 dB, and spike-rate intensity functions as well as temperature coefficients (Q_{10}) were determined. All neurons exhibited an increase of spike rate with higher temperature, as well as decreased first spike latencies and action potential durations. Amplitudes of action potentials did not consistently change with temperature.

Intrinsic variability of the neurons was assessed by comparing the trial-to-trial variability between spike trains of the five repetitions per stimulus intensity, and between eight repetitions of four model songs, using the spike train metric introduced by van Rossum (2001). The trial-to-trial variability of the spike trains of a given neuron decreased with increasing temperature. This was also true when we used amplitude modulated model songs instead of the short block-like stimuli. Responses of receptor neurons were least affected by rising temperature, while in local and ascending interneurons the variability decreased significantly. This was due to a higher precision of spike timing (decreased variation in inter-spike-intervals) rather than a lower variability of spike count, which actually increased with higher temperature.

van Rossum 2001, Neural Comput 13:751-763

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Anthropogenic effects on vibratory environments and orb-web spider foraging behaviour

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In nature, animals must contend with the presence of noise, which limits their ability to perform important behaviours. Sources of noise can be constant (e.g. "overall" background noise) or intermittent (e.g. wind-induced noise) as well as from natural (e.g. animal sounds, water) or anthropogenic (e.g. traffic, construction) sources. The vibratory modality has long been overlooked in the study of anthropogenic effects on wildlife. Human-induced changes may introduce noise sources and new substrates that alter the vibratory environment of animals. We conducted field measurements of vibratory noise on various substrate types (natural and artificial) in urban and rural habitats. Next, we conducted lab experiments on how vibratory noise affects prey detection ability of the European garden spider (*Araneus diadematus*). We found that anthropogenic sources were a significant source of noise on webs. Garden spiders showed improved responses to prey cues under noise levels similar to wind-induced vibrations on natural substrates while responses were diminished under noise levels similar to those on artificial substrates suggesting predatory abilities are impaired on artificial substrates.

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Calcium ions modulate transduction, and are strongly buffered in spider mechanosensory neurons

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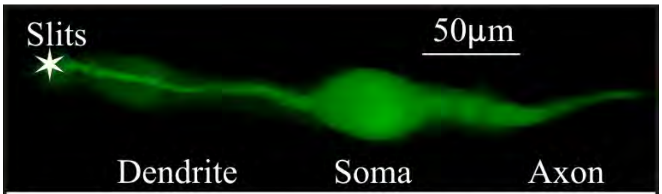
The numerous slit sense organs on the spider exoskeleton are believed to be involved in the detection of vibration produced by mates, prey, and predators. They also detect skeletal strains caused by muscular activity and hemolymph pressure. The VS-3 organ in the leg of the wandering spider, *Cupiennius salei,* adapts so rapidly that it must respond strongly to leg vibration. VS-3 organs consist of 7-8 cuticular slits, each innervated by a pair of bipolar sensory neurons. The neuron cell bodies are close to the slits and are accessible to intracellular recording, voltage clamp and pharmacological experiments during mechanical stimulation of the slits. Therefore, the preparation provides an important model system for studies of mechanosensory transduction and encoding.

VS-3 neurons contain low-voltage-activated Ca^{2+} channels that are only opened by action potential firing. The Ca^{2+} channels are widely distributed, and Ca^{2+}-sensitive dye imaging has shown that Ca^{2+} enters rapidly throughout the neurons when they are stimulated mechanically. We asked what roles Ca^{2+} play in the transduction and encoding of mechanical stimuli into action potentials, and how well is intracellular $[Ca^{2+}]$ regulated?



VS-3 Neuron filled with calcium-sensitive dye (Og488 BAPTA-1)

Intracellular $[Ca^{2+}]$ in VS-3 neurons was modulated by UV light-induced release of Ca^{2+} from cage molecules. $[Ca^{2+}]$ was simultaneously measured by a Ca^{2+}-sensitive dye. Both reagents were allowed to diffuse into the cell through a sharp glass microelectrode that also provided voltage clamp recording of mechanically induced receptor current, or current clamp measurement of receptor potential. $[Ca^{2+}]$ rise reduced receptor current and receptor potential in a dose-dependent manner. The data indicated that two Ca^{2+} bind to a substrate, possibly the mechanically–activated ion channels.

Endogenous Ca^{2+} buffering and clearance were estimated by allowing Ca^{2+}-sensitive dye to diffuse from electrodes into neurons over several hours, with the dye acting as both an intracellular $[Ca^{2+}]$ indicator and an added Ca^{2+} buffer. $[Ca^{2+}]$ was raised at intervals by firing action potentials with electrical pulses. The resulting $[Ca^{2+}]$ rise and fall were well fitted by a single compartment model of Ca^{2+} flows. Strong endogenous buffering (ratio ~700) was obtained, and most additional free Ca^{2+} was removed from the cell within ~50s after action potentials. This close regulation of intracellular $[Ca^{2+}]$ supports its role as a significant feedback regulator of mechanosensory transduction.

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Treehoppers follow an experimentally imposed amplitude gradient

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Vibratory communication facilitates many different social interactions, and often locating the vibratory source is important. However, small plant-dwelling insects face a potential constraint in sensing vibration directionality, because they obtain only a tiny spatial sample of a propagating wave with their leg vibration sensors. Despite this constraint, even insects under 1mm long can find a vibration source on a plant, but the mechanisms that underlie this ability are largely unknown. It has been posited that using amplitude gradients to locate a vibrating source would be inefficient due to the unpredictable nature of amplitude gradients along plant stems. However, our previous experiments suggest that amplitude gradients may be important during localization. Here we investigated whether insects can follow an experimentally imposed vibrational amplitude gradient on a plant stem.

We used male thornbugs (*Umbonia crassicornis*), which are small (~1cm) plant-feeding insects that use vibratory communication throughout their lives. When searching for mates, males produce a vibratory courtship signal to which a receptive female will respond. Males duet with the stationary female while homing in on her vibrational signals.

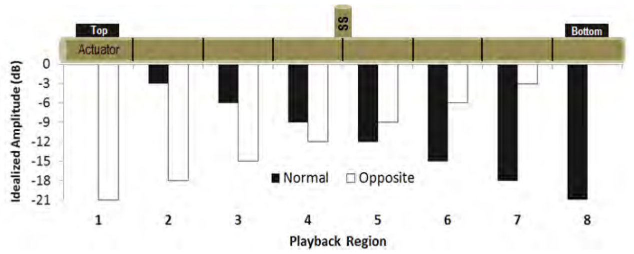

Figure 1: Diagram of the idealized playback arena.

The playback arena was a 24cm section of the mainstem of a potted 1.5m tall host plant. To simulate a receptive female, we affixed a playback device (a piezo-stack actuator) to the top of the arena. We then imposed one of two opposing amplitude gradients (in 3dB/3cm steps) onto the arena: In one treatment the gradient increased in amplitude from the bottom (low amplitude) of the arena to the top (high amplitude), while in the other the gradient increased in amplitude from the top (low amplitude) of the arena to the bottom (high amplitude) (figure 1).

A male was placed on a side stem, and the trial began when he duetted with the artificial female call and initiated searching. As males entered the arena, female signals were triggered immediately after the male's signals, the amplitude of the female signal varied depending on the male's position along the gradient. Trials continued until the male stayed at one end of the arena for longer than a minute, or walked off the arena.

Each of 42 males followed a gradient of increasing amplitude, even when the gradient led the male away from the vibration source. This outcome, combined with previous work, suggests that thornbugs may use a hierarchical approach when making directional decisions, sometimes ignoring information about the direction of wave propagation when other cues are present.

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Hearing of Aging Locusts

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In animal trials, scientists are careful to control for the age of their animals. Often older animals are less responsive, do not eat as much, and generally do not function as well as younger animals. We commonly think of these old animals as a bit 'geriatric', with their hearing amongst other senses fading. In mammals, older animals do not hear as well because their ears lose the ability to function. However, insect ears are different, with a sclerotized tympanum that formed during their final molt.

In locusts, this tympanum has the receptor neurons directly attached to the membrane and frequency determination results from displacement due to a traveling wave created with sound. Different sound frequencies result in a range of traveling wave shapes. We tested if locust hearing changes with aging animals. We measured their neurobiology as well as the physiological movements of their tympanal membrane.

As the locust ages it's hearing ability decreases. Younger animals have a shorter latency to neurophysiologically respond to sounds across all frequencies. In addition, younger animals have a greater neurophysiological response across all frequencies, especially at medium sound levels (70 & 80 dB SPL).

Interestingly, there are increasing differences between the sexes as they age. Males have a shorter latency than females across all age groups. However as they age, males also have a greater electrophysiology response, while no difference is seen in the youngest group. In addition, this data is reflected through larger physical movements of the tympanal membrane—ultimately deflecting the sensory neurons more. Understanding how hearing changes with age is important, not just for the physiological and biological implications, but as locusts are a model organism, it suggests the need for caution with using animals of uncontrolled ages.

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Mechanisms driving the evolution towards chorus synchrony – a case study on *Mecopoda elongata* (Orthoptera: Tettigoniidae)

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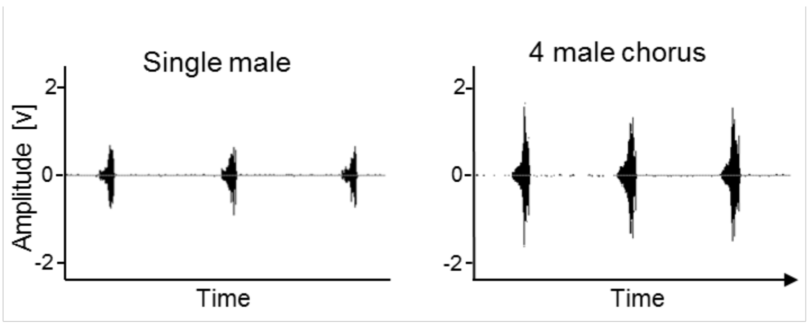
Mecopoda elongata males tend to display their acoustic signals in synchrony. Synchrony has also been observed in other taxa, but the mechanisms driving its evolution may be different. Theoretically, this group phenomenon can be either the outcome of inter-male competition or cooperation. Synchrony could be regarded as a cooperative act if males (1) increase the signal amplitude by calling in synchrony ("beacon-effect"), and/or (2) preserve their species-specific signal pattern. By contrast, chorus synchrony could be the by-product of inter-male competition, if females prefer signals that are timed in advance to those of competitors (leader preference). To distinguish between these alternatives we analyzed signal interactions of males in small choruses and conducted female choice experiments.

Males exhibited an exceptionally high chorus attendance where individuals often established consistent leader and follower roles for long periods of time. Signals produced in choruses showed a high degree of temporal overlap (see figure) with an average time lag between competing signals of only 73 ms. As a consequence, peak and rms signal amplitude increased by about seven dB when four males were active at the same time compared to solo singing males. Due to this resulting beacon effect males in a group likely attract a higher number of females compared to solo singing males. Against the "cooperative hypothesis", males in a chorus slightly increased their chirp rate compared to solo singing. Female choice experiments revealed that a time lag of only 70 ms was sufficient to bias female preference towards leader signals. Furthermore, a song model with a species-specific signal period of two seconds was more attractive compared to a song model with either a random signal period or a song model with a higher signal period of 2.5 s.

From these results we conclude that, in order to become attractive for females, males are forced to synchronize their periodic signals in a chorus. In doing so males compete for the attractive leader role, which results in a beacon effect due to a high degree of signal overlap. We argue for a trade-off between benefits gained through a beacon effect and costs associated with attaining leadership. The latter arises from a possible leader preference of a parasitoid fly species homing in on singing males. This may stabilize the follower role in *M. elongata*.



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How female crickets evaluate conspecific songs: a comparative view

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The songs of many crickets exhibit two time scales: a series of pulses is broadcast at a particular pulse rate on the short time scale, while groups of pulses, also called chirps, provide information on the long time scale. How do female crickets evaluate and weigh such pulse patterns for recognition of their conspecific song ?

For that goal we tested the phonotactic response of female crickets of several species (n = 7) within the genus *Gryllus* towards artificial song patterns. On the short time scale most species revealed preference functions tuned to a particular pulse rate (e.g. Fig. 1) that matched the song of conspecific males. On the long time scale the preference functions were more diverse. While some species preferred a minimal chirp duration, others responded best to a particular duty cycle of a song pattern, that is the ratio of the chirp duration to the chirp period. Further tests also revealed a large diversity between different species in terms of the relative weighting of both time scales. While some species appeared to evaluate the pulse rate alone irrespective of the chirp pattern, others required song patterns that contained information on both time scales.

In summary, for all species a preference for the conspecific pulse rate was observed. On the long time scale, however, species differed remarkably in their preference for a particular chirp pattern and in their relative weighting of the short and the long time scale. These results show that for an understanding of the evolution of preference functions in crickets both time scales have to be considered.

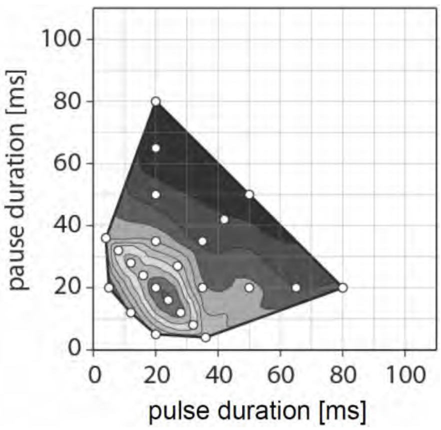

Fig. 1) The preference function of *Gryllus bimaculatus* for pulse rate. Females prefer test patterns with a pulse period of 40 ms over a wide range of pulse durations and pulse pauses.

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A comparison of cricket phonotaxis under outdoor and laboratory conditions

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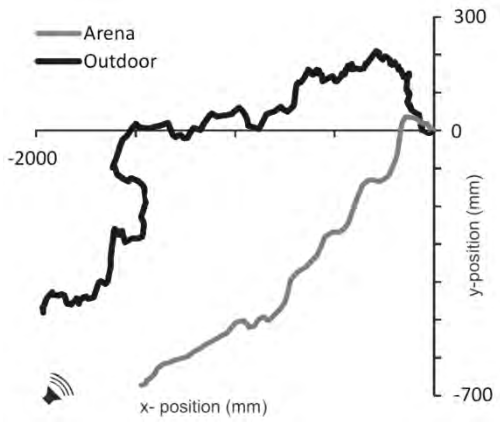
At the behavioural level, several methods have been used to quantify the degree of orientation or motor steering of female crickets towards song models (locomotion compensators, arena trials and outdoor tests). Each of these rather different approaches has its special advantages and limitations due to the freedom of movement of the females, the preciseness of control over stimulus parameters, or whether females perform phonotaxis under open or closed-loop conditions. However, since females usually make decisions in their natural grassland habitat, the laboratory approaches have to be complemented with outdoor experiments, where cricket phonotaxis has only rarely been observed and quantified. Outdoor conditions are challenging for receivers, because important signal parameters can be strongly degraded on the transmission channel and masked by noise (Römer 1998; Kostarakos and Römer 2010). Thus decisions based on small differences between signal variants may be less relevant under realistic natural conditions.

Here we present one of the first quantitative studies on phonotactic behaviour of *G. bimaculatus* in their natural habitat and can compare results of outdoor experiments with those of arena and trackball paradigms using identical stimulus situations. For example, in two-choice tests outdoors females discriminated between two song alternatives, and prefered the more intense, at a minimum difference of 5 dB. In contrast, on the trackball or in arena trials intensity discrimination and preferences were observed with differences of 2 or 3 dB, respectively. Similarly, females discriminated outdoors against song alternatives differing in chirp rate at a minimum difference of 50 chirps/min, whereas on a trackball this difference was only 20 chirps/min (Trobe et al., 2010). Furthermore, a comparison of phonotactic paths towards a single sound source demonstrated longer detours in outdoor experiments compared to arena trials (see figure). However, despite the many obstacles in the natural environment there was no difference in the walking speed of females. In addition, when presented with a change in the choice of song alternatives females responded with a similarly fast dynamic change in the orientation towards a new target.



Based on a direct comparison of phonotactic paths towards one or more conspecific signals obtained in three different behavioural paradigms, we discuss the advantages and limitations of the various behavioural methods.

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The effects of two similar acoustic signals on an active ear

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Masking is an ever-present problem for listeners in the real world. How an animal deals with noise – or other unwanted signals – in its auditory system, can be as important as how it processes relevant sounds. Often there are simple remedies – an ear that is narrowly tuned, for example, will reject noise not spectrally located within the bandwidth of the ear. This simple remedy has a drawback though – with a narrowly tuned oscillator as an acoustic sensor, one loses temporal acuity. Animals only interested in signals with almost pure-tone spectral content will likely have evolved a sensor that is some compromise between spectral sharpness, sensitivity, and temporal acuity.

For the mosquito, the presence of noise is an eternal problem – the male culicid *Toxorhynchites brevipalpis* listens to the sound of the female flight tone, which unfortunately occupies the same bandwidth (as defined by the antennal frequency response) as the male's own flight tone. Mechanical tuning cannot reject strongly a similar tone. Furthermore, the male has evolved an unusual mechanical response to a female sound that is thought to be the result of the synchronization of an ensemble of excitable nonlinear oscillators. How is this active, nonlinear, mechanical response affected by the sound of his own flying?

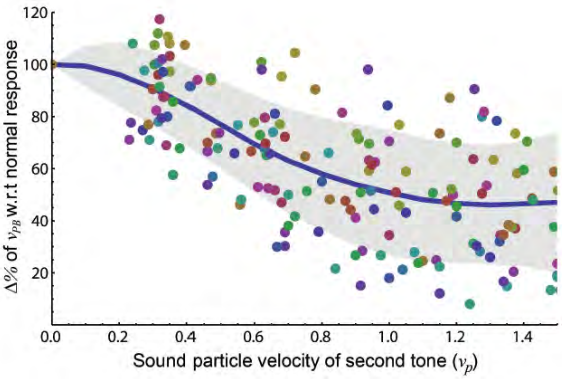

Figure 1. Effect of a second sound on the nonlinear amplification threshold. An increase in the amplitude of the second signal reduces the threshold percentage.

In order to determine the effect of a male sound impinging on the male ear, and the corresponding change in the typical nonlinear dynamics of the male ear, we performed a series of experiments that added male- and female-type sounds together. By monitoring the mechanical motion of the male antenna using laser Doppler vibrometry, and the neural output using extracellular electrophysiological measurements of the auditory nerve, we found that the presence of a male sound created a potentiation effect, in which the mechanical threshold for antennal amplification typically induced by a female is decreased. This counter-intuitive result suggests the male's auditory response is not hindered by the sound of his own flying, but instead aided in his quest for the female. Neurally, a frequency-decomposition reveals that the male tone is suppressed as the female tone increases in intensity. This rejection of the male tone suggests that the male ear can exploit the mechanical benefits of his own flight tone without compromising the neural output of his ear.

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Complex acoustic networks in the cricket wings

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Male field crickets produce loud musical songs by rubbing their raised forewings together to attract conspecific females. A plectrum on the anal edge of the left wing (LW) engages with a serrated vein on the underside of the right wing (RW). Each wing shows cells specialized in sound radiation (Fig. 1). The song emitted by the male must sufficiently loud to successfully attract females. Small sound-producing insects like crickets are therefore under strong sexual selection to maximize signal range. One way to increase song amplitude is to increase the area of sound radiation; field crickets do this by using two wings for sound radiation. They also use pure tones with carrier frequencies of ca. 5 kHz, and this is determined by wing resonance, which implies that the vibrations of both wings must be strongly coupled to maintain perfect phasing of the wing vibrations. Only if both wings vibrate in phase will the animal achieve an optimum in resonance and loudness for the combined acoustical output (through constructive interference).

Using Laser Doppler Vibrometry (LDV), high-speed video recordings and specialized acoustic equipment, we simultaneously recorded the vibration of both LW and RW during stridulation in field crickets (*Gryllus bimaculatus* DeGeer). Under the underlying assumption that the crickets cannot afford destructive interference and loss of sound radiating surface, we test the hypothesis that both wings should vibrate in perfect phase, and no destructive interference should be observed among wing regions.

Results show that wing cells of each freely vibrating wing exhibit independent local resonances with relatively broad spectra and damped resonances at variable frequencies. Amazingly, when wings engage in stridulatory motion, all wing areas resonate at a single identical frequency, and all broad-band patterns vanish (Fig. 1). In the crickets studied here, the wing-based stridulatory mechanism tolerates phase differences of up to ca 70º, while still maintaining reasonable song amplification in the combined waveform output. These results suggest that the escapement mechanism used by field crickets will not allow them to exploit high frequencies while maintaining both song purity and song loudness.

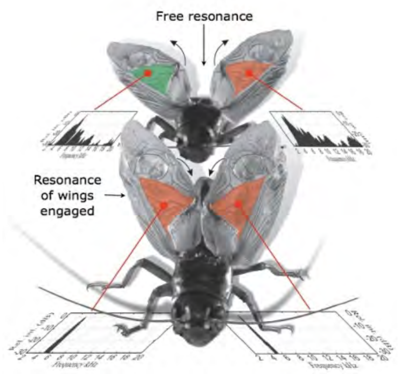

Fig. 1. Wing resonance in a stridulating cricket. Shown are the marked changes in resonance frequency that occur during stridulation, as measured with LDV. Bottom: wings engaged, sharp resonances. Top: wings free, broad resonance spectra.

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Calling song recognition in an insect brain

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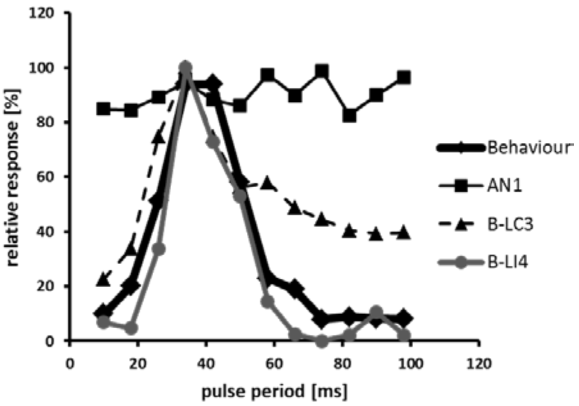
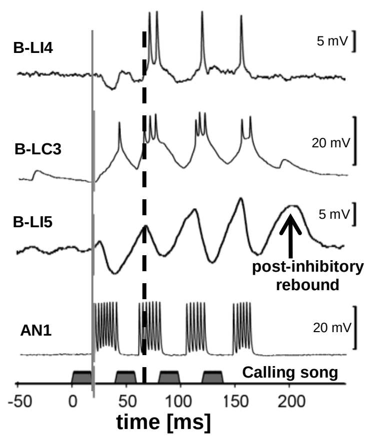
Acoustic communication is central to the lifestyle of many animals and crucially linked to mate attraction, rivalry behaviour and group formation. The calling song of field crickets consists of simple sequences of sound pulses and chirps with species-specific temporal features. Female crickets recognize the temporal structure of the song and specifically orient towards the signaling male by phonotaxis. The pattern recognition process resides in the brain but the underlying neural mechanism is not resolved.

