International Society for Neuroethology

Newsletter
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International Society for Neuroethology
c/o Panacea Associates
744 Duparc Circle
Tallahasee, FL 32312 USA

Voice/fax: +001 (850) 894-3480
E-mail: ISN@panassoc.com
Website: http://neuroethology.org

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ISN Officers

President: Albert S. Feng, Dept. Molecular & Integrative Physiology, Univ. of Illinois, Urbana IL 61801 USA. Phone: 1-217-244-1951; Fax: 1-217-244-5180; afeng1@uiuc.edu

Treasurer: Sheryl Coombs, Parmly Hearing Institute, Loyola Univ. of Chicago, 6525 N. Sheridan Rd., Chicago IL 60626 USA. Phone: 1-713-508-2720; Fax: 1-713-508-2719; scoombs@luc.edu

Secretary: Janis C. Weeks, Inst. of Neuroscience, Univ. of Oregon, Eugene OR 97403 USA. Phone: 1-541-346-4517; Fax: 1- 541-346-4548; weeks@uoneuro.uoregon.edu

Past-President: Malcolm Burrows, Dept. of Zoology, Univ. of Cambridge, Downing St., Cambridge CB2 3EJ, UK. Phone: 44-(1)223-336628; Fax: 44-(1)223-330934; mb135@cus.cam.ac.uk

President-Elect: Edward A. Kravitz, Dept. Neurobiology, Harvard Medical School, 220 Longwood Ave, Boston MA 02115 USA. Phone: 1-617-432-1753; Fax: 1-617-734-7557; edward_kravitz@hms.harvard.edu

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Next International Congress: August 9-13, 2004. Hotel Nyborg Strand, Nyborg, Denmark

This Issue Includes

The ISN President's Column

Albert S. Feng, ISN President (afeng1@uiuc.edu)
Univ. of Illinois,. Urbana, Illinois, USA

Happy New Year to all! 2003 has already been a busy year for the ISN. We are tackling many issues aimed at increasing the benefits of membership in the ISN in order to increase our numbers and to engage more students in our activities. Here I comment on several of them.

Management. As you know, this is the last year that Panacea Associates will be our management service provider. The Society is searching for a new management firm, with Sheryl Coombs leading this effort. We are delighted that more than 60 management firms responded to our initial Request For Proposals. With the help of our Council, we are narrowing down the list to a manageable size in order to study the individual proposals in greater detail. We are pleased that most of these firms can host the Society website and can handle on-line dues payment and on-line conference registration. In light of the competition, we may receive extra services at the same cost with the change in the management firm at year's-end.

Website. The Society is actively searching for a part-time web designer who can upgrade the appearance of the Society website and enrich its content. We have developed a job description for this position and posted it on our website. The Web Oversight and Education Committee will be responsible for screening the bids and selecting a designer.

The Nyborg Congress. Planning for the 2004 Congress in Nyborg, Denmark, is underway. I am pleased to inform you that, with the help of our Council, we have completed the selection of the Chair and Vice-Chair for the Congress Committee. Sarah Bottjer (University of Southern California, USA) will chair this Committee, with Martin Giurfa (Université Paul Sabatier, France) as Vice-Chair. The Chairs will be soliciting nominations (including self nominations) for membership on this Committee shortly. In addition, later in the spring, the Congress Committee will issue a Request For Proposals for symposia at the 2004 Congress. Please start thinking about the symposium that you would like to organize for the Nyborg Congress.