In order to analyze pattern recognition in female *Gryllus bimaculatus* we performed intracellular recordings from brain neurons and compared their responses with the temporal selectivity of phonotactic behaviour. Our morphological and physiological data show that brain neurons form a ring-like neuropil at the axonal projections of AN1 in the anterior protocerebrum and that temporal pattern recognition is established at this early stage of auditory processing. Fast interactions of inhibition and excitation seem to shape the temporal selectivity of neurons within the pattern recognizing network.

We identified local auditory brain neurons with spike responses that mirror the temporal selectivity of the behaviour. Contrary to the ascending neuron AN1, brain neurons are tuned to the temporal features of the song (left Figure). These neurons responded stronger to consecutive sound pulses of the calling song than to other pulses. One specific neuron (B-LI4) that matched best with behaviour, showed inhibitory inputs to the first sound pulse of a chirp and responded with spikes only to the consecutive pulses of a chirp. Our data also indicate that a non-spiking interneuron (B-LI5) plays a central role in the process of pattern recognition. In response to each sound pulse of a chirp this interneuron generates a transient inhibition followed by a post-inhibitory rebound depolarization. Only when the species-specific calling song is presented, does the delayed depolarization coincide with the ascending auditory spike activity of AN1 to the subsequent sound pulse (right Figure). At shorter and longer pulse periods the graded depolarization and ascending spike activity are not synchronized. This neural mechanism mirrors the concept of autocorrelation by delay-coincidence, a theoretical concept proposed for pattern recognition in crickets and matches the activity pattern of B-LI4. The delay is established by specific membrane properties shaping the time course of a post-inhibitory rebound rather than by synaptic or axonal delay lines. Our findings indicate a principle neural mechanism for the recognition of repetitive stereotyped pulse-patterns, which may occur in different species and sensory modalities.





This work was funded by the Royal Society (Newton International Fellowship) and the BBSRC

Insight into intraspecific interactions in the leafhopper *Aphrodes makarovi* (Hemiptera: Cicadellidae)

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In leafhoppers mate recognition and location is mediated by substrate-borne vibrational signals. Pair formation begins with emission of male calls and after partners establish a duet male searches for a stationary female. We investigated the role of male competition in mating behaviour of the leafhopper *Aphrodes makarovi*. In this species males emit long and complex calling signal and female reply always overlaps the end of male call. Furthermore, species-specific temporal parameters of female reply are crucial for recognition and successful localization. We focused our work on the following questions: (a) is precise timing of female reply necessary to ensure the recognition and to trigger searching behaviour; (b) do intruding males use alternative tactics like satellite behaviour and/or masking signals; (c) how energetically demanding is production of male calling signals and (d) do males in impaired condition show different competitive tactic than intact males?

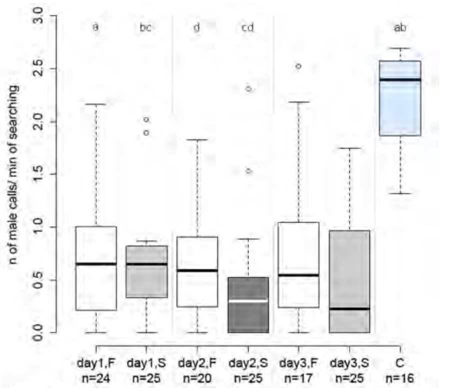

Figure 1: number of calls emitted per minute of searching regarding the male's physical condition. There were 3 groups: C = control group of males duetting with a female; F = group of fed males exposed to rival on days 1-3; and S = group of males exposed to rival on days 1-3 and starved on day 2. There is a significant decrease of calls/min of searching in groups exposed to rival compared to the control group (a, b) and there is a significant decrease of calls/min of searching on day 2 in starved group compared to the same group on day 1 (c) and fed group on day 2 (d).

We tested males in unilateral playback experiments in which we presented them a female reply with different time delays after the end of their call, as well as in bilateral playback experiments in which we presented from one side male call and from the other one female reply. We also measured oxygen consumption of calling and non-calling males. To obtain males in impaired condition we exposed them to starvation and then tested them in bilateral playback experiments. In all behavioural experiments we recorded vibrational signals, as well as leafhopper behaviour. We compared the proportion of searching males, number and duration of male calls during the search, rival call emission, time spent to locate the female and success in locating the female. In another set of experiments we measured oxygen consumption of calling and non-calling males.

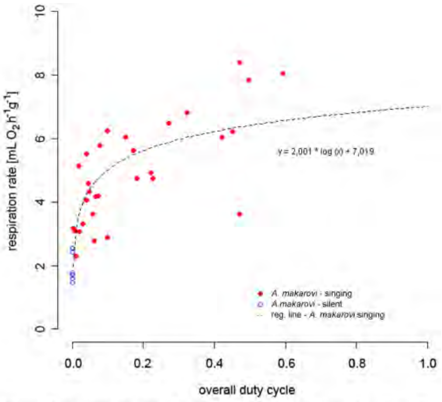

Figure 2: respiration rate of singing and non-singing males. Overall duty cycle is taken as the ratio between singing time and duration of the experiment. There is a significant difference between non-singing males and singing ones.

Results showed a crucial effect of the timing of female reply on mate recognition and successful location of the female. Intruding males expressed satellite behaviour, as well as emission of masking signals. Males regularly switched to satellite behaviour in the presence of an ongoing duet. The degree of its expression seemed to be related to male's physiological condition which is also supported by our results showing that singing is energetically demanding. Impaired males reduced the number of emitted calls, but not call duration, which indicates that male call duration may be under the influence of sexual selection.

Sound production of *Mecopoda elongata*: circadian rhythm and maturation

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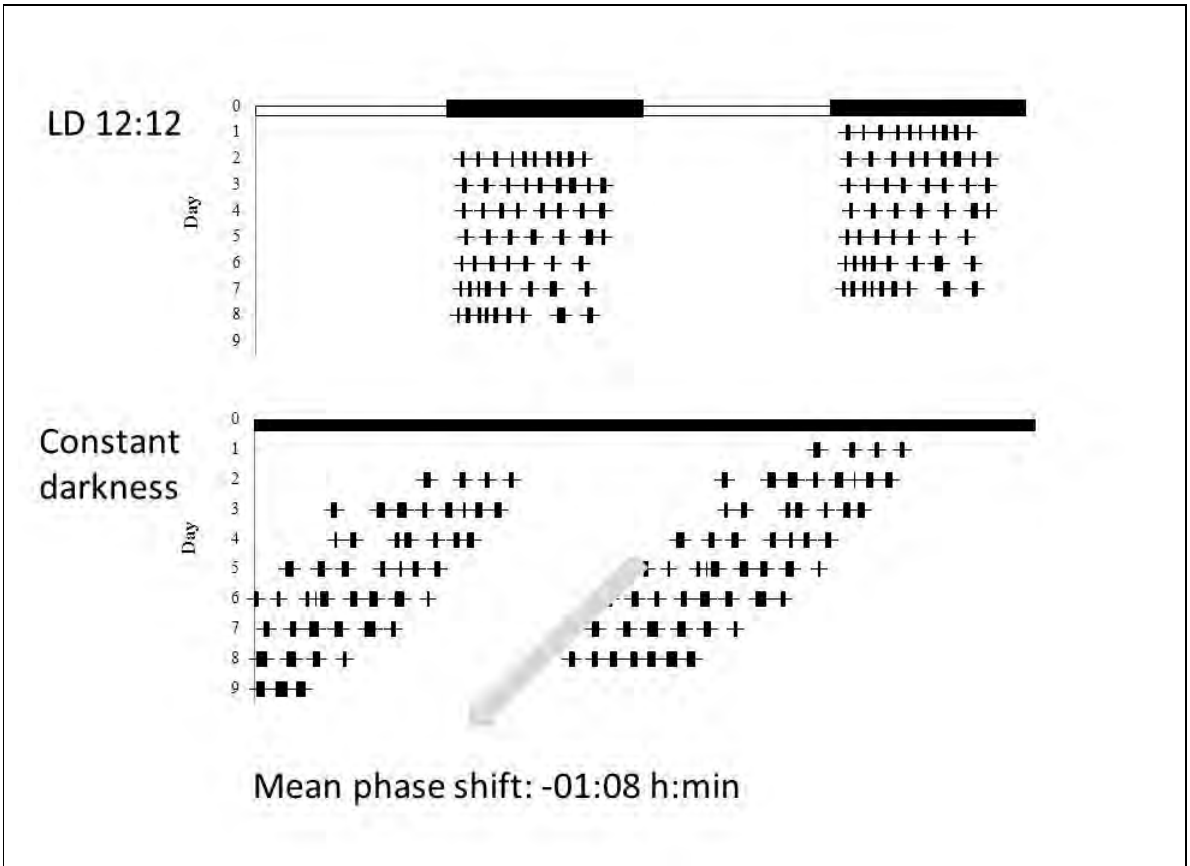
Insect acoustic communication underlies as many other behaviors the influence of circadian rhythms. Sound production is timed into acoustic niches in many insect species. With sound recordings of individually caged males the stridulatory activity could be demonstrated. Here we show how the rhythmicity of the stridulatory activity of male *Mecopoda elongata* develops and maturates after the adult moult. The mature stridulatory activity starts shortly after the onset of darkness and animals stridulate with pauses for a total of about 8 hours. The activity depends on the light-dark regime and shows in constant darkness a phase shift of about -1 hour. Analysis of the stridulatory patterns show the constant and variable components in different time scales of this behavior Additionally, the PDF immunoreactive neurons in the brain of tettigoniids are shown.



Stridulatory activity of *Mecopoda elongata* under two different light-dark regimes within 7 to 8 days. Stridulation occurs in LD 12:12 with about 9 verses per night, with a mean duration of 13 minutes per verse. Note the phase-shift in constant darkness.

What's the password? Female red turpentine beetles (*Dendroctonus valens* LeConte) grant access to their galleries based on an assessment of male signals

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Bark beetles (Coleoptera: Curculionidae: Scolytinae) exist unconcealed for only brief periods of dispersal, and otherwise inhabit an unseen world under bark. This natural history makes them difficult to study over much of their life; however, it is clear that many species employ acoustic communication through stridulation in contexts of distress, and inter- and intrasexual relations. At present, little is known of the function of acoustic signals, although a growing body of research exists describing signal characteristics.

The main objective of this study was to test the hypothesis that the signals produced during intersexual interactions function in female choice, using the red turpentine beetle, *Dendroctonus valens*, as a model.

We found that *D. valens* males produce significantly different chirps when interacting with females than during distress. During distress, "simple" chirps are prominent: 91% of individuals produced exclusively simple chirps when disturbed. Simple chirps are discrete units with descending amplitude envelopes that contain evenly spaced tooth strikes. Meanwhile, while attempting to gain access to a female's gallery, 71% of males produce a second type of chirp, broadly categorized as "interrupted". Interrupted chirps are longer (~12 times longer), contain more tooth strikes (~135%) and with larger intervals between tooth strikes (the tooth strike rate (# tooth strikes/second) for interrupted chirps is ~1/5 that for simple chirps). Interrupted chirps can also be identified by the large gaps they commonly contain (which interrupt the chirp into two or more components) and by their ascending amplitude envelopes. Once the male disappears under the frass, it is typical that he will switch from predominately interrupted chirps to mainly simple chirps.

We also found male size correlates with certain temporal and spectral characteristics of the signals. We found variability in the stridulatory apparatus which corresponds to size. We will discuss the significance of these findings with respect to the mating behaviour of bark beetles.

We demonstrate that signals produced during male-female interactions differ from those produced under disturbance conditions, and may reflect signaler effort. We also show that signal characteristics are dynamic between males and their relationship to signaler size suggests they contain information on male quality.

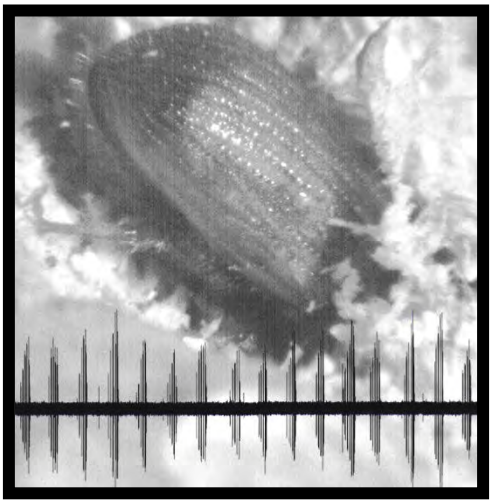

Figure: Male D. valens *digs through frass at a female's gallery entrance in an attempt to enter, all the while producing acoustic signals (a representative sample of which is illustrated in trace at bottom).*

This work was financially supported by funding from the Early Research Award and Canadian Foundation for Innovation to JEY, and from the Natural Science and Engineering Research Council for AAL and JEY

Model Locust Tympanal System: understanding the link between biomechanics and neurophysiology

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For over 50 years the auditory systems of insects have been of great interest to researchers in the field of acoustic systems. However, only recently have advances in technology allowed a more scrupulous approach to the study of the insect ear.

The locust hearing system consists of a stretched tympanal membrane backed by a tracheal air sac. The membrane has two distinct zones, the thin transparent membrane and anterior to this, the thick opaque membrane. At the internal boundary between these zones Müller's organ, a mechanosensory receptor organ, innervates the membrane, attaching at two areas of sclerotised cuticle - the pyriform vesicle (PV) and folded body (FB). Historical neurophysiological studies of the locust ear have shown that receptor cells coupled to the FB region are tuned to low and medium frequency stimuli in the range 1-12 kHz. In contrast, those cells linked to the PV are tuned to sound of frequency from 12-30 kHz.

This new work investigates the interesting and potentially valuable characteristics of locust ears. The properties which define the system have been studied using SLV and Scanning Electron Microscopy. Thereafter virtual computer models, representing the auditory system, have been built and finite element analysis applied. The finite element analysis uses a combination of the examination of standard free-resonating eigenmodes, and a simulation of the interaction of the tympanal membrane structure with a sound field.

For a wide range of stimuli, the model and simulations enable us to predict the unique membrane behaviour. The results are analysed with a view to linking the biomechanical response and corresponding neurophysiological response of a locust. This allows us to understand the mechanical processes undergone by the ear structures, as well as the influence of the nervous system.

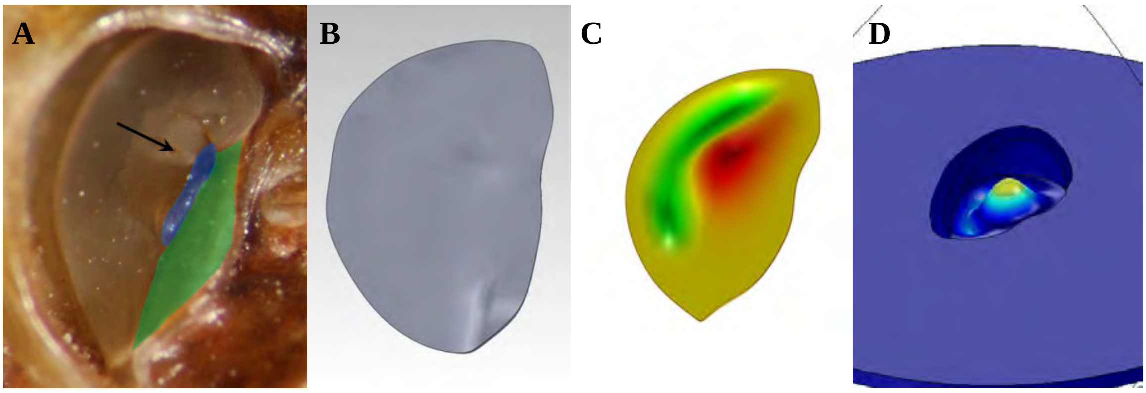

Figure 1 – **A.** Locust ear with thick membrane in green, FB in blue and arrow showing PV. **B.** Reconstructed 3D CAD model. **C** and **D.** Simulation results from 2 different locust model hearing systems.

This project is funded by the Engineering and Physical Sciences Research Council.

The Locust Ear: A General Mechanism for Tonotopy and Energy Localisation

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The ears of animals are exquisitely adapted to capture sound energy and accomplish diverse forms of signal analysis. In mammalian species, auditory signal processing enabling high sensitivity and frequency analysis is associated with the sophisticated histoarchitecture of the inner ear's cochlea.
Similar processing, namely frequency-dependent energy localisation, is possible using solely structural features of a tympanal membrane. The mechanical properties of the tympanum of the locust, such as distributed thickness and boundary conditions, are necessary and sufficient to generate sound-induced travelling flexural waves and energy localisation. The waveform transformation of the vibrational wave as it travels across the tympanum is reminiscent to that of a tsunami shoaling. Biologically, this localisation of deflection amplitude increases the vibrational energy delivered to the mechanoreceptors. In effect, this mechanism enhances the ear's sensitivity to sound.
Using finite element analysis, we show that a linear elastic membrane with a concentric thickness gradient and suitable boundary conditions are sufficient to produce frequency decomposition and energy localisation.
This work opens up the possibility of designing bio-inspired structural microphone membranes, a novel concept that provides interesting opportunities for sensitive and energy-efficient acoustic detection.

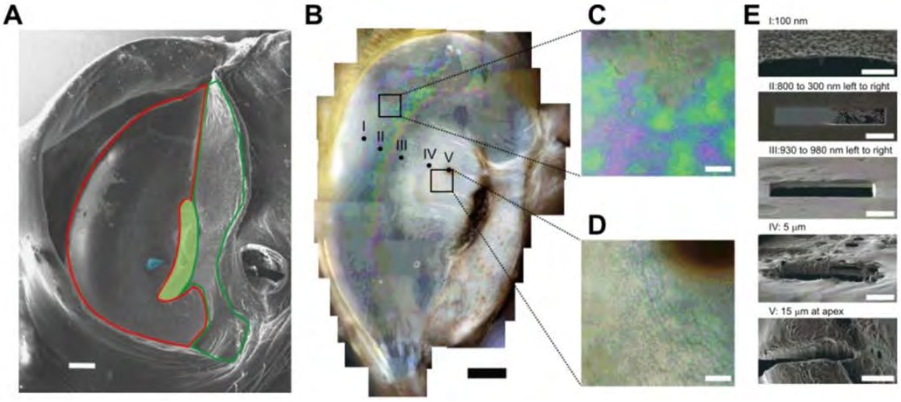

Figure 1 - Locust membrane structure. (A)SEM of external ear surface, thin region outlined in red, thick region in green, folded body (FB) in solid green and pyriform vesicle (PV) in solid blue. (B) Newton ring profilometry of membrane. (C) Thin region. (D) PV. (E) FIB millings at locations shown in (B).

NM is supported by a Marie Curie fellowship. DR is supported by the Royal Society of London and the Wolfson Foundation. The project was funded by a grant from the Biotechnology and Biological Sciences Research Council UK.

Mating Disruption of Insect Pests with Vibrational Signals: from Theory to Practice

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Mating communication in many insect species is mediated by substrate-borne vibrational signals that play a main role compared to other sensory cues. This is the case, for example, in leafhoppers (Hemiptera, Cicadellidae) in which are included many important crop insect pests. In these species mating signals are characterized by species-specific features (spectral and temporal) that allow the receiver to estimate identity, and to perform location and courtship, after establishing a vibrational duet with the partner.

As model species we used *Scaphoideus titanus* a grapevine leafhopper which is a vector of a phytoplasma disease Flavescence dorée. In this species rival males show complex rivalry behaviour which includes specific signals to interrupt a mating duet of another male with a female. Thus we hypothesized that playing back the male rivalry signals to grapevine plants we would be able to disrupt the mating behaviour of *S. titanus*, thus preventing the copulation.

First, we conducted laboratory tests on pairs placed on a grapevine leaf to demonstrate that mating disruption with vibrational signals is feasible.

As a second step we tested a system of potted plants inside plastic cages interconnected by iron wires, to simulate a typical vineyard trellis. Pairs of *S. titanus* were released into the cages for 18 hrs (4 pm to 10 am) and a prototype of a vibrational shaker with best transmission performances was used to vibrate the wire. As a result more than 90% of pairs remained unmated (in control treatment only 20% of pairs did not mate).

Later we applied vibrational mating disruption to mature plants in open vineyard. Pairs of males and females were released inside net sleeves including 3-4 grapevine shoots with fully developed leaves. Again the disruption signal was continuously applied to plants through the supporting trellis wire for 18 hrs. Results showed that even 10 m away from the shaker more than 90% of pairs were remained unmated, compared to 20% of non-mated pair in controls.

Finally, we applied the method to test new prototypes of shaker that may be effective at longer distances and with different disruption time regimes in order to spare energy consumption. We found that 65% of mating disruption is still achieved at 45m and that at least 18 hrs of disruption are necessary to have 80% of success. Now our aim is to further optimize the system in order to make the device an economically sustainable tool for agricultural use.

Two to tango: how tree cricket song changes with temperature and auditory tuning keeps up

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Placed against the wild variety of sounds and songs made by animals, insects may appear a bit staid. Their songs are repetitive, a single note sung over and over again. The simple but powerful explanation for this one note song is that insects use mechanical resonance to produce sound.

Analyses of their sounds and sound producing structures show that insects are sub-optimally sized for the frequencies they use. Mechanical resonance is an efficient mechanism to produce powerful songs, certainly more effectual than a non-resonant system. By definition, however, resonant systems operate best at a single frequency and hence, insect songs tend to be tonal with only little variation.

But this is not always the case; some insects can change their frequency. The songs of tree crickets change with temperature. Like other crickets they chirp at higher rates when warmer, but uniquely their song frequency also increases by as much as an octave. Using tree crickets as model systems, we investigate the biomechanical basis of this variable frequency song using laser vibrometry and finite element modeling. We find that the frequency response of the wing depends on its geometry. We show that the unusual high aspect ratio of their wings allows tree crickets to exhibit a broad frequency response and produce songs of varying frequency while still using an efficient resonant system.

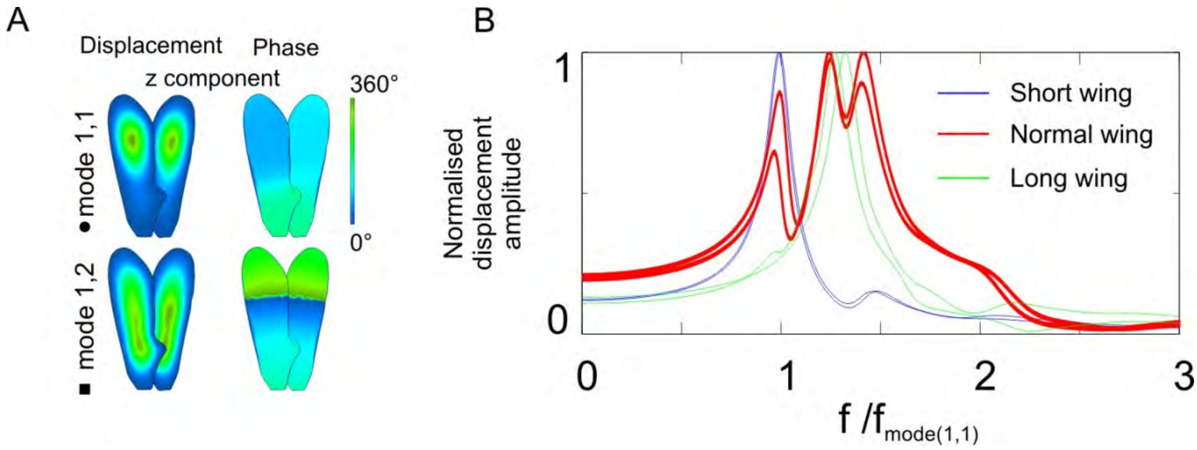

Figure: Finite Element Modeling of vibrational modes, wing geometry, and resonant responses. Modified from: Mhatre et al (2012), *PNAS*.

This varying song frequency, however, creates a reciprocal problem for the female receiver. Females must detect, identify and localize male song within a crowded and noisy environment. Like song production, female auditory capabilities are also thought to rely on resonance. The question then arises of how the auditory system of the tree cricket can keep up with changing, temperature-dependent male song. We are able to show using laser vibrometry, how female tree crickets solve this problem through the unique coupling of two independent resonant systems.

This research was funded by grants from the Biotechnology and Biological Sciences Research Council and the UK India Education and Reseach Initiative. NM was funded by a Marie Curie fellowship and DR by a Royal Society Wolfson fellowship.

What does a butterfly hear? Tuning and amplitude discrimination in the Blue Morpho butterfly

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The Blue Morpho butterfly, *Morpho peleides*, has an interesting and rather complex ear. As for most other butterflies that are diurnal, and mute, the function of hearing remains a mystery. The tympanic membrane is located at the base of the forewing (see figure) and comprises a dome-shaped inner membrane surrounded by an outer membrane. The inner and outer membranes are innervated by separate chordotonal organs (COII and COIIIa, b) that in turn are innervated by different nerve branches (NII and NIII). Why would such an ear evolve in a mute butterfly?

The first step towards answering that question is to determine what sounds the ear is capable of detecting with respect to frequency and amplitude, and to then relate this to what the butterfly might be exposed to in its natural environment. We recorded the extracellular responses of both nerve branches to sound pulses of varying frequency and amplitude.

Audiograms show that *M. peleides* is sensitive to frequencies between 0.5-20 kHz, with maximum sensitivity at 55 dB SPL between and 1-4 kHz. Both nerve branches have similar tuning curves. Compound action potential analysis of both nerve branches shows that the butterflies are capable of discriminating sound amplitudes over a dynamic range of ~30 dB.

What sounds might be important for a butterfly to hear? We propose that their ears function as ‘bird detectors’. We recorded flight sounds from foraging birds and demonstrated that insectivorous birds produce pulsed, broadband, acoustic cues. Through play-backs of bird flight, we show that both butterflies (sonic hearing) and moths (ultrasonic hearing) respond physiologically to the passive cues of approaching birds. Our results pave the way for future behaviour experiments with live birds, to explore the exciting possibly of an evolutionary arms race between birds and eared insects.

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Mechanical basis of self-generated sound in the locust ear

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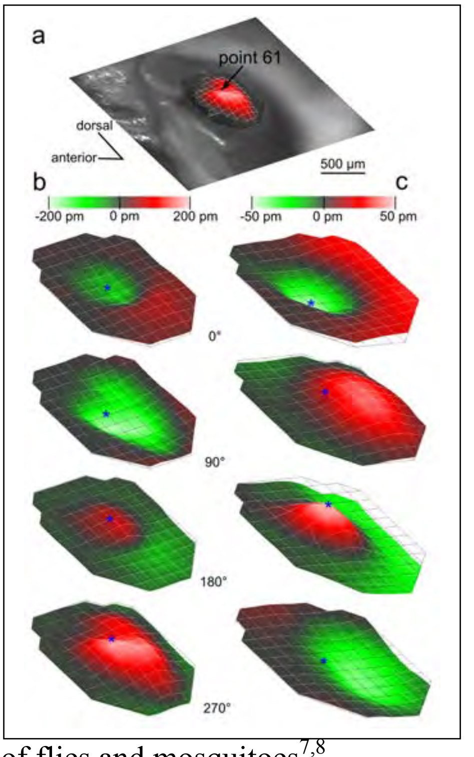
Insects, mammals and other vertebrates have a quite remarkable similarity: Their ears make sound while they are listening to sound. Such distortion-product otoacoustic emissions (DPOAEs) from tympanal organs have characteristics comparable to those of vertebrates[1], where they are used as indicator for nonlinear cochlear amplification[2-4]. Insect DPOAEs are highly vulnerable to manipulations interfering with the animal's physiological state[5]. Although previous studies gave first evidence for the involvement of auditory mechanoreceptors[4,6], the source of DPOAE generation in insects and possible active mechanisms in tympanal organs, however, are still unknown.

Here we show that DPOAEs mechanically emerge at the tympanum region where the auditory receptors are attached (a). Those emission-coupled vibrations (b) occurred locally restricted as standing waves around the receptor's attachment position, as the mechanical gradient of the tympanum probably prevented the spread of such locally evoked waves. They differed remarkably from tympanum waves induced by external pure tones of the same frequency (c) which displayed traveling-wave-like vibrations.



Selective inactivation of the auditory receptor cells by mechanical lesions did not affect the tympanum's response to external pure tones, but abolished the emission's displacement amplitude peak.

These findings provide strong evidence that tympanal auditory receptors, comparable to the situation in mammals, feed energy into the system, which in return deflects the tympanum. The cellular active amplification mechanism involved could be similar to that of low-frequency auditory particle velocity sensors of flies and mosquitoes[7,8].

Figure: (a) Laser measurement area. (b) Tympanal displacement pattern for the 2f1-f2 emission evoked by f1 15.72 kHz and f2 17 kHz (70/70 dB SPL). (c) Tympanal displacement pattern for the emission frequency used as pure tone stimulus (14.44 kHz, 20 dB SPL). Arrow and asterisks designate the laser point at the high-frequency receptor's attachment position.

Ref.: [1] Kössl et al. 2008 JCPA; [2] Kössl and Boyan 1998 JASA; [3] Kössl et al. 2007 JCPA; [4] Möckel et al. 2011 JCPA; [5] Möckel et al. 2012 JEB; [6] Möckel et al. 2007 JCPA; [7] Göpfert et al. 2005 PNAS; [8] Nadrowski et al. 2008 Current Biol.

This project was supported by a grant from the Deutsche Forschungsgemeinschaft (No. 841/1-1), and by a "Nachwuchswissenschaftler/innen im Fokus" grant from the Goethe Universität, Frankfurt, Germany.

Dynamics of pressure difference receiver tympanal membranes in a bushcricket ear (Tettigoniidae)

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Bushcrickets detect sound pressure waves using a system of paired eardrums (tympana) on each foreleg. Sound from the environment travels through the air and acts on the external surfaces of the tympana, setting them into motion. Furthermore, an air-filled tube, the acoustic trachea, conveys sound from an opening (the acoustic spiracle) on the side of the thorax to the internal surface of the eardrums (Fig. 1). Since both surfaces of the tympanic membranes (external and internal) are simultaneously excited by sound, it has been suggested that these ears function as pressure gradient receivers. In a pressure gradient receiver ear, sound waves reach both sides of the tympanum using two different paths. Here, the two paths differ in that the sound has to pass an acoustic resistor when travelling through the trachea to reach the internal tympanum surface while the external surface gets excited directly.

It is broadly accepted that the acoustic trachea is the main acoustic input of the Tettigoniidae ear. In several species with large thoracic spiracles the acoustic trachea is thought to produce a gain, increasing the pressure of sound waves acting on the internal side of the tympanic membranes. Therefore, sound pressure acting inside could significantly differ from that acting externally on the tympanic membrane. If the acoustic trachea does indeed produce a gain, the tympanal vibrations caused by such internal input should exhibit higher amplitudes than those compared to external input alone (i.e., ratio 1:>1). Also, a time delay in the arrival of sound to the internal surface is expected if the trachea imposes acoustic resistance.

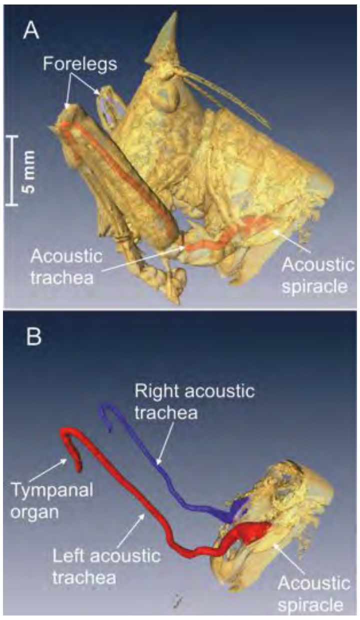

Fig. 1. 3D reconstruction of the bushcricket acoustic trachea.

We tested this hypothesis using µCT scanning, an innovative acoustic isolating platform, calibrated probe speakers, and µ-scanning Laser Doppler Vibrometry. We estimated the transmission gains of the trachea and measured the mechanical time resolution of the tympanic membranes in *Copiphora gorgonensis*, a neotropical bushcricket that communicates with pure tone songs at 23 kHz.

The acoustic trachea produces a delay in the transmission of sound, but also a gain of nearly 15 dB. Inside the trachea sound travels with speed of 215 ms^{-1}. Therefore we were able to discern the sound arriving externally and internally to the tympanic membranes from a single stimulus.

Control measurements show that the tympanic membranes are stable linear systems in a wide range of sound pressures used (10 mPa-25 Pa). Above that range the eardrums do not behave linearly but reach a maximum and stable displacement of about 200 µm.

Results and methodology are discussed and compared with early work.

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The proxemics and acoustic geometry of courtship in *Drosophila melanogaster*

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In *Drosophila melanogaster* acoustic communication is an important component of courtship (Manning 1967 *Science* 158, 136-137, von Schilcher 1976 *Anim. Behav.* 24, 18-26). They detect the particle velocity component of sound in the acoustic near-field, where the small size of the dipole sound source (the male wing) and the rapid attenuation rate of particle velocity produce a spatially divergent sound field. The bilateral, antisymmetric antennal ears of *D. melanogaster*, as well as the particle velocity stimulus they receive, are highly directional (Göpfert & Robert 2001 *Nature* 411, 908; Morley *et al.* 2012 *J Exp Biol* 215, 2405-2413) and the position of a singing male can change the amplitude at the female antennae considerably. Importantly, the antennae are actively tuned by virtue of the contributions from mechanosensory neurons in an amplitude dependent manner (Göpfert & Robert 2003 *PNAS* 100, 5514-5519). Amplification occurs at low input amplitudes where the antennae are tuned to frequencies of around 200 Hz, but at higher amplitudes there is no amplification and resonant frequency is increased to around 800 Hz. At low amplitudes the antenna should be tuned into song, but as amplitude increases the antenna tunes up towards frequencies far above those found in courtship. Spectral and temporal features of song have been analysed to try to determine the information conveyed to the female, however, little attention has been paid to spatial features of song production and reception. The position from which the male sings determines the amplitude at the female antenna, and hence, whether she is tuned in to his song.

We examined courtship in *D. melanogaster* from the behavioural proxemics of song production in males to the mechanics of the female receiver. Although courtship is dynamic and both male and female move around, the male predominantly maintains a position behind the female, directing song towards the antenna along an axis that ensures maximal stimulation of the ipsilateral receiver. From this position we empirically establish that courtship song produced by males is too loud to allow the female antenna to tune into song frequencies. There is therefore a mismatch between the amplitude of song and the tuning of the antenna. This raises questions as to why energy is expended to maintain active mechanics in these flies. Is the acoustic world of the fruit fly bigger than simply courtship?

D. melanogaster male (outstretched wing) courting a female.

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Tympanotriba vittata, another katydid with strange stridulatory acoustic adaptations

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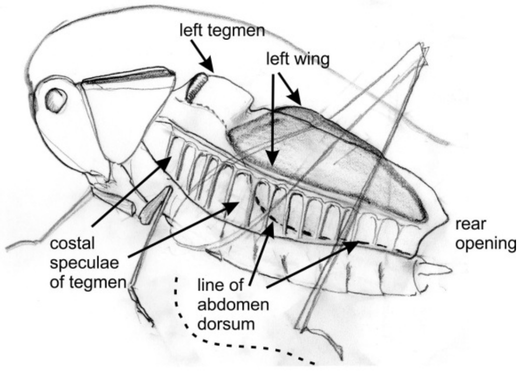
Males of a flightless katydid, *Tympanotriba vittata*, incorporate both tegmina and hind wings in stridulation. Females are apterous. First described in 1971 from southeastern Brazil, this conocephaloid has since gone unrecorded in the literature. It is abundant in Iguazú National Park, Argentina, singing from low herbaceous vegetation at high densities, day and night. Some sing amid the roar of the Iguazú cataracts.

Sound radiation involves an unusual air chamber, delimited by both tegmina and wings. Open rearward by a fluted aperture, this chamber is roofed by the fleshy wings that cantilever the length of the body. Laterally the tegmina abut the anterior margins of the (flexed) wings; the tegmina latch upon projections of the thoracic pleura and so splay slightly posterolaterally, exposing the wings between them in the midline. The chamber's lateral walls are a line of costal speculae, extremities lying against the abdominal pleura. A strongly depressed abdomen forms the chamber floor. The overlapped anal regions of the tegmina, bearing scraper and file, produce sound by to-fro scraper movement just as in more typical tettigoniids. Costal speculae are excited by the same file-scraper energy inputs that excite the mirror and harp. The whole chamber suggests a Helmoltz resonator that radiates from the rear aperture.

The nonresonant frequency spectrum is exceptionally wide: a band of frequencies extend from 20 to 60 kHz. Quieter sound is also produced in the audio range, making the call readily apparent to the human ear. The song has a low-rate 'plosive' quality. Each call lasts about 150 ms incorporating 4 time-domain elements, the third and fourth differing in spectrum. Calls are repeated continuously.



For a dozen specimens at 10-cm distances the sound field was explored for dorsal, left and right lateral, frontal and rear sound levels. We tested the effect of loading wing regions with wax and no costal enhancement of lateral sound levels was apparent via the lateral specular series. This insect's broad-band spectrum may be an adaptation for the distance-ranging localization of rival singers, relying on differential attenuation within the cluttered understorey vegetation of patchily distributed forest clearings.

Acknowledgement of support from the Natural Sciences Research Council of Canada.

Sonic properties of silks

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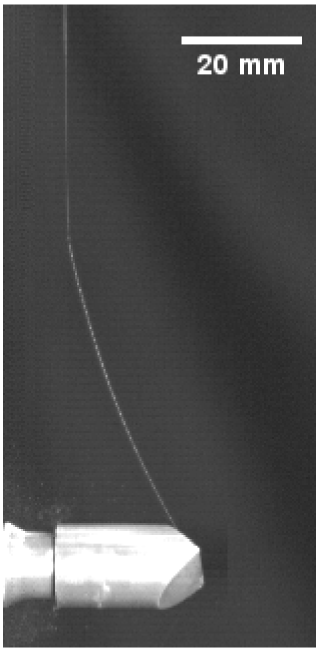

Silk is a biologically important polymer spun by various members of the arthropods for use outside the body[1]. The majority of silk research to date has focused on silk's mechanical properties[2-3]. However for spiders, as well as mechanical roles, silk plays a major functional role in vibration signaling[4-5]. Our work characterizes silks' sonic properties using independent complimentary techniques on single fibers, including ballistic impact (see opposite) [6] and laser vibrometry. This enables us to answer biological questions on the evolution of these fascinating materials, from web impact to spider 'sonar'.

Analogous to sonar, orb weavers will pluck silk strings, harnessing resonance, to locate prey items and other foreign objects in the web[7]. Our laser vibrometry work measures silk resonance at known lengths and tensions of single fibers. The resonant peak shape gives additional information on the suitability of the material to act as a signaler during resonance. We have found that multiple fibers signaling together increase the bandwidth at resonance, so frequency sensitivity. The role of multiple fibers has previously been overlooked when interpreting web function.

For spider silks, resonance is not always going to be the source of vibrations, as standing waves will not always form. We also present data on the Reynolds numbers of silks, linking fiber morphology to silks' dynamics in air at different speeds. This shows that spider silk's small diameter greatly impacts its sonic properties, in addition to increasing energy efficiency and strength[8]. Our data is also an important step forwards in linking deformation rate of silk to its ability to dissipate energy during web impact using air drag.

Spiders have highly sensitive vibration sensors above c. 1 kHz frequencies[9], well outside the expected frequency range of either web or insect vibration[4-5, 7]. This work allows us to make sense of these findings, by looking at impact events, characterized as multi-frequency, high-amplitude waves; to resonant events, characterized as high-frequency, low-amplitude events. Understanding the sonic properties of single silk fibers is the first vital step in understanding how spiders use these biomaterials as a signaler to influence all aspects of their biology.

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Thanks to Richard Duffin for technical support and building of equipment. For funding we thank The Leverhulme Trust, the US Air Force Office of Scientific Research, the European Research Council, Magdalen College, Oxford and the Engineering and Physical Sciences Research Council.

Acoustic communication in Pear psyllids (*Cacospylla pyri* L.) and occurrence of stridulatory organs in the genus *Cacopsylla* (Hemiptera: Psylloidea)

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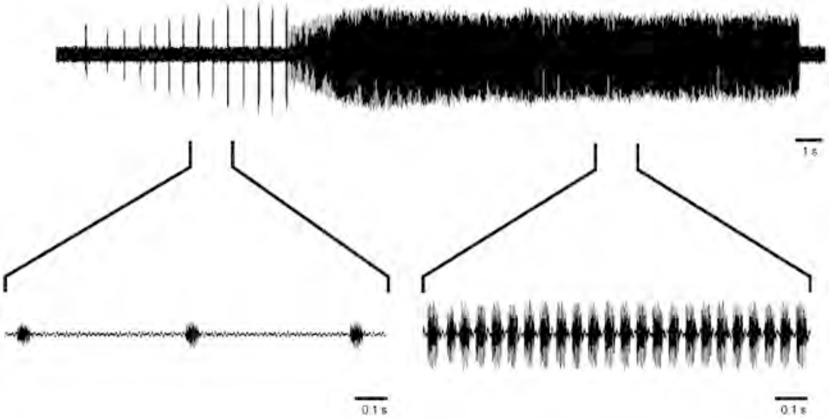
In Hemiptera intraspecific communication through substrate vibrations is well known and documented for many species. The often highly specific signals are mostly used during pre-mating behaviour for search and recognition of a potential partner. However little is known on sound production for species of the family Psyllidae (Psylloidea), most observations of sound production in psyllids are reported from species of the family Triozidae (Psylloidea).

Jumping plant lice of the family Psyllidae are economically important as vectors of pathogenic phytoplasmas in fruit crops. Pear psyllids of the species *Cacopsylla pyri* L. (Psyllidae) are the most damaging pest of pear trees in Europe. These phloemfeeding insects transmit pear decline (PD), a disease caused by Candidatus Phytoplasma pyri. Detailed knowledge of the biology and ecology of the vector is indispensable for the design of innovative and ecologically sound control strategies against these insects.

We could record for the first time acoustic signals emitted by this species. This is the first evidence for the existence of vibrational communication in the intraspecific communication of this species. Furthermore, we found potentially sound producing stridulatory organs in male and female individuals of *C. pyri* and three other *Cacopsylla* spp. The acoustic signals recorded are described and presented, possible stridulatory organs are depicted as SEM pictures. The implications of these findings for the taxonomy and phylogeny of the group and for its potential applications in pest control are discussed.



Oscillograms of a male call of *Cacopsylla pyri*. - Top. Complete call at 1s temporal resolution. - Left. Section of the first part of the call at higher temporal resolution. - Right. Section of the second part of the call at higher temporal resolution.

We thank Juliane Gaestel (Museum für Naturkunde, Berlin) for providing SEM pictures, Constanze Süttinger and Kai Lukat (JKI, Dossenheim) for rearing *C. pyri* and Karl-Heinz Frommolt for archiving the sound samples (Tierstimmenarchiv, Museum für Naturkunde, Berlin).

Male Courtship Song Disrupts Orientation Flight in the Yellow Peach Moth, *Conogethes punctiferalis*

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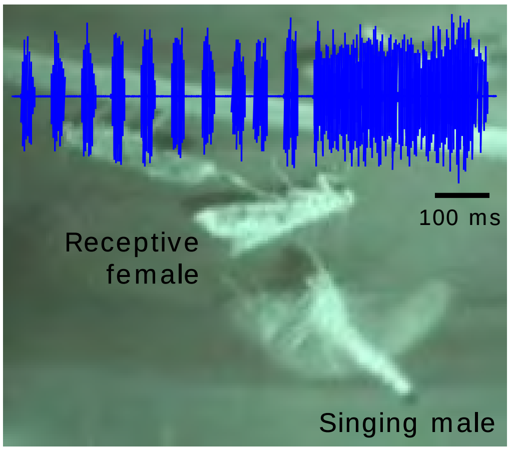
Nocturnal moths have evolved ears sensitive to ultrasound against predation by insectivorous bats emitting ultrasonic echolocation calls. Flying eared moths generally evade ultrasonic pulses to avoid bat predation by means of a power dive, zigzag flight, looping flight, and/or changing their flight path. These evasive behaviors could be used for pest management with artificial ultrasound. This was first attempted by P. Belton and R. H. Kempster in 1962 (*Entomol. Exp. Appl.*) to our knowledge. Since then, bat echolocation calls have been simulated to repel moth pests in crop fields; however, marked prevention of moth infestation has not been reported, so the ultrasound technique has not replaced other control methods, such as pesticides. Previous trials were not based on direct behavioral/neural evidence of the evasive response of moths. Ultrasonic pulses hitherto used were mostly simple simulations of frequency-modulated bat calls with short pulses of <10 ms. Thus, application of ultrasonic pulses, which efficiently cause an avoidance response in target moth species, would enable us to guard crops against economic moth pests.

Here we tested whether ultrasonic pulses (see figure below), which are emitted by courting males of the yellow peach moth *Conogethes punctiferalis* (Lepidoptera, Pyraloidea, Crambidae), are useful to control their infestation. In successful mating, receptive virgin females raised their wings in response to a long burst (>100 ms) consisting of consecutive pulses. On the other hand, short pulses (14–47 ms) emitted in the early phase of the male song repelled the approach flight of rivalry males for mating. In a small flight tunnel, male's orientation flight toward a synthetic sex pheromone was significantly suppressed by playing back short pulses rather than long bursts. This result coincided with the previous mating experiment. We anticipated that male short pulses reduce a female's orientation flight toward an oviposition substrate as well as the male's flight. Again, in the flight tunnel, we found that mated females hardly landed on apple fruit as an oviposition substrate when the short pulses were played back. We discuss the evolution of the evasive response against short pulses in the yellow peach moth.