New Student Travel Awards. A resolution that emerged from the ISN Executive Committee meeting in November was to establish Student Travel Awards, ideally named after a distinguished neuroethologist. We are delighted that the Heiligenberg family has given us permission to name these merit-based awards *The Heiligenberg Student Travel Awards*. As many of you know, Walter Heiligenberg was a distinguished neuroethologist, and a pioneer in the field; he was the President-Elect of the ISN when he died in an untimely air accident in the mid-nineties. Several of these awards will be made *annually* to qualified students who wish to present their work in neuroethology at national and international scientific meetings, consistent with the aims and goals of the ISN (e.g., meetings in neuroethology, neuroscience). A Selection Committee will be appointed shortly in order to make the first of these awards in 2003-2004. The Executive Committee believes that significant benefits will result from these awards: (1) they will promote the dissemination of results of research in neuroethology; (2) they will encourage and assist ISN student members to travel to scientific meetings; (3) they will increase attendance of students at the International Congress for Neuroethology and at other conferences; (4) they will provide benefits during non-congress years for students who join the ISN; (5) they will increase the retention of ISN members during non-congress years. The ISN will provide seed money for these awards. We hope that donations from members and funds raised from outside sources can support the Heiligenberg Awards in the future. If you wish to contribute towards these awards, you can do so when you submit your annual dues payment by checking the appropriate box on the form. In the future, a mechanism will be established to accept contributions towards the awards at any time through the ISN website.

Discount for Journal Subscription. We have received the official word from Springer-Verlag that the publisher will continue to offer a special discount rate (US $179, or 169 Euro) for ISN members to subscribe to the hard copy version of the *Journal of Comparative Physiology A*. Also, ISN members can continue to enjoy a special subscription rate to the *Journal of Experimental Biology* from the Company of Biologists (personal online subscription is US $58 or UK£34).

Questionnaire. The Long-Range Planning Committee will soon send out a questionnaire to solicit member input on topics including the newsletter, the possibility of establishing visiting lectureships during non-congress years, the possibility of establishing chapters of the ISN, and the content and frequency of the upcoming and future International Congresses. Please respond to the questionnaire promptly so that we can better meet the interests and needs of the membership on these topics.

Thank you in advance, and see you in Nyborg!

Web Research Spotlight

Zen Faulkes (zfaulkes@panam.edu)
Univ. of Texas - Pan American, USA

The Web Oversight and Education Committee wishes to begin a regular series of short articles on ISN's website, http://neuroethology.org, to spotlight neuroethology research by ISN members. These articles might be a little like 'News & Views' in *Nature*, only aimed at more general readers. These would be archived, becoming an educational resource for those interested in neuroethology. The guidelines are:

- Approximately 700 words in length.
- Research should be published. Recent work is slightly preferred, but reviews of older 'classic' work would also be welcome.
- Provide about three pictures. Suggestions: one picture of the animal studied, one of a neuron or brain, etc., and one of data. Images that are clear when their length or width is reduced to ~400 pixels are preferred.
- A few relevant references.

The goal is to post one new article at the start of every month. Anyone who wishes to contribute an article, or would like more information, can e-mail me at the address above.

Add our link to your website!

Adding a link to ISN (http://neuroethology.org) on your website will help raise our profile in the scientific community.

Add your website address to the ISN Member Directory!

To keep our membership directory current, check your current listing at http://neuroethology.org and send any updates to our webmaster at Panacea Associates, <lampman@panassoc.com>. We are adding members' website addresses to the directory so please submit this information as well. ✥

Seeing the World Through a Locust's Eyes

Roger Santer (r.d.santer@ncl.ac.uk)
Univ. of Newcastle upon Tyne, UK

If you want to understand how insects avoid high-speed collision, the answer could be to take one to a movie, at least according to current research by Claire Rind and Peter Simmons at the University of Newcastle upon Tyne. Roger Santer, their Ph.D. student, gives his perspective on how their work could, one day, help improve safety on our roads.

Animals live in a complicated and dynamic world, so their visual systems must cope with shadows, moving objects and variations in colour and contrast whilst still extracting the information they need to go about their lives. Many visual systems 'filter' their input, disregarding unnecessary detail and preserving those pieces of information that are important to the animal — such as how far it is to a nearby object and whether or not a predator is swooping towards them. Man-made 'seeing machines' are not so efficient. They're unable to extract this important information as quickly and efficiently as biological systems; but this should come as no great surprise. The visual systems of animals have been perfected by millions of years of evolution whilst, by comparison, artificial visual sensors are a recent invention. Many scientists believe that the solution is to copy what we find in nature; this is called biomimetics.