We thank T. Takanashi and Y. Ishikawa for valuable comments on our work. This study was supported by Grant-in-Aid for Young Scientists (B) from the Japan Society for the Promotion of Science (#23780053), the Ono Acoustic Research Fund, Kurata Grant (#1172), and research grants from the Nagano Techno Foundation and the NARO (#38).

Frequency analysis in the bushcricket ear

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In a previous study we discovered that traveling waves form the physical basis of the mechanical frequency distribution along the high-frequency hearing organ in the bushcricket, called *crista acustica*. We also could show that longitudinal (proximal-distal) traveling wave characteristics are comparable to those measured in mammals (Palghat Udayashankar et al. 2012). Now, we studied in detail the radial (anterior-posterior) structure of traveling waves and the discrimination of complex signals *in-vivo* in our model system, *Mecopoda elongata*.

Under pure-tone stimulation, the maximum velocity response of the sound-induced traveling waves along the *crista acustica* was tonotopically distributed, with the maximum velocity response found in the proximal part under low-frequency stimulation and in the distal part under high-frequency stimulation. A detailed radial analysis revealed that the response maximum was always shifted towards the anterior part of the *crista acustica* (Fig. 1) and not on top of the mechano-electrical transduction place (scolopidial cell complex). This lateralization of kinetic energy led to a tilt in the magnitude response that could be relevant for signal transduction in the *crista acustica*. When complex signals, like the conspecific song, were used for stimulation, the tonotopic distribution is in principle present but dominated by amplitude responses of the low-frequency range.

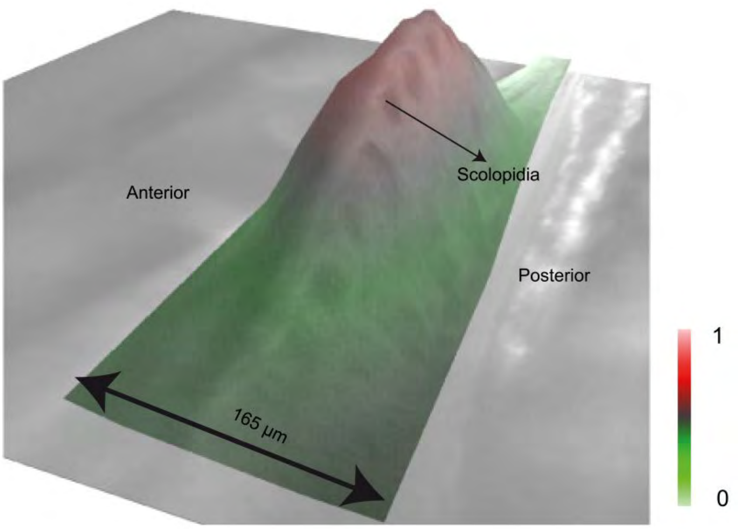

Fig. 1. Lateralization of kinetic energy along the crista acustica*. Maximum velocity was always found at the anterior part of the* crista acustica*. This shift of energy causes a complex organ motion, which can provide an important indication of stimulation direction. The degree of lateralization of energy correlates with the curvature of the organ.*

Ref.: Palghat Udayashankar A, Kössl M, Nowotny M. (2012). Tonotopically arranged traveling waves in the miniature hearing organ of bushcrickets. PLoS One. 2012;7(2): e31008.

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Drumming call variation and female response specificity in a group of closely related species of stoneflies (Plecoptera)

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Inter-sexual vibratory communication by drumming signals is a widespread phenomenon amongst stonefly species of the suborder Arctoperlaria. Similarly to the acoustic sexual advertisements of other insect groups plecopteran drumming calls serve to help conspecific males and females to find each other. If signal differences are distinctive and female preferences are specific, drumming communication may be an important behavioural component of the premating isolation between closely related species. Thus examining signal variation may yield a new insight into the species-level taxonomy of these insects. Our study focuses on the examination of Capnia bifrons, a species which is a common member of the Plecoptera fauna of most European countries. Previous studies reported drumming call variants and morphological variation mostly in Western European populations of that species, but no taxonomic consequences had been clarified. We studied 13 populations of Capnia bifrons in the Carpathian basin and Balkan peninsula (regions from where no data on drumming signals of C. bifrons had been available). Male drumming calls were recorded using mid-frequency-range speakers as vibration transducers. Five rhythmic parameters were measured on the oscillograms of the recorded calls. Our results show that four drumming signal type can be recognized in the 60 examined specimens. In each population only one call variant could be found. The four call types show a rather clear separation along two call parameters: mean inter-beat interval and beat-group duration. Populations using different call variants are distributed in an interspersed, allopatric pattern. To measure the attractivity of different call variants to females we made play-back experiments. Since pair-formation is achieved during a male-female drumming duet in these insects, the attractivity of play-back stimuli could be quantified by counting female responses and using female response ratio as an estimator of attractivity. Virgin females from three populations (each using a different male drumming pattern) were tested. Each female produced the highest response ratio to play-back stimuli representing the drumming type of their own population. All these results are in good accordance with newly discovered morphological differences in external genitalia and molecular phylogenetics of the examined populations. Based on the above detailed results we consider the examined populations to belong to four different species. Our play-back experiments with three of them suggest that divergence in their vibratory communication should result in strong assortative mating in case of sympatric occurrence.

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Are calling song characteristics affected by anthropogenic noise in the tree cricket, *Oecanthus pellucens*?

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There are several studies indicating that increasing noise pollution -as a concomitant of the development of traffic and urbanization- has an effect on the acoustic communication of animals. Even if there is an increasing amount of information about the effects of noise pollution in vertebrates much less is known about insects in this respect.

For that reason, we examined the male calling song of the Italian tree cricket (*Oecanthus pellucens* [Scopoli, 1763]) in habitats with different levels of noise (from bushes and hedge rows along busy roads to near-natural state habitats) in Hungary. The calling song of that species interferes easily with noise because of its' low fundamental frequency. Our question was whether parameters of the calling songs show some alteration which can be related to the level of noise pollution. To answer this question we measured 4 song parameters in 84 cricket songs recorded at 22 different sampling sites. We measured the noise level of the habitats and the momentary ambient air-temperature after each recordings.

We found significant association between the inter echeme interval and the noise level (measured in dB SPL) taking the temperature as a covariant variable into consideration: the duration of inter echeme interval decrease with increasing noise level, thus the repetition rate of echemes of the cricket song becomes faster in noisy environment. This modification increases signal redundancy and may increase the possibility for the females to receive the information encoded in the males' signals.

A mixed effect model shows that fundamental frequency of male calling songs increases with the noise level. That frequency shift may increase the signal/noise ratio of the male calling song in habitats with high levels of low-frequency dominated noise caused mainly by traffic activities.

Background of the technical part of research was partially supported by the project OTKA, K81929.

Mapping the auditory pathway in heliothine moth

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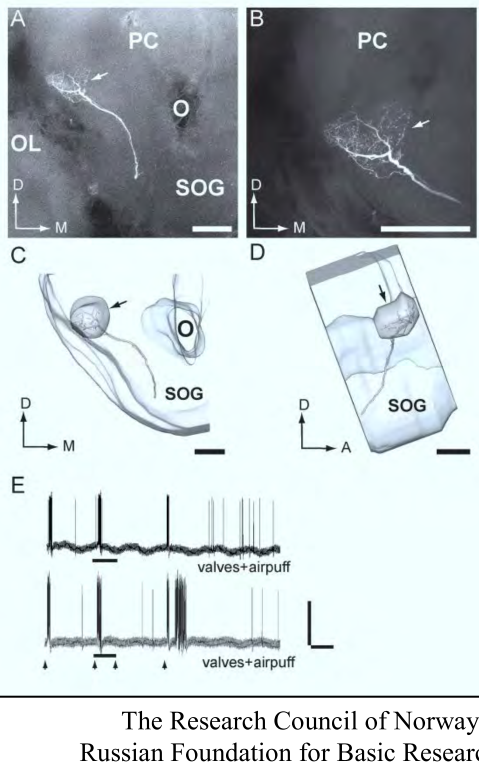
Many noctuid moth species perceive ultrasound via tympanic ears that are located at the metathorax. Previous staining experiments and behavioral research has shown that sound information is being processed in the brain (Paul, 1973; Surlykke & Miller, 1982; Anton et al., 2011). The particular regions involved have not yet been explored, however. By means of the intracellular recording and staining technique, we found higher order sound neurons in the lateral protocerebrum in the brain of three noctuid moth species, *Heliothis virescens, Helicoverpa armigera,* and *Helicoverpa assulta.* The majority of the auditory neurons ascended from the ventral cord and ramified densely within the anterior region of the ventro-lateral protocerebrum. The physiological and morphological characteristics of these auditory neurons were highly similar. The position of the soma and the neural processes in the thoracic ganglion, as seen in one of the preparations, resembles the 506 neuron found by Boyan and Fullard (1986). Mass-staining of ventral-cord neurons supported the assumption that this particular region is a main target for the ascending auditory neurons projecting into the brain. Also, we found one sound-responding brain interneuron having its soma positioned near the calyces of the mushroom bodies. This neuron extended numerous neuronal processes in the ventro-lateral protocerebrum as well. This indicates a sophisticated auditory processing despite a sparse initial encoding.



The Research Council of Norway (Project No. 219827/F11)
Russian Foundation for Basic Research (Project No. 09-04-01042-a

Phenotypic plasticity in response to food quality and anthropogenic noise in the grasshopper *Chorthippus biguttulus*

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Phenotypic plasticity can relay on experiences during an individual's lifetime, but can also be based on parental effects. In the latter case, plasticity results from experiences in ancestors. Such trans-generational responses might be adaptive by allowing fine-tuning of offspring traits to the current environment. Likewise phenotypic plasticity resulting from experiences in ontogeny can be adaptive. We examined whether the parental environment and the environment during ontogeny have effects on offspring life-history traits and sexually selected acoustic signal traits in the grasshopper *Chorthippus biguttulus*.

To examine the effects of food quality during early ontogeny or during the parents' lifetime has on such traits, we use a full factorial design by rearing parents and offspring on high-quality or poor-quality diet. We tested for cross-generational and ontogenetic effects by measuring the effects of manipulating the environment and measured effects in offspring traits in *C. biguttulus*. We found significant parental effects, i.e. positive effects of high-quality food treatment, on signal loudness and gap duration as well as on growth rate, condition of offspring, and weight of egg cases laid by female offspring. In all cases these effects were larger than the effects of the environmental conditions during ontogeny, even though some of the latter were significant, too. Interactions between parental and ontogenetic treatments were non-significant in all cases, indicating that offspring traits are not fine-tuned in response to parental experiences. We conclude that parental effects, potentially caused by epigenetic effects, are unexpectedly stronger than effects of the ontogenetic environment in *C. biguttulus*. These effects do not seem to constitute adaptive phenotypic plasticity but nevertheless show that the nutritional environment of the parents has a large influence on traits in *C. biguttulu*s grasshoppers.

A comparison between male grasshopper songs from roadside habitats and countryside populations showed a significant difference in the location of the lower frequency maximum. The upward shifted frequencies in roadside grasshoppers may be an adaptive response to avoid the potentially masking effect of the low frequency road noise. To examine the potential causes for the observed differences in song frequencies, we used grasshopper larvae collected at noisy roadsides and from the countryside, where they were less exposed to noise. Half of the grasshoppers were exposed to road-noise playbacks and the others were kept as a control without noise exposure. The analysis of song traits showed that noise exposure as well as the origin, but not their interaction, explained a significant proportion of variance in grasshopper song frequencies. We conclude that adaptive phenotypic plasticity as well as genetic or epigenetic effects are responsible for the observed differences in song frequency in *C. biguttulus*. Since males can be assumed to reduce the masking of their courtship signals by road noise, being most intense at low frequencies, we assume that the observed differences are adaptive.

We thank Bielefeld University for providing a "Rektoratsstipendium" to Ulrike Lampe and the Research Centre for Mathematical Modelling (RCM^2) for financial support.

Grasshoppers use local but not global cues for acoustic pattern recognition

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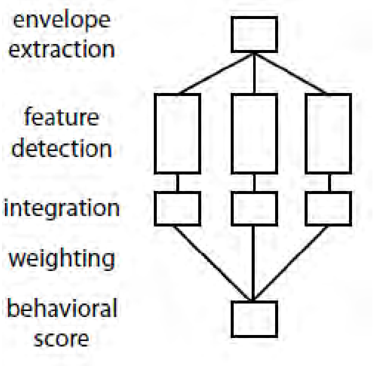
Acoustic signals of grasshoppers are decisive to identify and attract mates. Behavioural experiments have shown that the temporal pattern of amplitude modulations yields the decisive cues for signal recognition. A model for pattern recognition has been developed that relies on a set of feature detectors (each consisting of a filter plus nonlinearity). The output of the detectors is the integrated over time – i.e. the exact temporal position of a feature is discarded – and combined to yield a prediction of the stimulus attractiveness measured by the behavioural response. We found the specific shapes of the filters and nonlinearities using a genetic learning algorithm that started from a set of random solutions and was trained on a subset of behavioural data obtained with a large sample of different stimulus patterns.

Two results are remarkable: (i) with a combination of only two features already a very good prediction of the behaviour was possible ($r^2 \sim 0.9$) – including a third feature did not substantially improve model performance. (ii) if one considers the output of the detectors separately, one showed a reasonable correlation with behavioural data, while the other showed no correlation at all ($r^2 \sim 0.0$). This has implications for our search for neurons in single cell recordings that may transmit behaviourally relevant information.



This work was funded by grants from the DFG (SFB 618, B1 and GRK 1589/1) and from the German Federal Ministry of Education and Research (01GQ1001A)

Amphion floridensis and the Backthroat Boys: How are these caterpillars producing sound?

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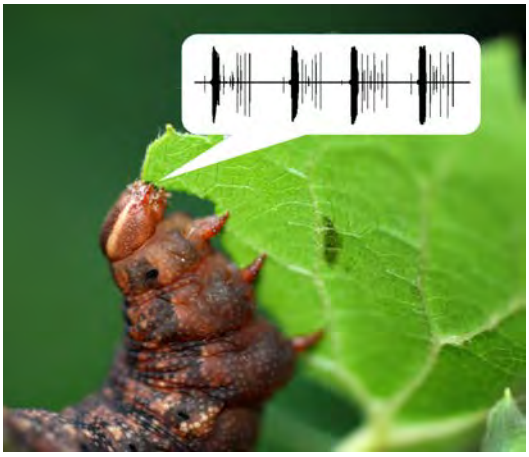
Caterpillars have many antipredator defences, but only recently has it been shown that many species of silk moths and hawkmoths (Bombycoidea) produce defensive sounds when attacked. It has been confirmed that they can make these sounds by whistling through spiracles, and clicking and stridulating with their mandibles. In this study, we report a novel mechanism of sound production, which we hypothesize to be analogous to vocalizing. This study had two goals: to characterize the sounds produced by four species of hawkmoth caterpillars (*Amphion floridensis, Sphecodina abbottii, Pachygonidia drucei* and *Nyceryx magna*) and to test their mechanism for sound production.

Following a simulated predator attack using blunt forceps, *A. floridensis* caterpillars produced a train of pulsed sounds for an average duration of 12.6 seconds. Most of the energy is in the ultrasound, with a dominant frequency of 32.9 kHz. All the four species produce pulsed sounds called echemes. The echemes can have from 1 up to 511 pulses, but the first echeme produced is typically longer than 100 pulses, which is followed by several shorter ones.

We propose that sounds are produced by the oral cavity through a mechanism akin to vocalization. All four species open the mouth when producing sound, which is evidence they are using the oral cavity for sound emission. Supporting the vocalizing hypothesis, the caterpillars slightly contract the thoracic segments prior to sound production and we found that *A. floridensis* possesses enlarged dilator and contractor muscles of the pharynx. We propose that they regulate the air flow through the pharyngeal and oral cavities. Video analysis revealed that the epipharynx of *A. floridensis* vibrates during sound emission. The epipharynx could operate as a valve that modulates the sound amplitude in pulses or as a vocal fold that generates sound.



Vocalizing occurs in mammals, birds, amphibians and reptiles. Although experimental evidence is currently lacking, some adult hawkmoths have also been suggested to use airflow through the pharyngeal cavity to produce sound. Still, vocalization remains rare in invertebrates and the occurrence of this mechanism in caterpillars attests to the diversity of sound producing mechanisms in this group.

We will propose a model for sound production and will discuss the functional significance of these high frequency defense sounds in these interesting caterpillars.

This research was funded by NSERC, CFI, ERA and OIT to J.E. Yack, and by National Council of Technological and Scientific Development of Brazil (CNPq) to C.A.R. Denadai.

The evolutionary history of the diversity of *Neoconocephalus* acoustic communication

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During the last thirteen years we studied the diversity of the acoustic communication system of the katydid genus *Neoconocephalus*. This new world genus includes about 25 species in North and Central America and the Caribbean. The ancestral call pattern is an extremely fast pulse rate (>200 Hz) produced as a continuous trill. Three derived call patterns occur in this group: 1) pulses are produces as pairs (double pulses), 2) slower pulse rates below 50 Hz, and 3) discontinuous calls with pulses grouped to regularly repeated chirps. Each one of these derived call traits has evolved several times independently.

We tested female call recognition for pulse and chirp patterns. We found at least 5 different recognition mechanisms for the pulse pattern and three mechanisms for the chirp patterns of male calls. In addition, we found some species where male calls have derived characters but female call recognition remained in the ancestral state.

In species with discontinuous calls, neighboring males synchronize their calls. At least two types of synchrony occur. First, males settle into stable leader follower relationships, seemingly cooperating to preserve the chirp pattern. Second, males compete for the leading position of the duets. This competition is the outcome of female preferences for leading calls. Phylogenetic analyses indicate that competitive synchrony as well as leader preference have evolved at least twice in this genus. The phylogenetic pattern indicates that leader preferences are not the result of a preexisting sensory bias.

Comparative analyses of the processing of the temporal call patterns and their timing relationships in the ascending sensory pathway provide additional evidence on the evolutionary mechanisms shaping the communication system.

Molecular clock approaches reveal that the diversity of communication in this genus evolved extremely rapidly, with divergence times orders of magnitude less than found in comparable systems.

In this talk, we attempt to integrate the various data sets into a comprehensive view of the evolutionary history and the mechanisms generating the diversity of this communication system.

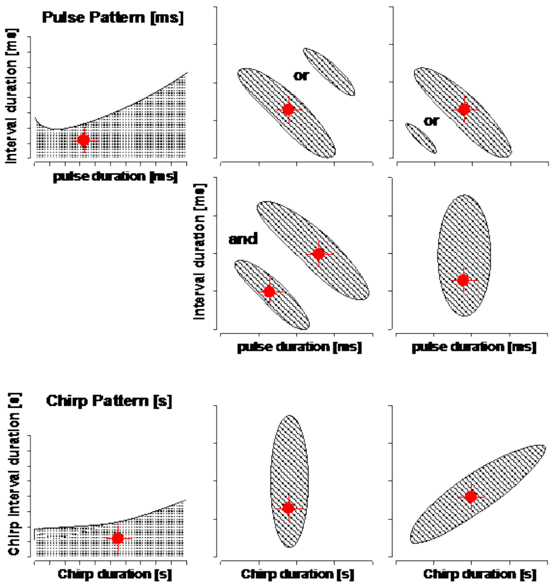

Figure: sketches of attractive parameter spaces for female call recognition among Neoconocephalus *species. Top: pulse pattern, bottom chirp pattern.*

Supported by several grants of the National Science Foundation to JS and SLB.

Vibratory communication in a black widow spider (Araneae: Theridiidae): From signal production to reception

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Vibratory communication is widespread among spiders (Araneae), and in many species, vibratory signals have been shown to play an important role during courtship. However, much of our understanding of the ecology and neuroethology of vibratory communication in spiders comes primarily from studies focused on hunting spiders (e.g. jumping, wolf, and wandering spiders); while other groups, specifically the web-builders, have received less attention. In many web-building spiders, males courting on a female's web have been observed to engage in various behaviors associated with the production of web-borne vibrations. Despite this, however, very few studies have measured and characterized web-borne courtship vibrations, and to date, no study has examined the details of the signaling mechanisms involved – previously, three types of signaling mechanisms have been described for spiders: 1) percussive; 2) stridulatory – rubbing two body structures together (usually involves a file-and-scraper mechanism); and 3) tremulatory – rapid oscillation of a single body structure.

In this study, we used the western black widow spider (*Latrodectus hesperus*), and examined: a) the courtship and vibratory behaviors of males on female webs; b) the mechanisms involved in signal production; and c) the sensory physiology of vibration reception. Using a laser Doppler vibrometer we recorded and characterized male courtship vibrations. Males performed three general types of behaviors, each resulting in distinct vibratory signals: web plucking (~117 Hz), web bouncing (broad frequency range, > 5 kHz), and dorso-ventral abdominal vibrations (~125 Hz). Using synchronized high-speed video and laser vibrometry, we showed that web-bounces were caused by upward flexion of all eight femurs, resulting in the male propelling towards the web surface; and abdominal vibrations were associated with the ventral movement of the abdomen. We then conducted ablation experiments where we: 1) immobilized abdominal movements to determine its necessity for vibration; and 2) prevented contact between the abdomen and the cephalothorax, to determine whether abdominal vibrations were stridulatory or tremulatory. Lastly, we conducted extracellular neurophysiology to determine vibration sensitivity in females. Females showed broad tuning, with increasing sensitivity at higher frequencies.

Our results contribute novel information about vibratory-signaling mechanisms in web-building spiders, and present black widows as excellent model organisms for future comparative work on the behavioral ecology, neuroethology, and evolution of vibratory communication and reception in spiders.

We would like to thank Dr. Maydianne Andrade for providing spiders to conduct experiments. This project was funded by the Ontario Graduate Scholarship (OGS) to Sen Sivalinghem; and grants from the National Science and Engineering Research Council (NSERC) to Dr. Andrew Mason

Sensory hair motion in oscillating air-flow is matched by neuronal filter properties of filiform sensilla

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Filiform sensilla are exceptionally sensitive mechanoreceptors of terrestrial arthropods that have a thin sensory hair, which is deflected by air flow. Recently a lot of effort has been put into understanding the mechanics of sensory hairs and their interaction with the air-flow. One of the most surprising discoveries was the fine tuning between the position and the length of hairs and the fine details of the biologically relevant aerodynamical stimuli. What is now missing is the connection between the hair motion and the actual information that is transmitted to the brain by sensory cells. In this poster we present a study of an oscillating air-flow around the abdomen of a firebug (*Pyrrhocoris apterus*, Heteroptera), and compare its characteristics with nerve impulse response of filiform sensilla that detect the flow. We used the PIV (Particle Image Velocimetry) method to describe both qualitatively and quantitatively the air-flow, and to determine the air-hair coupling of the sensilla. In a separate set of experiments we stimulated the sensilla directly with a piezo-ceramic actuator, driven by white-noise and sine voltage input. The characteristics of the response were determined from nerve impulse train that was recorded extracellularly using tungsten electrodes. Due to low number and well-defined locations of filiform sensilla we could characterize the response of a particular sensillum and compare it to its motion in the air-flow.

Our results show that the amplitude of close-field air-flow oscillation is greater at the position of sensilla, both in longitudinal and transversal directions of the far-field air-flow, with respect to the anteroposterior (AP) body axis. Surprisingly, even in pure transversal direction of the far-field flow we measured a significant longitudinal component of the close-field flow, suggesting that the sharp edge of the abdomen transforms some of the transversal flow into longitudinal flow. The longitudinal component lies in the plane of maximal nerve impulse response of most sensilla, which is in parallel to the AP axis. With increasing frequency of the flow the boundary layer above the abdomen gets thinner, resulting in an increasing sensory hair displacement. In the longitudinal far-field flow the hair starts to move at frequencies of a few Hz; at a few tens of Hz the movement is already substantial, and at 250 Hz there is one-to-one lock-in with the air movement. This seems to correspond to the frequency characteristics of the nerve impulse response. The gain of the response is indeed very low at low frequencies, but starts to increase rapidly as the stimulus frequencies increase towards 10 Hz and more. Thus, the neuronal responses of filiform sensilla are suppressed for frequencies of the air flow that do not move the sensory hair. This suggests that the physiological response of sensilla is adapted to the characteristics of the actual hair movement.

This work was supported by Slovenian research agency grant Z1-4228.

Males Influence Both the Phonotactic Responsiveness of Female *Gryllus bimaculatus* and Song Encoding by their ON1 and AN2 Neurons

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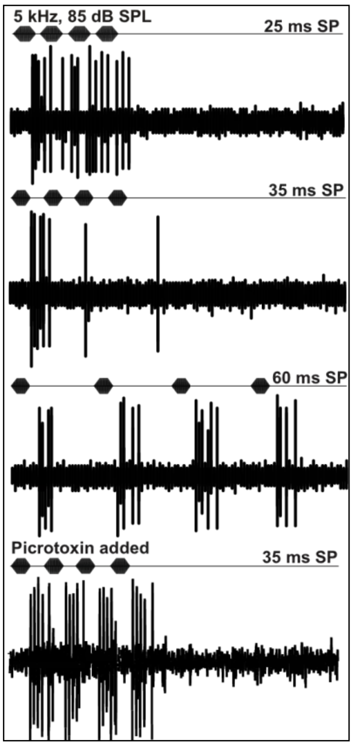
Most studies of phonotaxis and ON1 and AN2 responses to model calls by female *Gryllus bimaculatus* have used virgin females. We have evaluated female phonotaxis, using male exposed (raised in the same container) females. Although about 60% of male exposed females responded phontactically to model calling songs (CSs), these responses were quantitatively different from virgin females, as seen in their frequency of response and choices for syllable periods (SPs) to respond to phonotactically. Nanoinjection of juvenile hormone III (JHIII) into the prothoracic ganglion immediately following initial tests of phonotaxis of male exposed females that did not respond to model CSs, resulted in most females (about 80%) responding phonotactically.

For male exposed females, responses of the ON1 neurons to model CSs revealed greater variability than is the case for virgin females. Many recordings exhibited reduced spiking and ON1's responses were frequently influenced by the SPs of the model CSs presented. In the recordings shown, ON1's spiking responses to syllables 2 – 4 of CSs with a 35 ms SP (characteristic of the males' CSs) were almost eliminated. Responses to syllables 2 – 4 were greater when shorter or longer SPs were presented. These results might suggest a carefully timed, delayed inhibition following each syllable. Adding picrotoxin to the bath surrounding the ganglion could increase the response to syllables 2 – 4 (e.g. 35 ms SP), suggesting inhibition based on ionotropic Cl^- channels. In some experiments, nanoinjection of JHIII into the prothoracic ganglion of male exposed females increased ON1's responses to CSs and/or changed its' relative responses to sequential syllables.



It has been repeatedly demonstrated that in gryllids, including *G. bimaculatus,* the AN2 auditory interneuron receives inhibitory input from the ON1 neuron that is stimulated by the ear that is contralateral to the ear providing input to the AN2. AN2 neurons recorded from male exposed females demonstrate substantial variability in their responses to CSs with different SPs. It is reasonable to suggest that this greater variability might reflect a greater variability in the input inhibition provided by the contralateral ON1 neuron, or might reflect different degrees of synaptic coupling between the ON1 and AN2 neurons of male exposed females.

We thank the Department of Cellular Neurobiology, University of Goettingen and Prof. Dr. Reinhold Hustert for providing the research facilities, and Andrews University for financial support via faculty research grants (JS) and an undergraduate research scholarship (SL).

Airborne and vibratory signal production in the purring wolf spider, *Gladicosa gulosa*

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Many spiders produce complex multimodal signals, making them excellent models for testing hypotheses about the evolution of signaling behavior. Wolf spiders, in particular, are excellent models for vibratory communication as males of most North American species utilize vibrations in courtship. Initial observations of the "purring" wolf spider *Gladicosa gulosa* (Araneae: Lycosidae) describe an audible, airborne sound produced by males that can be heard from up to several meters away. Only minimal research has been conducted on this species, but early studies describe the volume of this signal. Though coupled with a simultaneous vibration during courtship, the production of this airborne signal is unique in that the spider itself does not possess any known structures for detecting it. This poses several questions regarding the possible adaptive or maladaptive qualities of this behavior and the pressures that may have driven its initial and continuing evolution within the communication network of this species. Using Laser Doppler Vibrometry and sensitive microphones, we recorded and characterized the airborne and vibratory components of male courtship in the field and lab. Recordings suggest, like previous descriptive work, that courtship displays by males of this species produce both airborne and vibratory signals, and that these complex signals are produced by both stridulatory and percussive mechanisms. Additionally we demonstrate that the airborne signal, like the vibratory signal, is fully attenuated on a non-vibrating substrate. These data indicate that substrate resonance may play a role in production of the airborne signal, and that the production of airborne sound may be the physical byproduct of vibratory communication in this species.

We also identified and measured the organs involved with signal production, scaled for body size, in relation to production of signals in both modalities. We compared the morphology of the sound-producing organs of this species with several other genera within the Lycosidae. These data may shed some light on the mechanisms underlying both the physical production of the sound and its potential role in the sexual behavior of this species.

This research was supported by grants from the National Science Foundation and the Wieman-Wendell-Benedict Foundation at the University of Cincinnati

Several Octopamine Receptor Subtypes are Involved in Modulation of Spider Mechanosensory Neurons

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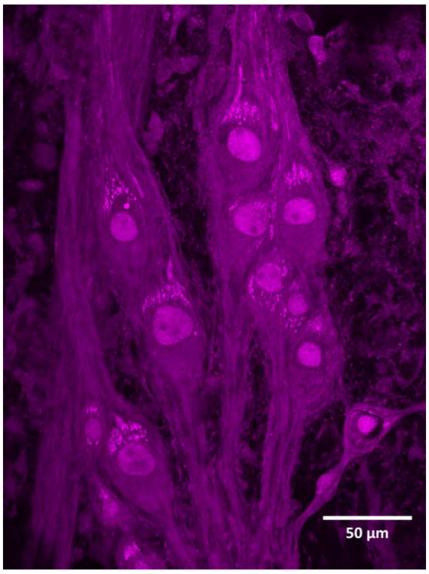
Octopamine (OA) is a biogenic amine that modulates many biological processes in invertebrates, including those involved in sound and vibration. OA is released from neurosecretory endings to the circulation and from efferent nerve endings directly to target neurons where it binds to G-protein coupled receptors. Based on similarities in structure and signaling properties with vertebrate adrenergic receptors, OA receptors are currently classified as α-adrenegic-like, β-adrenergic-like and OA/tyramine receptors (Evans and Maqueira 2005).

Mechanosensory neurons in spider (*Cupiennius salei*) legs receive extensive efferent innervation, including GABAergic, glutamatergic, cholinergic and octopaminergic efferents. The VS-3 neurons of the lyriform slit sense organ that detects strains in the spider patella, respond to OA with a long lasting enhancement in sensitivity to mechanical or electrical stimuli. This effect was significantly reduced by KN-62, an inhibitor of Ca^{2+}/calmodulin kinase II (CaMKII) and the Ca^{2+}-chelator BAPTA-AM, suggesting that the OA signals at least partially via a Ca^{2+}-CaMKII pathway, that also mediates long-term potentiation in neurons (Torkkeli et al 2011).



To characterize the OA receptors on spider mechanoreceptors, we extracted and purified total RNA from the leg hypodermis. A cDNA library prepared from mRNA was sequenced by RNAseq (Illumina HiSeq 2000 process, Génome Québec). The resulting 100 base pair reads were assembled without a reference genome (*de novo*) by searching the transcriptome for homologous sequence fragments to OA receptors of several related arthropod species, and then assembling putative transmitter receptor genes by transcriptome walking method (French 2012). Expression of putative OA genes was confirmed by RT-PCR. Candidate OA receptor RNA targets were localized in the spider leg hypodermis by *in-situ hybridization* using nucleic acid probes conjugated to fluorochromes (*Figure*). Two putative α-adrenegic-like and two β-adrenergic-like OA receptors were found in VS-3 and other mechanosensory neurons. These results suggest that octopaminergic modulation of spider mechanosensory neurons is a complex process involving several subtypes of OA receptors.

References: Evans and Maqueira 2005: *Invert Neurosci. 5:111-118*
French AS 2012: *BMC Research Notes 5:673-680*
Torkkeli PH, Panek I. and Meisner S 2011: *Eur. J. Neurosci. 33:1186-1196*

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Crabs Unquiet in Noisy Seas

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Anthropogenic noise has fundamentally changed the acoustic environment both of terrestrial and aquatic ecosystems, with growing evidence that even short-term exposures to this noise can affect the behaviour and physiology of many vertebrates. While invertebrates represent a considerable portion of marine fauna and are essential components in ecosystem dynamics, how they are impacted by anthropogenic noise has received scant attention. We used a series of carefully controlled experiments to investigate how the playback of ship noise affects both the behaviour (foraging and anti-predator) and physiology (oxygen consumption) of the shore crab (*Carcinus maenas*).

Compared to exposure to playback of ambient harbour noise, ship-noise playback resulted in crabs becoming more distracted from food, taking longer to find shelter in response to a simulated predation event, and righting themselves more quickly when turned on their backs. Single exposure to playback of ship noise also led to significantly higher oxygen consumption (indicating a higher metabolic rate and potentially increased stress), with larger individuals affected more strongly. When repeatedly exposed to ship-noise playback, crabs continued to consume oxygen at an elevated level, providing no obvious evidence of habituation or tolerance.

In combination, these results highlight that invertebrates, like vertebrates, may also be susceptible to the detrimental impacts of anthropogenic noise, and that elevated risks of starvation and predation may arise. Moreover, our study showcases that more detailed studies into the impacts of anthropogenic noise on marine invertebrates offers the opportunity for a greater understanding of this pervasive global pollutant.

We are grateful to the Bristol Aquarium for housing the study animals, to Sophie Holles and Irene Voellmy for the original sound recordings, to members of the Bristol Bioacoustics and Behavioural Ecology Group for thoughtful discussions, and to Defra for financial support.

Contributed Poster Abstracts

The Swarm and the Mosquito: Information transfer, co-operation and decision making in a group

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Mosquitoes form swarms which selected functions during mating behaviour. Males fly together in a "coherent" group, which attracts the attentions of nearby females who approach in search of a mate. The exact mechanisms that support swarm formation and cohesion are unknown, yet they are deemed to rely on acoustic communication between the males as they adjust their positions within the aggregation. A dynamic process of wing beat frequency modulation takes place when pairs of mosquitoes interact. Individuals are able to infer gender and species membership based on the sound produced by their neighbour's wing beats. Furthermore, in male-female duets, individuals attempt to meet at a common frequency value in a courtship phenomenon that has been termed "harmonic convergence".

A swarm can be considered to enhance individual chances of of each male to mate with an incoming female. However, whilst co-operative in swarm formation and maintenance, the male's behaviour must switch to selfishness if he is to encounter an approaching female first. The nature of the information leading to this decision, and its effect on swarm structure and stability (and hence other males) has never been considered.

We present experimental data investigating the nature of pairwise interactions between mosquitoes. A particular emphasis is placed on efforts to quantify the effect of harmonic convergence between males and females, something which is lacking in the literature to date. We discuss a suite of analytical tools designed to probe the intricacies of this process, and place them in the broader context of our investigations into swarm structure, dynamics and stability.

Acknowledgements go to the Bristol Centre for Complexity Sciences (BCCS) and Engineering and Physical Science Research Council (EPSRC)

Spatial Release from Masking: quantifying the effect of peripheral directionality & central inhibition in katydids and crickets

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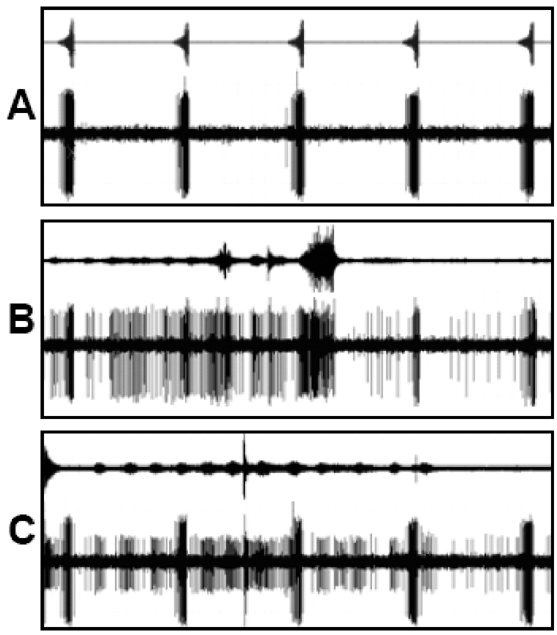
Acoustically communicating insects in a noisy habitat encounter the problem of interference of relevant and irrelevant signals from conspecifics or predators. “Spatial Release from Masking” affects the segregation of sound sources by improving the ability to distinguish signals that are spatially separated. Thus, spatial release of masking is basically related to mechanisms of directional hearing.
The aim of a current study was to determine, in which way both the peripheral directionality of insect ears and central nervous mechanisms via lateral inhibition contribute to the total amount of spatial release from masking. In a neurophysiological approach in katydids and crickets, we recorded simultaneously the activity of a pair of direction-sensitive Interneuron (omega-neuron or AN1-neuron, respectively) while presenting conspecific signals and noise from either the same or different sides of the insect. The activity of both neurons and the thresholds to signal and noise are quantitative measures for spatial release of masking.



Results indicate strong masking when the masker acts on the same side as the signal. But when the masker is shifted to the contralateral side the release from masking is perfect up to 20-30 dB above the threshold of the masker (crickets: 12 dB). When central neural processing via lateral inhibition cannot play a role, and only peripheral directionality is left for spatial release from masking, we found a strong masking effect even when the masker was shifted to the contralateral side. The peripheral directionality caused a release effect of only about 5-7 dB SPL in both taxa. Thus, in katydids the main contribution to spatial release from masking in the order of about 20 dB results from CNS mechanisms.

Fig. 1: Simultaneous recording of both omega-neurons (small and large spikes of left and right neuron) when (A) conspecific chirps are presented from right side, (B) noise & conspecific chirps are presented from right, and (C) noise is shifted to the left side. Note that in the latter case the representation of the conspecific signal is almost unaffected by noise.

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FWF, project P20882-B09 to HR

Geographic variation in acoustic signals in the bladder grasshopper *Bullacris unicolor*

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Bullacris unicolor (Orthoptera; Pneumoridae) is a species of bladder grasshopper endemic to the west coast region of South Africa. It has a fairly wide geographic distribution, spanning two vegetation biomes (succulent Karoo and Fynbos), and feeds on a variety of host plant species. *B. unicolor* is adapted for long-range acoustic communication. The inflated abdominal bladder of males enables them to produce an extremely loud advertisement call at night, to which females reply with a softer call.

The aim of the study was to examine the extent of geographic variation in the acoustic characteristics of the male advertisement call, as well as in morphological (body size) measurements. Furthermore, we wanted to evaluate whether any observed geographic variation may be related to environmental conditions that differ locally, including temperature, rainfall, humidity, altitude and vegetation type.

Individuals were sampled from five locations across the geographic range of the species (Fig. 1). The host plant species of each individual was noted. Sound recordings of the advertisement call were obtained from spontaneously calling males and analysed for their acoustic characteristics. Morphological measurements were taken from adult males and females. Environmental variables for each location were obtained from archive data sets.

We found that there was significant variation in the temporal and frequency components of the male advertisement call among individuals from the different locations. However, this variation was largely unrelated to environmental conditions. Morphology of males and females also differed significantly among the five locations, and this was correlated with local differences in mean annual temperature and precipitation, but unrelated to host plant species. The variation in acoustic signals also did not correlate with differences in male morphology.

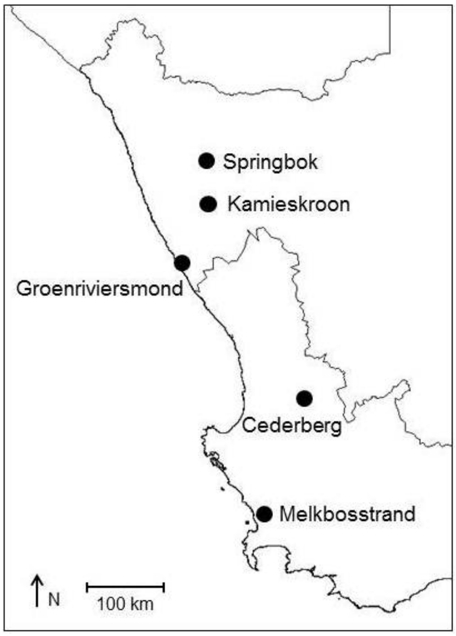

Fig. 1: Map of the west coast of South Africa showing the areas where *B. unicolor* was sampled

We therefore conclude that while ecological factors such as temperature and rainfall may influence morphology, there must be alternative selection pressures acting on acoustic signals that operate independently of environmental effects on body size. Further studies will examine female mating preferences in this species to determine whether sexual selection may be responsible for the observed geographic variation in male calls.

We thank N. Potgieter for assistance in the field. Funding was provided by the National Research Foundation of South Africa (grant 80582 to VC).

Complex substrate-vibrations and calling songs in a bushcricket of the Mecopoda elongata complex (Orthoptera: Tettigoniidae)

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Males of a trilling species of the tropical katydid in the *Mecopoda elongata* complex produce complex air-borne sound signals to attract females from a distance. Males and females also produce substrate vibrations by shaking their body (tremulation) or by front leg tapping. Calling songs of this species consist of an amplitude-modulated part, which is followed by a trill of variable duration. Here we investigated signaling via air-borne sound and substrate vibrations in isolated males on bird-of-paradise plants (*Strelitzia reginae*).

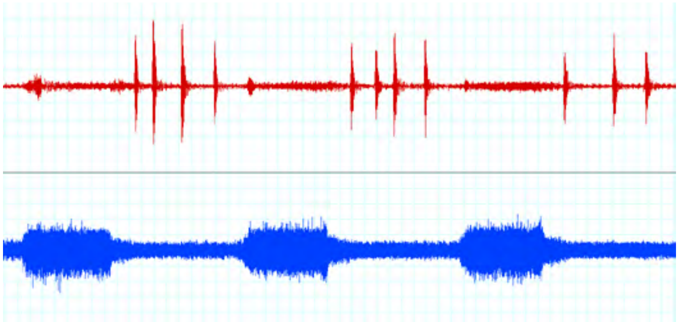

Figure 1.
Sound (blue) and substrate vibrations (red) of a signaling male. (Total duration of recording is 54 s.)

Tremulatory signals of males exhibit a rather variable temporal structure. They can be classified into three different types: 1) Longer lasting tremulation signals preceeding male calling songs. 2) A train of vibration pulses generated during the soft part of the amplitude-modulated section of the calling song, but never during the high amplitudes of more than 100 dB SPL (see one example in figure 1). 3) A train of brief vibration pulses with regular temporal structure produced immediately after males ceased singing. Finally, front leg tapping occurs infrequently either during singing or when males are silent. Tremulations preceding air-borne sound signaling exhibit a dominant carrier-frequency of about 20 Hz on the plants, whereas carrier frequency is ~40 Hz induced by sound production.

From these preliminary results we conclude that males make use of an unusual high repertoire of vibratory and sound signals for mate attraction. We suggest that active production of species-specific vibrations facilitate species recognition and localization of males in a complex structured habitat. Since a previous study conducted with another tropical katydid revealed rather high energetic costs associated with the production of tremulatory signals (Römer et al. 2010), advertisement signals in this trilling Mecopoda species seems to be energetically expensive and likely conveys information about the quality of senders.

References: Römer, H., Lang, A., and Hartbauer, M. (2010). The signaller's dilemma: A cost–benefit analysis of public and private communication. PLoS ONE, 5, e13325.

The research was funded by the Austrian Science Fund (FWF): P21808-B09. We thank Prof. Hashim Rosli for generous support in collecting these insects in Malaysia.

Listening to the Environment: Hearing Differences from an Epigenetic Effect in Solitary and Gregarious Locusts

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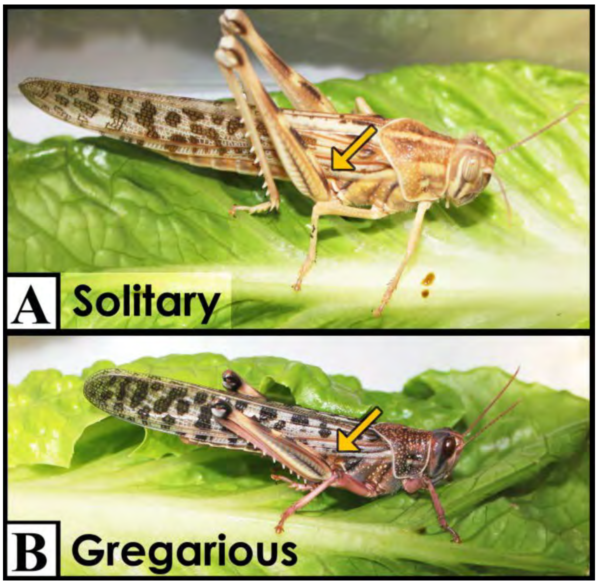
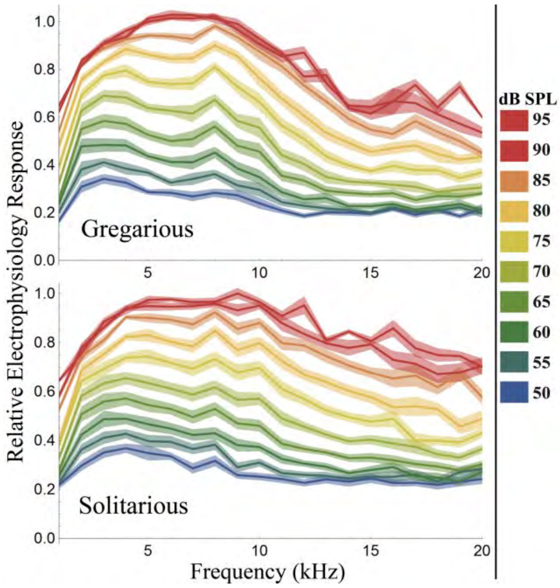
Developmental plasticity enables animals to adapt to the environment they experience during growth. Locusts exhibit epigenetic effects resulting in two phases (solitarious & gregarious) differing in appearance, behaviour, and physiology (figure below).

For hearing, our results show solitarious locusts have a relatively higher electrophysiological response at higher frequencies. Conversely, gregarious locusts reach their maximum with lower decibel levels at low frequencies, and thereby have a more narrow response to sound levels. Gregarious animals also have a faster response time across low frequencies. Next, we link this data with the nanometre mechanical responses of the ear's tympanal membrane to sound, finding that solitarious animals exhibit more displacement movement. Finally, we identify significant differences in the shape of the tympana that may be responsible for their hearing sensitivity.

Solitary locusts presumably need to hear their predators, such as bats, more precisely as they are not protected by the numbers of the swarm and gregarious locusts are more active during the day where they may be spotted by bird predators. Together, these data highlight the importance of how epigenetic effects set forth during development equip animals to match their immediate environmental needs.





Solitary (A) and gregarious (B) phases of the locust, *Schistocerca gregaria*.
Electrophysiology response with increasing sound levels by phase (right).

Work was funded through BBSRC (JFCW and SDG, BB/H004637/1),
EPSRC (JCJ, EP/H02848X/1), and a Society of Experimental Biology travel grant (SDG).

Do vibrations produced by feeding larvae mediate egg-laying decisions in populations of the cowpea beetle?

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The cowpea beetle *Callosobruchus maculatus* (Chrysomelidae: Bruchinae) is subjected to strong larval competition within the seed and vibration may play a role not only mediating larval competition, but also mediating egg-laying decisions by the mother females. This species exhibits large strain differences in larval competition and life-history traits and two distinct strains of this species, one from Southeast Brazil and one from South India, display such differences. The Brazilian strain exhibits scramble larval competition (with several larvae emerging per seed) and the females are not selective regarding the egg-laying substrate. The Indian strain exhibits contest larval competition (with few larvae emerging per seed) and choosy females less likely to lay eggs in seeds already containing either eggs or larvae.

The detection of larval feeding vibrations by egg-laying adult females may provide efficient means of detecting active larvae within the seed, preventing egg-laying in infested seeds and minimizing larval competition. To test this hypothesis, we carried out free-choice bioassays of seed selection for egg-laying by females of both strains where one seed was clean (i.e., free of eggs and larvae) and one containing either egg, live larva or dead larva. We expected that the Indian females would avoid laying eggs on seeds infested with either egg or live larva, while the Brazilian females would not be so choosy. Indeed, while the females of the Brazilian strain were able to discriminate seeds with eggs from clean seeds, they were not able to distinguish clean seeds from (live and dead) larva-infested seeds. In contrast, females of the Indian strain distinguished clean seeds from seeds containing either egg or live larva (they did not distinguish clean seeds from seeds with dead larva). Eggs of these species seem to contain a chemical deterrent of egg-laying, which does not remain active for more than a week or so, requiring another mechanism to assess seed infestation by larvae. Vibrations produced by feeding larva are likely to mediate egg-laying decisions and our results provide support for this hypothesis.

We further tested the hypothesis of vibration-mediated egg-laying decisions in the India strain by recording vibrations produced by feeding larvae using a laser vibrometer and playing them back to females of both strains. Again the results obtained supported our hypothesis in that Indian females discriminate against vibrating seeds (simulating larval feeding) preferring to lay their eggs in clean seeds, unlike the females of the Brazilian strain, which did not exhibit such preference.

This research was funded by the Natural Science and Engineering council of Canada (JEY), the Canadian Foundation for Innovation and the Ontario Trust Fund (JEY), an Early Researcher Award (JEY), and the Brazilian National Council of Scientific and Technological Development (RNCG).

Adaptive form in the thorax, pteralia, and wings of male *Metrioptera sphagnorum* (Ensifera, Tettigoniidae)

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Males of the flightless tettigoniid *Metrioptera sphagnorum* generate a rare and complex dual-spectrum signal via stridulation, using highly adapted acoustic tegmina. Complex-wave pulse trains make a non-resonant broad-band (17-25 kHz) spectrum upon the distal half of the file; ultrasonic sinusoidal (35 kHz) pulses comprise trains over the file's proximal half. We studied how *M. sphagnorum* generates and alternates these two different spectra with (nominally) the same tegmina. Wax loading tested the role of the scraper pit in scraper movement. Non-resonant spectra were more substantially affected.

Several species of tettigoniids are capable of generating trains of ultrasonic pure-tone pulses. The storage of elastic energy in the scraper is hypothesized to play a key role in driving the scraper over the file at a necessary tooth-contact rate. Fluorescence microscopy with pH shift was used to explore for resilin, a highly elastic cuticular protein commonly found in arthropods; we supposed this material might contribute to scraper speed during the ultrasonic sinusoidal pulses. Results indicate no resilin present anywhere in the tegmina of *M. sphagnorum*. Instead scraper speed during these pulse trains may be interplay between cuticular stiffness and scraper shape.

While the action of pteralia in Orthoptera is explained in the context of flight, to date there has been no investigation of their alignment and role during sound generation. Differences in form and function of these pteralia and associated musculature were observed in several katydids, including macropterous species that employ their tegmina for both flight and stridulation, and in brachypterous non-flying species (as in the case of *M. sphagnorum*) that use their abbreviated forewings only for stridulation. We also looked in these tettigoniids for the resilin 'springs' (i.e. prealar arm and pleural wing process hinge) as seen in locusts.

Complex signalling, song interaction, and mate choice in a bushcricket of the *Mecopoda elongata* complex (Orthoptera: Tettigoniidae)

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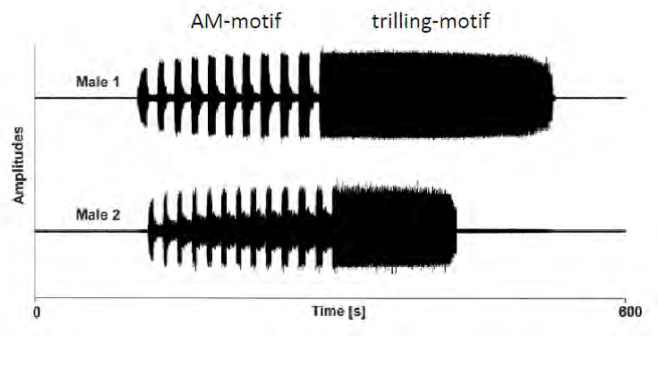
The behavioral background of producing complex calling songs in the context of sexual selection and the influence of different song motifs were examined in a trilling song variant of a bushcricket in the *Mecopoda elongata* complex. Calling songs of this species consist of two different modes, an amplitude modulated part with high and low amplitudes (AM-motif) that is usually followed by a loud continuous trill (see figure). The structure and duration of songs were compared between males either singing in isolation or interacting in a duet. In addition, a possible preference of females for certain signal traits was investigated in choice experiments in which females were given the choice between two songs differing in song structure.

The SPL during loud episodes of the AM-motif was 103.2 ± 1.7 dB and 86.0 ± 3.9 dB during soft episodes (fast recording mode, distance = 15 cm). Wing motion analysis revealed that for the production of loud song episodes males opened their wings twice as wide (12.4 mm ± 2.09, N = 5) compared to soft episodes (6.3 mm ± 0.87, N = 5). In summary, soft song episodes are characterized by a rather low intensity and shorter syllables compared to loud episodes. The size of males correlated strongly with the average SPL of loud song segments of AM-songs (Pearson correlation; $R^2 = 0.85$, $p < 0.01$, n = 11).

When males were free to sing their song bouts in relation to those of another male in an interaction, their song bouts overlapped on average by 39% (see example in figure 1). A comparison of total time spent singing in the dark period of solo singing and acoustically interacting males revealed no difference (Wilcoxon signed rank test, p = 0.49, N = 10). However, the duration of song bouts of males singing in isolation was significantly longer compared to song interactions (paired t-test, p<0.01, N=10).



In two-choice experiments females preferred a continuous loud trill over AM-songs ($p < 0.01$). After equalizing RMS amplitude of continuous trills and AM-songs, the preference for the trill was abolished (p = 0.84). Females appear to prefer acoustic signal traits that are more expensive to produce and indicate male body size.

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The Cricket Auditory System Responds to Bilateral Phase-Shifts

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The cricket's auditory system is a highly directional pressure difference receiver (Schöneich and Hedwig, 2010). Its accuracy seems to depend on phase shifts of sound waves propagating through the auditory trachea that connects the left and right hearing organs in the front legs.

We tested whether experimentally induced phase shifts of sound signals lead to changes in the cricket's (*G. bimaculatus*) phonotactic behavior, the response pattern of the tympanic membrane, and the activity of the auditory afferents. To create this phase shift, the same artificial calling song was played simultaneously from speakers at both the left and right sides of the cricket, at 75 dB SPL. One sound pattern, however, was shifted in phase by 90°. Phase shifts were tested for carrier frequencies in the range of 3.6-5.4 kHz. A trackball system was used to quantitatively monitor phonotactic steering behavior (Hedwig and Poulet, 2005), tympanic membrane oscillations were measured with a laser vibrometer, and the activity of the auditory afferents was recorded with a hook electrode.

Individual crickets were different in their phonotactic responses. Pooling data over all animals tested revealed that between 3.6 and 4.4 kHz the crickets steered away from the calling song pattern that was leading in phase. This effect was strongest at 4.1 kHz. Steering around 4.5 kHz was indifferent and showed no preference. In the range from 4.7-5.5 kHz the animals oriented more strongly towards the side that was leading in phase.

Qualitatively similar response patterns were obtained with the laservibrometric measurements and the afferent recordings. We calculated the response differences for ipsi- and contralateral stimulation with sound leading in phase. In the range of 4.0-4.5 kHz a stronger response occurred when the contralateral speaker was leading in phase. Between 4.6 and 5.4 kHz the ear responded stronger when the ipsilateral speaker was leading in phase.

These experiments demonstrate that the cricket's auditory system is sensitive to experimentally induced phase shift of acoustic stimuli. They also indicate and that the response properties of pressure difference receivers may be analyzed with phase shifted sound stimuli in a systematic way to further our understanding how insects use phase shifts within their auditory systems.

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Frequency processing of the conspecific song in the bushcricket ear

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For reproduction, males of the tropical bushcricket species *Mecopoda elongata* produce calling songs to attract females. These calls contain a broad frequency spectrum ranging from about 5 to 90 kHz. Within the frequency spectrum of the call, several distinct frequency peaks (7, 17 and 31 kHz) as well as a high-frequency plateau (>45 kHz) can be identified. To investigate the frequency-dependent response of the high-frequency hearing organ (*crista acustica*), we combined electrophysiological recordings of tympanal nerve activity with Laser-Doppler-Vibrometer measurements of the sound-induced hearing organ motion under stimulation with the conspecific song and several frequency-filtered versions of this song.

Electrophysiological measurements of the summed nerve potential of the hearing organ showed highest neuronal activity to stimulus frequencies below 20 kHz and especially to the first frequency peak of the song at ~7 kHz. High frequency components of the song (at least >37 kHz), however, seem to have no major influence on the electrical response intensity of the *crista acustica*, although the spectral energy of the song is maximal at the high-frequency plateau (>45 kHz).

Mechanical measurements of the hearing organ were performed at a proximal, medial and distal point along the *crista acustica* under stimulation with the conspecific song. The most striking characteristic of these mechanical investigations was that all three regions showed highest displacement amplitudes in response to the first frequency peak of the verse spectrum (~7 kHz). This finding was unexpected, since it does not correspond to the tonotopy along the *crista acustica*. To investigate the reason for this, we measured mechanical responses under pure-tone stimulation. The normalized displacement amplitudes during pure tone stimulation revealed a tonotopical representation of frequencies along the entire organ, with low stimulus frequencies represented proximally and high stimulus frequencies represented distally on the organ. The absolute displacement amplitudes, however, exhibited maximal responses at frequencies <27 kHz indicating a dominant influence of the low-frequency traveling waves, that dominates even the high-frequency region. This dominant influence of the low-frequency component within the conspecific song might be due to amplification by the tympanal membranes, which are known to be most responsive to stimulus frequencies below 25 kHz, with distinct resonances at about 7 and 16 kHz.

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The effect of a noisy calling song on the auditory response of a Mediterranean cicada

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Many animals have evolved sound production and detection to dictate courtship. It is often thought that, for effective communication, noise must be minimised. Unfortunately for some animals, noise is implicitly generated during sound production, and it is assumed to be detrimental for communication. The male Mediterranean cicada *Cicadatra atra* produces a calling song that comprises a series of pure-tone pulses. While the pure-tone pulses are spectrally relatively clean, unless the inter-pulse interval is consistent, the signal is implicitly noisy, and spectrally smeared. We hypothesised that an idealised perfect *C. atra* song with a constant repetition rate would, as an ostensibly cleaner signal, lead to a greater auditory response than an imperfect sound.

We generated artificial *C. atra* songs with varying amounts of randomness in pulse repetition, based on recordings of singing *C. atra* and their known mechanical sensitivity. Females, sourced from Cuges-Les-Pins, France, were then subjected to these sounds, while the neural response was monitored electrophysiologically. A typical response to a *C. atra* calling song is a small period of latency, followed by a volley of spikes that decays in amplitude to a steady electrophysiological response.

Analysis of the steady response showed that, counter-intuitively, a normalized electrophysiogical response is stronger for a noisy signal, than the ostensibly better, noise-free signal.

The origin for this effect is unclear. We hypothesise that the noisier signal decoheres the response of the ensemble of neurons in the cicada ear, such that energy is temporally smeared. In the field, noisier signals correlate with either a noisier singer, or the sum of many singers that are unsynchronized. This suggests the possibility that the cicada ear has a greater sensitivity to a chorus of cicada songs than to an idealized song of the same sound level. Noisier signals might also be better transmitted through the habitat and better localized by the receiver. In any case, that the *C. atra* ear is more sensitive to a noisy signal means that the typically noisy acoustic scene for *C. atra* is not a hindrance to communication.

The Mediterranean cicada *Cicadatra atra*

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Comparative neuroanatomy of the subgenual organ complex of orthopteroid insects

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The subgenual organ (SGO) is a scolopidial sense organ present in the tibia of most insect taxa. It ranks as one of the most elaborate scolopidial organs, together with the femoral chordotonal organ. Comparative studies have unvailed that in different taxa the SGO is not the sole scolopidial organ, but rather forms a "subgenual organ complex" as it is accompanied by other scolopidial organs. This sensory complex is also discussed to be the evolutionary origin of the hearing organ in Ensifera. In recent years we have accumulated detailed data on the subgenual organ complex with respect to neuroanatomy, cell numbers, and innervation. The focus of these studies was especially different taxa of Ensifera, stick insects, and praying mantids. These data provide the basis for a comparative analysis of the neuroanatomy of orthopteriod taxa.

All orthopteriod insects possess a SGO, which therefore represent a basic feature with 3 (Dermaptera) up to 70 (tree weta) sensory cells. The innervation is highly conserved between taxa. In many lineages, additional scolopidial organs are present, which can be classified by neuroanatomical characters into distinct groups (figure 1). The distal organ (DO) and intermediate organ (IO), as well as the tympanal organ (TO) of crickets are likely to be homologous. In some groups of atympanate as well as tympanate Ensifera a distinct crista acustica CA) or its homolog (CAH) have been evolved. An accessory organ (AO) or "Nebenorgan" (NO) with unconfirmed functions is found repeatedly in several lines, always located in the posterior tibia adjacent to the posterior subgenual organ.

These findings are discussed in respect to the phylogenetic relationships of orthopteroid insects (figure 1).

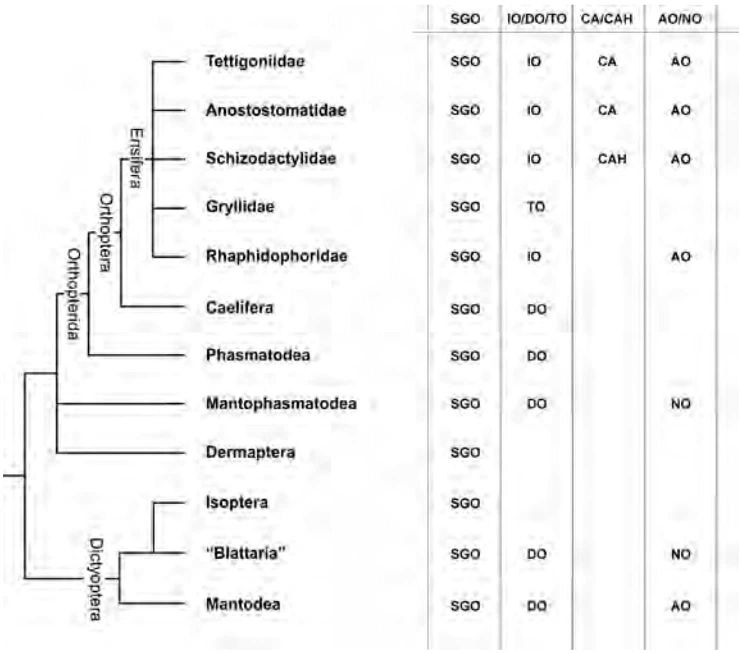

Figure 1: Phylogenetic relationships of orthopteroid insects with documented sensory organs in the subgenual complex in the respective groups. Abbreviations: AO, accessory organ; CA, crista acustica; DO, distal organ; IO, intermediate organ; NO, Nebenorgan; SGO, subgenual organ; TO, tympanal organ. References can be provided on request.

Useless hearing in male *Emblemasoma auditrix* (Diptera, Sarcophagidae) - a case of intralocus sexual conflict?

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Distinct behavioural functions were ascribed to the diverse insect hearing systems even if they were sexually dimorphic. Here we describe a first case, where a trait of an evolutionary novelty and a highly specialized hearing organ is adaptive in only one sex. The main function of hearing of the parasitoid fly *Emblemasoma auditrix* is to locate the host, males of the cicada species *Okanagana rimosa*, by their calling song. This task is performed by female flies, which deposit larvae into the host. We show that male *E. auditrix* also possess a hearing sense. The morphology of the tympanal organ of male and female *E. auditrix* is rather similar, with the female ear 8% larger than the male ear. In both sexes the physiological hearing threshold is tuned to 5 kHz. Behavioural tests show that males are able to orient towards the host calling song, although phonotaxis is often incomplete. However, despite extensive observations in the field and substantial knowledge of the biology of *E. auditrix,* no potentially adaptive function of the male auditory sense has been identified. This unique hearing system indicates a novel quality of intralocus sexual conflicts, as the complex sense organ and the behavioural relevant neuronal networks evolved *de novo* whereby it is adaptive for only one sex. The correlated evolution of the sense organ in both sexes might impose substantial constraints on both, the sensory properties of the organ for females as well as on the fitness for males. Similar constraints, although hidden, might also apply to hearing systems of other insects.

Intraspecific communication (mate finding, spacing, aggression) (Orthoptera, Cicadas)	**Predator avoidance** (Lepidoptera, Orthoptera)	**Host detection** (Diptera)

Main described functions of tympanal hearing in insect (together with main representative taxa). None of the functions seems to have a specific adaptive value for male *Emblemasoma auditrix*.

Local neurons in the auditory system of the bush cricket *Ancistrura nigrovittata*

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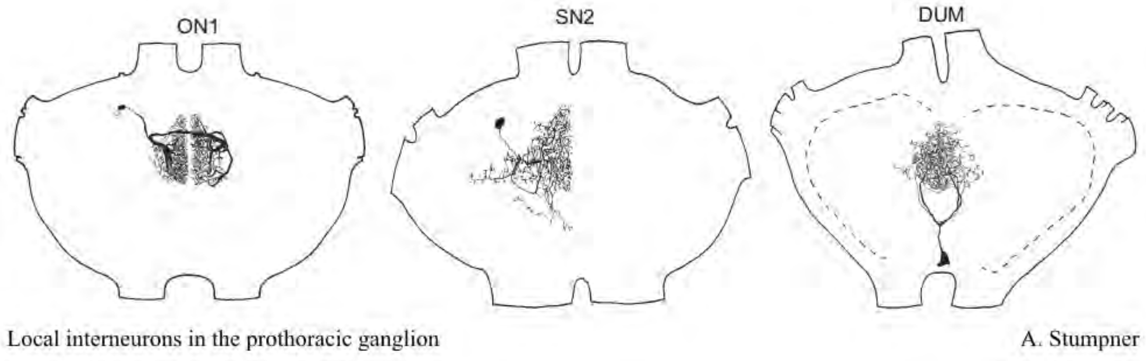
Auditory processing in insects involves sensory neurons in the ears and local neurons and intersegmental neurons in the CNS. Much attention has been directed to sensory cells, intersegemtal neurons projecting into the brain and very few large local neurons. Experiments like cell killing indicated that, more neurons than the studied local neurons must provide important contributions to auditory processing. Compiled data on a bush cricket demonstrate the likely importance of local neurons for frequency processing, directional processing and also temporal processing.

In the prothoracic ganglion, the first level of auditory processing, frequency dependent inhibition, directional inhibition and temporal inhibition are found. The only well characterized local neuron, the omega neuron (homologous to ON1 in crickets) has been demonstrated to produce strong directional inhibition [1].

Additionally, frequency dependent inhibition has been found, which may rely on groups of DUM-cells. Preliminary data show that there exist several DUM-cells, directly responding to acoustic stimuli in bush cricket [2]. They exhibit a huge variety of frequency tuning: From cells responding only to vibratory stimuli to cells responding best in the audio range, to cells responding best in the ultrasonic range, and cells exhibiting clear IPSPs at certain frequencies. Therefore, these cells are well suited to evoke frequency dependent inhibition in intersegemental neurons as has been hypothesized [3]. Processing in the prothorax appears to involve specific inhibition as well, since blocking Cl^--channels with picrotoxin changes the response of temporally selective neurons like AN2.

The identification and characterization of local DUM neurons are currently investigated in order to further investigate their action on local auditory processing.



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DFG Deutsche Forschungsgemeinschaft

Visualisation and Quantification of Diffraction

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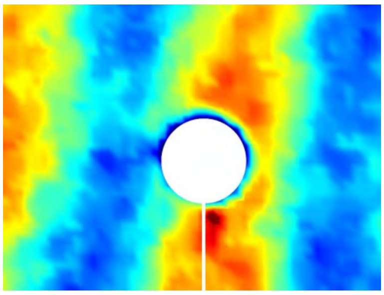
The visualisation of sound waves can be achieved in a number of ways. Most techniques however lack the ability to fully quantify the sound fields in question. A recent and very promising technique for sound field visualisation and quantification relies on laser Doppler vibrometry.

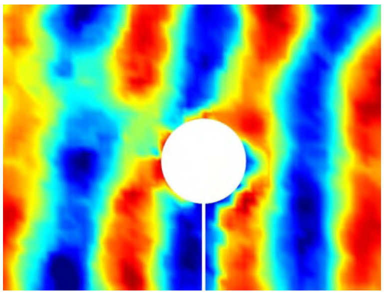
The refractive index of air is modulated by sound pressure, which causes small but measurable changes in the speed of light. The resulting change in the speed of light can thus be used to measure the change in refractive index, which is proportional to the acoustic pressure. In combination with a scanning of the acoustic field a quantified visualisation of the field can readily be achieved. The method can therefore be used to investigate a number of acoustic phenomena, such as; reflection, diffraction and interference.

Figure 2shows the diffraction patterns around a plastic tube at right angles to incoming sound radiation, as measured using the method. As the frequency of the sound increases the wavelength approaches the tubes dimensions, the condition at which diffractive conditions occur.

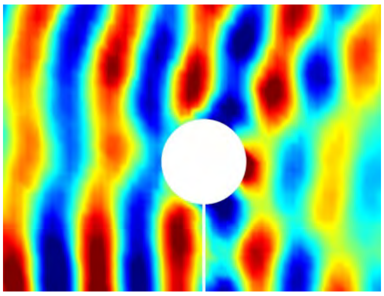
The poster will illustrate aspects of the method with emphasis on it's use in bio-acoustics, it's limitations and future directions.



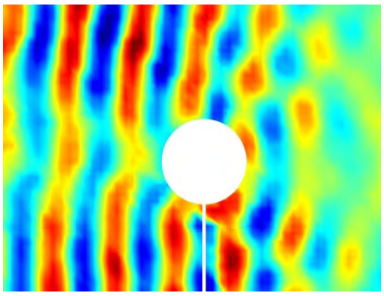
5kHz - λ=70mm



10kHz - λ=35mm



15kHz - λ=23mm



20kHz - λ=17mm

Figure 2 - Acoustic diffraction around a tube (diameter 20mm) at different frequencies. Diffraction phenomena become more pronounced as the wavelength in air approaches the dimensions of the tube.

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The Genomic Architecture of Song and Recognition traits in Teleogryllus Cricket Species

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Understanding the genetic architecture of animal communication systems and the dynamic interplay of factors driving their evolution is of central importance in evolutionary biology. Divergence in mate recognition systems can play a primary role in curtailing gene flow and maintaining genetic boundaries between diverging species. However, the genetic basis of mate preferences and the coevolution of signal-response traits remains poorly understood. Detailed empirical data, from both natural and experimental populations, is needed in order to validate theoretical predictions on the evolutionary genetics of communication systems.

In this study, I will use the two closely-related Australian field cricket species *(Teleogryllus oceanicus* and *Teleogryllus commodus)* and next-generation DNA sequencing technology to examine the genomic architecture of male calling song and female preferences and the role these traits play in reproductive isolation. These species provide an exceptional model system, to address important hypotheses on the evolution of mate recognition systems, as there is a rich body of knowledge on their acoustic behaviour and a potential hybrid zone in which to examine experimental findings in a natural context. Using both natural populations and laboratory crosses, I will combine behavioural experiments, quantitative genetics and genome wide molecular approaches to accomplish two interrelated goals. The first is to identify genomic regions involved in male calling song and female preferences through QTL (Quantitative trait loci) mapping. By determining the genetic basis of these traits inferences can be made on the evolutionary history and trajectory of this acoustic communication system. The second goal is to examine the pattern of genomic divergence within and between species and how this relates to variation in acoustic behaviour. If calling song plays a primary role in reproductive isolation, we may expect reproductive character displacement in the area of species overlap. If gene flow between species is reduced due to divergent acoustic behaviour we may expect the associated genomic regions to be divergently selected for in each species. Therefore, loci identified in the QTL mapping of song and preference traits should colocalize with divergently selected regions of the genome revealed through genome scans for outlier loci.

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First description of substrate-borne signals emitted by males of *Macrolophus pygmaeus*

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Vibrational communication is widespread in insects where it represents the main communication channel for more than 70% of families. The sexual behaviour of numerous species is characterized by the use of substrate-borne signals. In Heteroptera the vibrational communication has been deeply investigated in the Pentatomidae family, but very little is known about other families, including the Miridae for which olfaction has always been considered the main intraspecific communication channel.

Macrolophus pygmaeus (Rambur) (Hemiptera: Miridae) is an economically relevant species for the biological control of several pests in the Mediterranean region. In Europe, it is commercially reared for biological control of whiteflies *Trialeurodes vaporariorum* (Westwood) and *Bemisia tabaci* (Gennadius) (Sternorrhyncha: Aleyrodidae) in tomato greenhouses.

In the present study we investigated the ability of *M. pygmaeus* males to produce substrate-borne signals during mating behaviour. Two different experiments were carried out using a laser vibrometer. The first one aimed to record the vibrational signals produced by a male on a tobacco leaf in three situations: male alone, male with a female, and male with another male. The second experiment used a minishaker to playback male signals to evaluate if they affect the behaviour of conspecifics.

3- Male of *M. pygmaus.* Photo by G. Baldo

The results showed that males of *M. pygmaeus* can emit two different substrate-borne signals that we onomatopoeically called "roaring", a long broadband signal and "yelping", a train of short repeated signals with harmonic structure. We also found that the playback of "roaring" modifies the behaviour of receiver males, in terms of increased locomotion. "Yelping", instead, did not induce any significant variation either in listening males or females. This signal, however, was always recorded in test 1 before mating attempts. This suggests that "yelping" would function as stimulus of male acceptance from a female.

In conclusion, this is the first report of the use of substrate-borne vibrational signals by a mirid species for mating behaviour and a contribution to better understand its reproductive biology.

Modelling insect directional hearing

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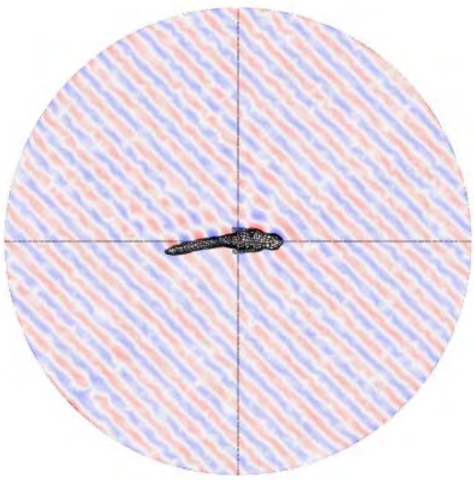
One of the main factors in the evolution of hearing is the ability to localize the origin of a sound source. This work has investigated the effect of an invertebrate's body on the received sound field. The locust *Schistocerca gregaria* was chosen as the subject for this work. It is known to utilize directionality in its hearing via a pair of tympanate ears, located on either side of its body. *S. gregaria* is sensitive to a range of acoustic frequencies, from below 1 kHz to above 30 kHz. This means that the locust is responsive to sound wavelengths with a range from over 340 mm to below 11 mm. The locust's thorax is typically 10 mm in diameter, and total body length is ~50 mm. This scaling overlap between body size and wavelength suggests that the body of the locust will have a diffractive effect on the higher frequency sounds, potentially altering the sound reaching its two ears.

Previously, experimental and behavioural studies have indicated that the locust's body affects incident sound waves at frequencies above 10 kHz. In order to investigate what happens to the sound field about a locust we utilised a combination of computer modelling and physical measurement of the sound field at different frequencies. In order to accurately model this interaction the body of a locust was scanned using a Faro 3D laser scanner. Wings and legs were removed in order to simplify and reduce the model. This produced a computer based three dimensional 'point cloud' measurement of the locust body surface. This point cloud was converted into a 3D computer aided design model, and then imported into finite element analysis software (COMSOL). The interaction of the locust body with different sound waves was then simulated in 3D (as shown for example in the figure below). The 3D model was also used to create a 'rapid prototype' resin based locust body, which was then fitted with microphones at the ear locations and subjected to different frequency sound from different incident angles.

The computer simulations, and measurements from the 3D printed rapid prototype locust body, reveal that the previous behavioural and experimental observations about the effects of the body on sounds above 10 kHz are correct. It has been found that the pressure on the incident side of the locust body is increased from that of the plane wave. There are clear diffractive effects in the sound field about the body. The angle of the incident wave has a large effect on the pressure difference. This work considers only the body of the locust, and will be extended in future to consider the more complex, and computationally challenging, investigation of a winged model mimicking the locust's body position in flight.



Acoustic field around the body of a wingless locust for a sound frequency of 25 kHz

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Morphological Diversity and the Evolutionary Origins of Vogel's Organs in Nymphalidae Butterflies

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Butterflies have been studied extensively for their visual and olfactory systems, but their auditory system remains poorly understood. Many species of the brush footed butterflies (Nymphalidae) have been shown to possess a tympanal ear at the base of the forewing, known as Vogel's organ. At present, very little is known about the distribution and evolution of ears in butterflies, a largely mute and diurnal group of insects.

We sought to; (1) Examine the diversity of Vogel's organ across Nymphalidae; (2) Code the external morphology of Vogel's organ as well-developed, intermediate, or absent; (3) Use this information to pose hypotheses regarding the evolutionary origins of hearing.

Papilionoidea, the true butterflies, is comprised of 5 families: Papilionidae, Pieridae, Nymphalidae, Riodinidae and Lycaenidae. With approximately 6000 species, Nymphalidae is a very diverse group of butterflies. In this study, a total of 90 nymphalid species were examined spanning 11 sub-families and 30 tribes. In addition, 16 specimens from outside of Nymphalidae were used as out-groups. Our results show that ears are found only in Nymphalidae, which is consistent with previous reports. 'Well-developed' ears occur in four sub-families; Satyrinae, Nymphalinae, Apaturinae, and Biblidinae. Exemplars from typically basal sub-families, (e.g. Libytheinae and Danainae) lacked ears and were deemed 'atympante', while the remaining five sub-families all possessed at least one species having a tympanal membrane deemed 'intermediate'.

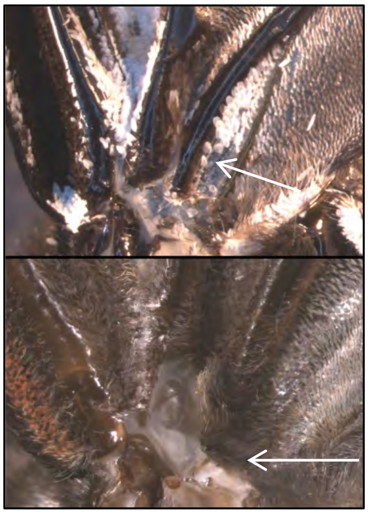

Figure 1. Atympanate state (top) seen in *Ideopsis juventa*, and well-developed tympanal membrane of *Morpho peleides,* (bottom).

In the species we surveyed, ear structure and state were conserved at the tribe-level. However, across sub-families there were noticeable differences in the development of the ear with some having elaborate vein enlargements or pronounced accessory structures. Satyrinae was the only sub-family in which all species examined to date have well-developed ears. Comparatively, ear morphology varied extensively in the sub-family Nymphalinae, with representatives of each of the three tympanal state classifications observed.

We conclude that within the true butterflies, Vogel's organ appears to be restricted to Nymphalidae, but within this family, there is great variability in the development and structure of the ear. We will discuss possible scenarios for the evolutionary origins of hearing in Nymphalidae, and why we think that this hearing organ is restricted to this family.

This research was funded by CFI, OIT, NSERC and ERA to J. E. Yack.

Directional Hearing in Masking Noise in the Grasshopper *Chorthippus biguttulus*

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For many tasks in animal acoustic communication the signal must be localized by the receiver. Localization ability can have especially strong consequences in mate-attraction contexts in which the ability to move quickly towards the source of signals can both improve the likelihood of mating and reduce the costs, such as predation risk, associated with such movements. The results of laboratory tests show that many animals have excellent directional hearing capabilities. Nonetheless, animals' localization abilities may be compromised in nature because acoustic communication typically takes place under high levels of noise. Noise may mask critical features of the signal and render tasks such as localization far more difficult than in the idealized laboratory condition.

I explored the impact of noise on sound localization in the grasshopper *Chorthippus biguttulus*. Males of this species show an unambiguous lateralization response towards the source of female response songs. This behavior has been used in previous experiments to examine the minimum directional cues necessary for sound localization. Despite their small size, because the ears of these grasshoppers act as pressure-difference receivers, they are capable of discriminating very fine inter-aural differences in both time (inter-aural time differences; ITDs) and intensity (inter-aural intensity differences; IIDs).

I examined two questions in this study. First, I asked whether, and to what extent, masking noise affects males' localization abilities. Second, I asked whether there were differential effects of noise on the two cues that may be used for sound localization: ITDs and IIDs. To test this, I exposed males to female song stimuli from two speakers, positioned at an angle of 180 degrees from one another and at 90 degrees to the animal's longitudinal body axis. Masking noise was presented from an overhead speaker. I manipulated the stimuli so that one speaker's broadcast was either slightly delayed (to simulate ITDs) or broadcast at a slightly lower or higher sound-pressure level relative to the other (to simulate IIDs). I measured males' lateralization responses to these stimuli and determined the minimum ITD and IID for a significant lateralization response at different levels of masking noise.

Preliminary data show that noise has a strong impact on the ability of males to localize female signals. These data have important implications for our understanding of grasshopper acoustic communication in the noisy social environment in which mating takes place. These results also complement our understanding of the neural basis of directional hearing, and these techniques can be applied to electrophysiological studies to better understand the proximate bases for adaptations related to directional hearing in challenging acoustic conditions.

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Microscale Acoustic Systems – Bio-inspired Micro-Electro-Mechanical Systems

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The auditory system of the parasitoid fly *Ormia ochracea* has a remarkable directional sensitivity allowing the insect to locate a sound source to within 2º azimuth. This sensitivity, comparable to that of humans, is more remarkable when the scale of the auditory system is considered: the tympanal membranes of *Ormia ochracea* are spaced less than 0.5mm apart. The directional cues available from phase differences and inter aural intensity differences are therefore extremely limited. The key to the fly's directional hearing lies in the coupling of the two tympana via a flexible cuticular membrane, christened the inter-tympanal bridge. This coupling amplifies the interaural intensity difference to 20dB at 45º azimuth and the interaural time difference by a factor of 20.

The aim of this research is to apply the coupling mechanic of the *Ormiine* ear in a Micro-Electro-Mechanical System (MEMS) and therefore develop a new form of directional microphone. The focus of the research has been on the identification of regions of linear directional sensitivity which was demonstrated by Miao Yu in models mimicking the *Ormiine* ear. The optimisation of the *Ormiine* ear to provide a linear directional sensitivity to incident sound at up to 30º azimuth appears to tally with behavioural observations of the fly turning to face the sound source. Unfortunately the occurrence of linear sensitivity is heavily dependent on the damping of the system which is difficult to recreate, or to predict accurately, in a MEMS device. Modelling via COMSOL and MATLAB has observed similar regions of linear sensitivity at a range of damping ratios by tailoring the ratio of the frequency of the first two resonant modes to the damping.

More detailed models of MEMS devices intended to be constructed by the POLYMUMPS service in MEMSCAP have been created, with the modelled devices offering the capability to tune the resonant modes of the diaphragm via electrostatic comb drives. The completed devices are then to be tested using a laser Doppler vibrometer and the sensitivities compared to the modelled results.

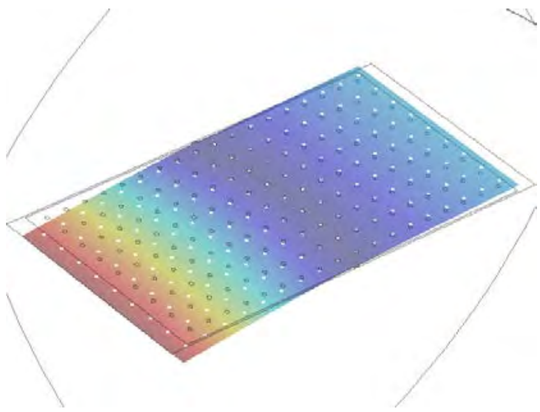

Figure 4: COMSOL image grab from thin film damping test of perforated membrane. Image shows acoustic structure interaction model of the membrane with sound frequency at 10 kHz and azimuth angle of 45º

When to Kick? Cues Triggering Collective Mechanical Defence in *Aphis nerii* (family: Aphididae)

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Aphids are omnipresent and regarded as pest as soon as numerous individuals exert harmful effects on the vitality of host plants. Due to a high number of natural enemies, growth rate of aphids mainly depends on their defence strategies. Defence of colonies lacking ant protection and a specialised soldier caste includes avoidance reactions, chemical defence and a recently described collective kicking and twitching response (CKTR) (Hartbauer, 2010). CKTR is recognisable by a high degree of synchronized abdomen shaking accompanied by hind leg kicking.

In our new research project we test the hypothesis that CKTR is effective against predators approaching aphid colonies from the air. Flying insects generate a visual stimulus, wind and substrate sound during the final approach phase. Besides visual cues literature describes vibration-mediated colony responses in young *Acyrthosiphon pisum* aphids (Gish, Dafni & Inbar, 2012) as well as in *Aphis nerii* colonies (Hartbauer, 2010). For example, the combination of breath and vibration mimics the approach of a large herbivore which resulted in a threefold increase in dropping rates of *A. pisum* individuals.

In a preliminary experiment we tested the potential of sound as a trigger for CKTR in *Aphis nerii* colonies. Brief frequency modulated (FM) sweeps were broadcast to oleander (*Nerium oleander*) twigs infested with *A. nerii* colonies (see figure) either through an attached mini-shaker or through a loudspeaker positioned close to aphid colonies. First results show that playback of FM sweeps frequently elicited CKTR in both stimulus situations.

So far our project is at an early stage and we are confident that further experiments will reveal the cues efficiently triggering CKTR from outside the colony as well as local cues synchronizing collective defence within a colony. In an accompanying phylogenetic approach we are going to test the hypothesis that CKTR evolved several times in non-ant tended aphids.

References:

Gish M, Dafni A, Inbar M (2012) Young Aphids Avoid Erroneous Dropping when Evading Mammalian Herbivores by Combining Input from Two Sensory Modalities. PLoS ONE 7:e32706.

Hartbauer M (2010) Collective Defense of *Aphis nerii* and *Uroleucon hypochoeridis* (Homoptera, Aphididae) against Natural Enemies. PLoS ONE 5:e10417.

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Asymmetry in the song of crickets: Preferences of females and proximate mechanism of discrimination

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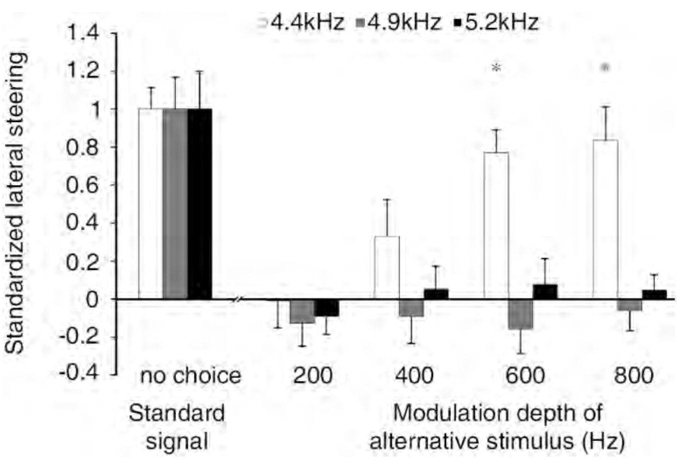
Subtle random deviations from perfect symmetry in bilateral traits are suggested to signal reduced phenotypic and genetic quality of a sender, but only little is known about the related receiver mechanisms for discriminating symmetrical from asymmetrical traits. We investigated these mechanisms in behavioural and neurophysiological experiments in the Mediterranean field cricket, *Gryllus bimaculatus*. A downward frequency modulation at the end of each syllable in the calling song has been suggested to indicate morphological asymmetry in sound radiating structures between left and right forewings. Even under ideal laboratory conditions on a trackball system female crickets only discriminated between songs of symmetrical and asymmetrical males in two-choice experiments at carrier frequencies of 4.4 kHz and large modulation depth of 600 and 800 Hz. Under these conditions they preferred the pure tone calling songs over the modulated (asymmetrical) alternative, whereas no preference was observed at carrier frequencies of 4.9 and 5.2 kHz.

These preferences correlate well with responses of a pair of identified auditory interneuron (AN1), known for its importance in female phonotaxis. The interneuron is tuned to an average frequency of 4.9 kHz, and the roll-off towards lower and higher frequencies determines the magnitude of responses to pure tone and frequency modulated calling songs. The difference in response magnitude between the two neurons appears to drive the decision of females towards the song alternatives. We discuss the relevance of song differences based on asymmetry in the morphology of song producing structures under natural conditions.



Mean lateral steering response of phonotactic tracks (mean ± s.e.m.; n = 14). Positive values indicate a preference for the non-modulated signal. Note that increasing modulation depth caused a significant increase in lateral steering towards symmetrical signals only for a CF of 4.4 kHz. Asterisks denote mean lateral steering significantly different from zero (one-sample t-test).

The research was funded by the Austrian Science Fund (FWF): P20882-B09.

Vibratory Communication and Putative Vibration Receptors in the Masked Birch Caterpillar *Drepana arcuata* (Drepanoidea)

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The use of solid-borne vibrations to communicate with conspecifics has been documented in immature stages of several holometabolous insect species. But, at present we know little about how signal characteristics confer information to recipients or how they are detected. Masked birch caterpillars, *Drepana arcuata* (Drepanoidea), defend silk leaf shelters using ritualized acoustic displays composed of three signals: anal scraping, mandible drumming and mandible scraping. These three types of signals vary during territorial encounters between conspecifics and have been shown to vary in rate and type as contests escalate. The objectives of this study were to assess how these signal types differ from one another, to assess what information they can confer to conspecifics, and to identify possible mechanoreceptors that might detect these vibratory signals.

Differences were observed for each signal in terms of temporal and amplitude properties within an individual. Anal scrapes have longer duration when compared to mandible scrapes and mandible drums. Mandible scrapes have the lowest relative amplitude of the three signals. The different characteristics of each signal suggest that each may confer information about the signaller. When comparing individuals of different weights, mandible drums produced by heavier individuals were higher in relative amplitude than lighter individuals. This has implications for conferring information about the signaller's size and body condition.

In addition to analyzing the signals, we conducted morphological studies in search of structures that may function as vibration receptors. We describe a mechanoreceptor complex in the prolegs composed of two chordotonal organs and two bipolar sense cells. The two bipolar sense cells are associated with the SV1 and SV2 setae of the proleg. These two setae, in addition to a third called V1, make direct contact with the leaf surface and vibrations could be detected by the sense cells when the setae are perturbed. The two chordotonal organs are located at the base of the prolegs. One is attached to two points on the wall of the proleg located near the V1 seta. The other chordotonal organ is attached to an aggregate of adipose tissue and to a point on the proleg wall which is located near the SV1 seta.

We propose these mechanoreceptors work as a unit to detect different characteristics of the signals. By doing so the mechanoreceptors may also determine the information content of the signals. Alternatively, the two receptors may be responsible for detecting different signals within an acoustic display.

Figure: *D. arcuata* defends its territory through ritualized acoustic displays (a trace of this display is seen at the bottom), a scanning electron micrograph of the proleg shows a detailed view of the crochets, SV1, SV2 and SV3 setae.

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Neuronal coupling of ventilatory and chirp rhythm in singing field crickets

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Male field crickets sing to attract conspecific females and during aggressive encounters with rivals. The neuronal network that generates the singing motor pattern is located in the anterior abdominal neuromers (Schöneich & Hedwig 2011, 2012). This organization suggests that the singing pattern generator may have evolved from the ventilatory motor network which is also located in the abdominal ganglia. In the calling song of *Gryllus bimaculatus*, chirps consisting of 3–5 short sound pulses (also called syllables) are perseveringly repeated at a rate of 2–3 Hz. A neuronal linkage between the singing and ventilatory motor pattern generator is indicated by a strict coupling between the chirp rhythm and the abdominal pumping cycles during singing (Huber 1960; Kutsch 1969; Paripovic et al. 1996).

Here we investigated the neuronal basis of the coupling between ventilatory and chirp rhythm by intracellular recordings of corresponding interneurons in the abdominal ganglia before and during fictive singing. The two motor patterns were monitored by extracellular recordings from transverse abdominal muscles and the mesothoracic wing nerve N3A, respectively. At the beginning of each singing episode the frequency of ventilation cycles increased considerably and the two rhythms always needed several cycles before their typical phase relationship was established. Although abdominal pumping then usually occurred in phase with the chirp cycles, from time to time the two rhythms became transiently uncoupled and then resynchronized. Intracellular recordings of ventilatory interneurons revealed that they receive additional EPSPs during singing, which strictly reflected the syllable pattern of the singing motor pattern. However, we never recorded synaptic input reflecting the ventilatory rhythm in the dendrites of singing interneurons.

Based on our data we conclude that ventilation and singing rhythm originate from discrete pattern generating networks. Coupling of the two rhythms is established by sub-threshold excitatory synaptic inputs forwarded from the singing to the ventilation network which then entrain the somewhat slower ventilatory rhythm.

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Courtship songs in a new hybrid zone between *Chorthippus albomarginatus* and *Ch. karelini* (Acrididae: Gomphocerinae) in Russia

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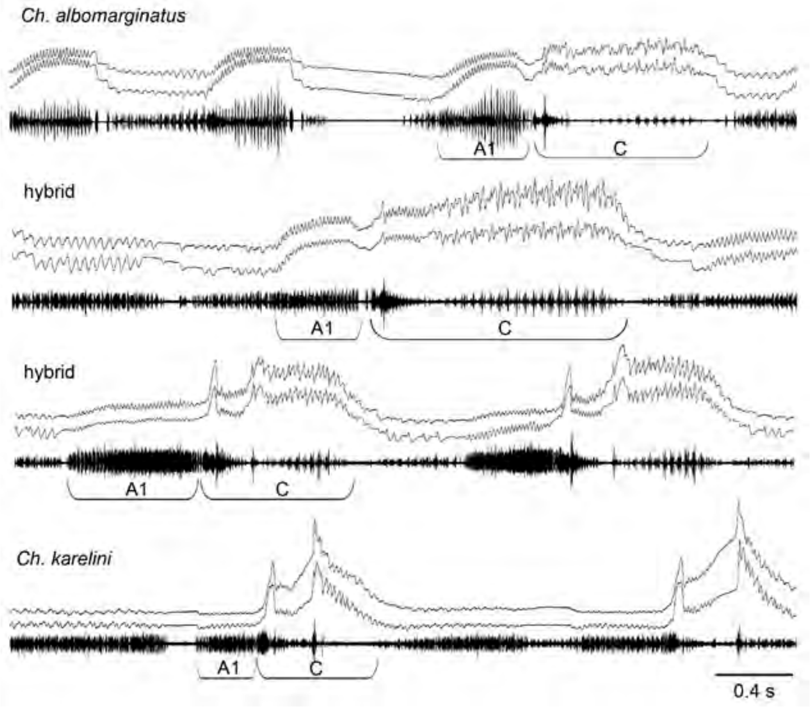
Sibling species of the *Chorthippus albomarginatus* group are very similar in morphology and calling songs, but they have different courtship songs. They are outstanding among all European grasshopper species since they have an extremely complex and elaborate courtship behaviour. The two species, *Ch. albomarginatus* and *Ch. oschei*, were previously shown to hybridize in a wide mosaic zone in the Ukraine and Moldova (Vedenina, Helversen, 2003, Beh Ecol Sociobiol 54: 44-54; Vedenina, 2011, Biol J Lin Soc 102: 275-291). Recently, we found a new hybrid zone between *Ch. albomarginatus* and the third species of this group, *Ch. karelini,* in the territory of European Russia. On the basis of analysis of the courtship songs and stridulatory movements of the hind legs, we found individuals whose songs were intermediate between the *albomarginatus* and *karelini* type. Figure shows a transition between A1 and C elements of the *albomarginatus* song and *karelini* song through intermediate variants. Similarly to the hybrid songs between *albomarginatus* and *oschei,* the songs recorded in the two new localities showed novel element combinations and increased among- and within variability. A distance between the two localities, where hybrid songs were recorded, appeared to be 70 km. This indicates that the hybrid zone between *albomarginatus* and *karelini* could be relatively wide, similarly to the zone between *albomarginatus* and *oschei*.



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Stable and variable parameters in vibrational songs of sympatric pentatomid bug species (Heteroptera, Pentatomidae)

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Vibratory signals play an important role in communication and premating behavior of pentatomid bugs. We investigated vibrational songs of sympatric bug species of genus *Carpocoris* (*C. pudicus, C. purpuriepennis* and *C. fuscispinus*). These species are very widespread in European Russia and often occur syntopically. Taxonomic identification of these species is difficult, since the most reliable feature are male genitalia. We found that the males of these species emitted the same signals towards individuals of both sexes; therefore, this type of signal may serve as rivalry and calling song. Females emitted only non-specific repellent song. Male song comprised series of relatively short pulses with a stable period that differed significantly in all three species. We suggest that differences in pulse period and duration may play a role in reproductive isolation. We measured coefficient of variation (CV) within and between males for five parameters of the songs in three species. Pulse duration was the most stable parameter: CV within males varied from 7 to 12 % in all three species. Pulse period was also stable in *C. purpuriepennis* and *C. fuscispinus* (CV within males varied from 8 to 11 %), and variable in *C. pudicus* (CV within males 17%). On the contrary, duration and period of the song were the most variable parameters: CV varied from was 38 to 61% (Table). Thus, vibrational signals of the studied species were shown to be stable at majority of the parameters and to have species-specific structure; the most variability was observed at the highest level of the song rhythmic organization.

Table. Coefficient of variations (CV) for five parameters of male songs in three *Carpocoris* species.

Song parameters	***C. pudicus* CV (%)**		***C. fuscispinus* CV (%)**		***C. purpuriepennis* CV (%)**	
	among ind	**within ind**	**among ind**	**within ind**	**among ind**	**within ind**
pulse duration	8	12	7	9	6	11
pulse period	10	17	6	8	9	11
pulse dominant frequency	5	10	7	9	10	9
song period	52	61	46	58	38	49
song duration	28	32	32	53	45	48

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The role of different courtship song elements in mate recognition of *Gryllus bimaculatus*

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Acoustic signals play an important role in cricket mate recognition. The importance of calling song parameters in mating success in *Gryllus bimaculatus* is well studied, whereas the role of courtship song parameters has not been studied in detail. It is suggested that courtship songs comprise two different elements: high-frequency ticks (12-16 kHz) and low-frequency pulses (4-5 kHz). However, we found that most of the courtship song elements in *G. bimaculatus* were quite variable (coefficient of variation in the range of 20-50%). In particular, the courtship ticks often contained substantial low-frequency power. In experiments with playback of synthesized courtship songs to 3- to 7-day-old virgin females, we studied the importance of two variable song parameters for mating success. In positive control (intact males), 84 % of females demonstrated mounting response, whereas in negative control (muted males), only 25 % of females mounted courting males. The synthesized songs with different carrier frequency of ticks (5, 8, 11, 14, 17 kHz) were as attractive to female as the natural courtship (positive control). Efficiency of stimuli without low-frequency pulses was also comparable with that in positive control; moreover, courtship latency appeared to be significantly lower for this stimulus ("11kHz_no pulses" and "17kHz_no pulses" in Fig. 1). Thus, changing of variable parameters did not decrease song attractiveness and in some cases, even increased it. Our results consistent with the idea that variable courtship traits give a female an opportunity for evaluation male quality and provide a substrate for directional selection.

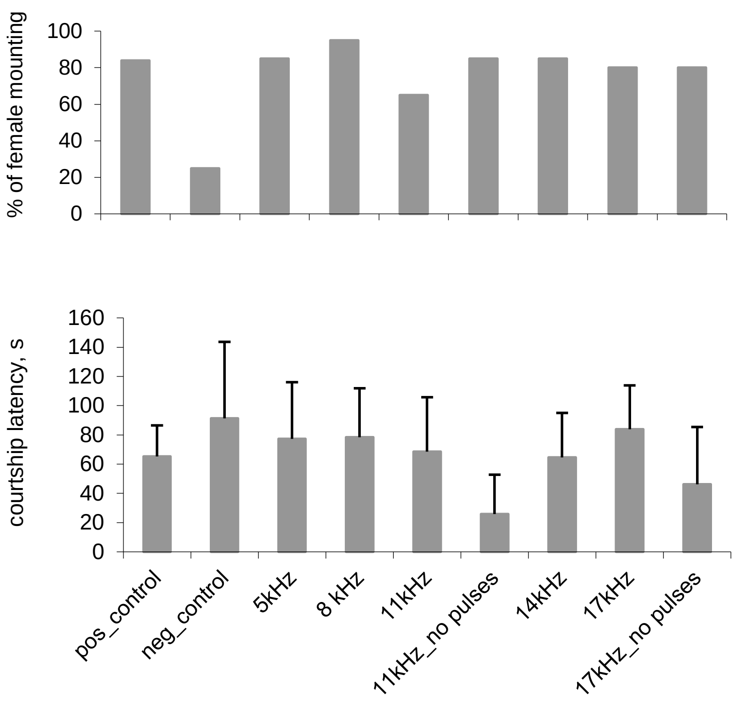

Fig. 1. Percent of females that mounted males (upper graph) and latency (mean + confidence interval) from onset of courtship song to the mounting response (lower graph). Data are shown for courtship by intact males (pos_control), by muted males with no playback (neg_control), and by muted males accompanied by playback of the test songs with different frequency of ticks.

Singing in the Rain:
Spiders Signaling on Sodden Substrates

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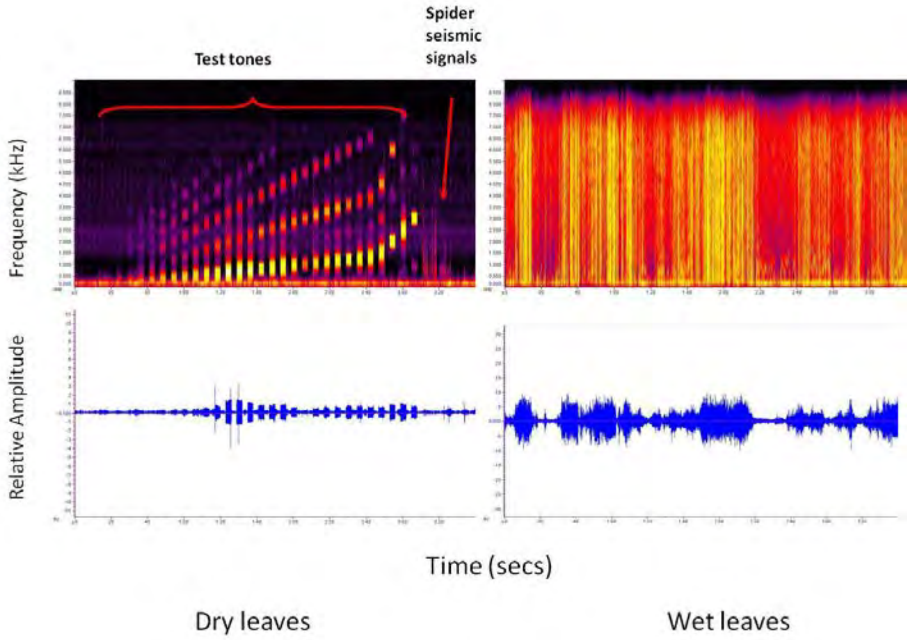
Communication in complex environments poses challenges of potential signal loss, but some wolf spiders may compensate using multimodal signaling. Courtship of male *Schizocosa ocreata* (Hentz) is multimodal, consisting of visual and substrate-borne vibration signals. Previous studies have shown that efficacy of vibratory communication varies with transmission properties of microhabitat substrates (leaf litter, rock, stone, wood). Because our 2011 field season had record-breaking levels of rainfall, we wondered whether adverse environmental conditions might dampen spider communication, and if leaf moisture affects substrate-conducted signals and mating success. We tested vibration transmission properties of wet vs. dry leaves using playback of both pure frequency tones and spider vibration signals. Dry leaves transmitted test tones and spider signals clearly, but wet leaves did not, obscuring signal structure across all frequencies. While wet leaves had higher levels of noise overall, dry leaves had higher signal to noise ratios. In addition, in dry leaves, signal amplitude may increase in a limited range of frequencies, suggesting potential for differences among leaves in resonance and/or signal filtering.

Males courted females equally on both wet and dry leaves, but mating success was significantly greater on dry leaf litter. Male spiders used significantly more visual signals (waves and arches) on wet leaves. Results suggest that although environmental conditions (e.g., heavy rains during the breeding season) can influence efficacy of individual signaling modes and negatively impact mating success, behavioral flexibility in multimodal signaling may compensate for constraints on communication.



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Substrate vibrations mediate startle behavior via femoral chordotonal organ in a cerambycid beetle

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Most insects can detect substrate vibrations in order to recognize predators and conspecifics. However, little is known about how coleopteran insects respond to vibrations. We investigated vibrational responses and associated sense organs in a cerambycid beetle, *Monochamus alternatus*. This beetle showed startle responses, such as freezing or fast movement against vibrations with low frequencies below 1 kHz, indicating that they detect low-frequency vibrations. We identified the sense organ responsible for this freezing behavior for the first time in a coleopteran species. The femoral chordotonal organ (FCO), located in the mid-femur, contained multiple sensory neurons and was distally connected to the proximal tibia via a cuticular apodeme. Beetles with all FCOs surgically ablated did not show freeze response to low-frequency vibrations during their walking whereas intact beetles did. These results suggest that the FCO is responsible for detecting low-frequency vibrations and mediating the startle behavior. We discuss the behavioral significances of vibrational responses in *M. alternatus* with respect to antipredator behavior and conspecific recognition.

A novel bio-mimetic MEMS microphone with better directional sensitivity performance in the low frequency range

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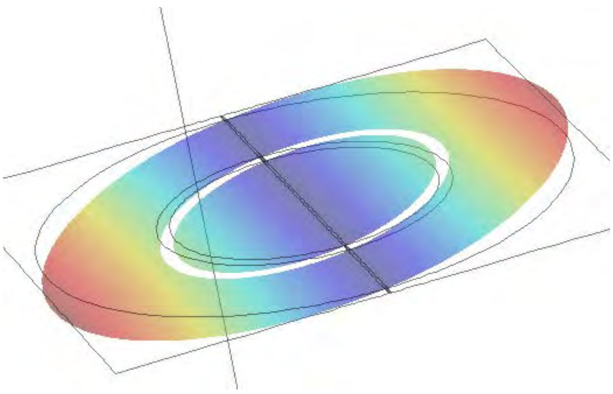
The development of Micro-Electro-Mechanical System (MEMS) microphones, including conventional condenser microphones, piezoresistive microphones and piezoelectric microphones, has been undertaken for over 25 years. However, these traditional MEMS microphones consist of complex further signal processing hardware, which complicates fabrication process and enlarges dimension. During the last 30 years, it was discovered that a parasitic fruit fly, *Ormia ochracea*, has high directional sensitivity (DS) when locating their hosts' mate calling (within 2° azimuth). This special capability of *Ormia* has already been applied in building new types of MEMS microphones to enhance their DS, to cut down physical size and to reduce post processing. However, since these MEMS microphones are inspired by the mechanical structure of *Ormia ochracea*, they have maximum and constant DS for azimuth incident angles in the range of 0° to 30°, which is not wide enough for some commercial applications.

The novel bio-mimetic MEMS microphone developed in this work aims to enlarge the range of azimuth incident angles with high and stable DS without sacrificing response sensitivity. Also, in order to increase the possibilities for civil use, such as hearing aids and mobile devices, this microphone was designed to have better performance (i.e. higher response sensitivity and DS) in a low frequency acoustic bandwidth based on the general human speech frequency range (roughly between 200 Hz and 4000 Hz). The model combines an annular structure with a concentric circular plate built by single crystalline silicon, separated and supported by a slim beam rotating along the diameter (see Figure below). Therefore, both the inner plate and outer ring react to incident sound waves, and the mechanical intensity difference (mIID) and mechanical phase difference (mIPD) between these pieces of the structure can be measured by using capacitive transduction, which expands the range of incident wave angles with a flat DS and thus increases the accuracy of locating. The first four resonance frequencies of this microphone are approximately 616Hz, 1721 Hz, 2292 Hz and 4099 Hz, and the COMSOL simulation of its directivity pattern reveals that it works well as a first order directional MEMS microphone.



Simulation of the new microphone

Do cave crickets *Phaeophilacris bredoides* Kalt. perceive sound signals?

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It is not known yet whether cave crickets *Phaeophilacris bredoides* perceive sound. These species of crickets have no tympanic system, which is the main auditory system in other insect species. However *Ph. bredoides* have a well-developed cercal system. The cercal system functions as a distant mechanoreceptor system and hence works in detecting predators. Singing crickets *Gryllus bimaculatus* employ the cercal system for detection of low frequencies in the range of 30 - 2000 Hz, presumably together with the popliteal and the Johnston organs (Knyazev, 1987, J. Evol. Biochem. Physiol., 202) but use the tympanic system for detection of interspecific signals with carrier frequency about 4 kHz. Here, we investigated whether the cave cricket can perceive low-frequency sounds in the absence of a tympanic system.

Methods: We tested cave crickets individually in a sound-proof chamber (V = 349000 cm^3) suspended above a light ball of foam plastic, i.e. a trackball. The signal was a sinusoidal stimulus ranging from 10 to 6000 Hz applied in steps of 50 Hz. Stimulation was from behind and lasted 5 seconds. Sound intensity was set at 102.2 ± 10 dB SPL. The response of the cricket was recorded with an infrared video camera. Two observers scored the behavior as shuddering, squeezing, negative phonotaxis, or searching behavior. The latter was defined as scanning movement of the antennae. Data was analysed in Statistica 5.0.

Results: The crickets *Ph. bredoides* responded to sound signals in the range of 10–6000 Hz. The strongest response was to signals in the range of 50–2000 Hz. The crickets showed different types of reactions especially protective behavior, i.e. shuddering, “squeezing” into the substrate, negative phonotaxis. In addition, the crickets showed searching behavior. Above 2000 Hz the number of reactions decreased.

Discussion: Perception of the low-frequency sounds in these crickets seems to be due to the activity of the cercal system. This might be mediated by the popliteal (vibrosensitive) and Johnston organs as in singing crickets. Since the cave crickets do not emit high-frequency sound signals, we speculate that the perception of the low-frequency sounds serves in interspecies communication, which includes shaking (vibrations) and wing-flicks (low-frequency signals). In addition, the perception of low frequencies through the cercal system may add in anti-predator behavior. A detailed analysis of the cercal system could answer that.

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From the tympanum to the brain: projection pattern of auditory cells in the moth *Heliothis Virescens* (Noctuidae)

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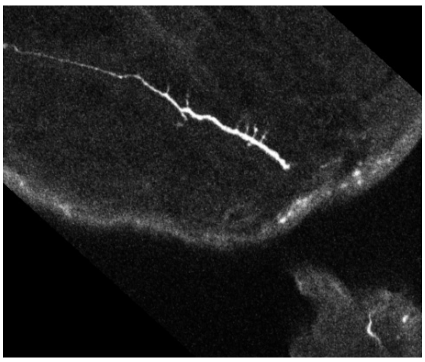
Noctuid moths have a notably simple tympanic ear housing two auditory sensory neurons; both specialized for detecting ultrasound calls of an echolocating bat. In the heliothine species, *Heliothis virescens*, one of the two so-called A cells, which enter the thoracic ganglion, is reported to ascend via the suboesophageal ganglion (SOG) directly to the brain (Surlykke and Miller, 1982, J Insect Physiol. 28). Whereas the neural processing of auditory information is relatively well studied at the peripheral and first synaptic level, little is known about the features characterizing higher order levels in the moth brain. Thus, the target region of the auditory afferent ascending from the thoracic ganglion to the brain in this insect group has not yet been described. In the current study we marked the sensory neurons of the heliothine moth ear by retrograde staining and then visualized, by means of confocal microscopy, the neural projections in the ventral cord and the brain in a three-dimensional view.

Methods: We either inserted the fluorescent dye, tetramethylrhodamine dextran (Microruby), into the peripheral nerve ends of the auditory cells (disrupting the tympanon) or we applied dye crystals into the IIINb nerve. After dissection and fixation we scanned the central nervous system of the moth using a confocal laser scanning microscope.

Results: In addition to rich ramifications mainly confined to the thoracic ganglion we found one fiber projecting upstream the ventral cord. This axon ascends further into the SOG on the ipsilateral side, giving off short neural processes before it bends off towards the lateral protocerebrum of the brain (see image below).

Discussion: The direct connection to the lateral protocerebrum, which is a higher association area in insects, suggests an efficient and fast integration of auditory information with other sensory modalities like olfaction.



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