Rather than attempting to understand an entire visual system, a simpler task is to concentrate on a particular aspect of its function. At the University of Newcastle upon Tyne, we're trying to understand one such function — the detection of looming. 'Looming' is a visual signal that indicates an object approaching the observer. It is defined by a number of 'features.' A looming object appears to expand and the rate at which it expands increases as it gets closer to the observer. Recognising these features allows animals to detect and avoid potential collision. If we are able to understand how the animal achieves this, we may be able to use this information to create our own biologically-inspired collision detector.

Our model animal is the locust, *Locusta migratoria*. Locusts are remarkable animals as they possess only about one million nerve cells but are able to operate within the same visual world as we do. The compound eyes of insects are highly specialised and are not like the camera eyes of vertebrates. Instead of a single lens, the locust (for example) possesses some 8,500 separate lenses in an eye that measures only a few millimetres across. These divide the world, as perceived by the insect, into a mosaic. As a result, these eyes have difficulty seeing fine detail. However, compound eyes have a massive advantage over vertebrate eyes in resolving rapid events. They work incredibly fast so they see movements almost as if they had occurred in slow motion. Furthermore, a massive proportion of the insect's brain is dedicated to dealing with visual signals and efficiently coding them into the information it needs to successfully accomplish a range of tasks. If you're left in any doubt as to how amazing these eyes really are, try to recall the last time you attempted to swat a fly with a newspaper!

The locust is a good subject for studies of looming detection. It possesses two large and easily identifiable neurons that respond particularly to objects coming towards the animal. The first of these is the LGMD (lobula giant movement detector; Fig. 1), which receives input from the optic lobe, the area of the locust's brain behind its compound eye. This neuron extends to the lateral protocerebrum of the brain where it excites the DCMD neuron (descending contralateral movement detector). The DCMD extends to the thorax where movements such as flight and jumping are coordinated. The two cells effectively form a 'cable' down which information received at the eye can be carried to the thorax where it may be converted into an evasive behaviour. Spikes in these neurons are monitored experimentally. These spikes are elicited when the locust is challenged with an imminent collision.

We wanted to find out exactly how the locust LGMD and DCMD were able to detect the visual features defining a potentially colliding object. To do this, we needed to find a way of making the locust think that an

Figure 1. Collision-detecting LGMD2 neuron in the locust optic lobe.

object was coming towards it. We achieved this by showing the locust clips from the Star Wars movie (Fig. 2), allowing its reaction to rapidly approaching spacecraft on collision or near-miss trajectories to be studied. We were able to monitor the locust's nervous system as it watched these clips and determine which kinds of visual stimuli caused the LGMD and DCMD neurons to become excited. We discovered that the two nerve cells were particularly interested in objects that expanded. Through further research using computer-generated stimuli, we discovered that the cells were also interested in the rate at which the stimuli expanded — these important features define a looming object.

But how are these features identified? Behind the insect compound eye, each of the lenses sends information down parallel processing channels through the optic lobe. These neural channels preserve the insect's mosaic view of the world through several different stages of processing; this is crucial to the function of any visual system. Each of the optic lobe's parallel processing channels makes contact with the LGMD dendrites (the input area of the cell), mapping on to it the view of the world perceived at the compound eye. These channels are excited by movement so that, as a looming object appears to expand over the eye, more and more channels are excited. Due to their arrangement, these channels pass an expanding area of excitation, which mirrors the perceived growth of the looming object, on to the LGMD. Studies using electron microscopy and antibody labeling techniques have shown that, as well as exciting the LGMD, each of these input channels inhibits its neighbour on activation. The identification of these lateral inhibitory interactions led us to hypothesise how the LGMD is able to detect potential collision. We suggested that just as excitation expands over the dendrites of the LGMD during a loom, so too does lateral inhibition. The neurons that carry this inhibition delay its spread to their neighbours. Meanwhile, excitation is limited only by the growth of the looming image. Thus, in the early stages of a loom, when the object appears to expand rather slowly, excitation and inhibition travel at approximately the same rate and effectively cancel one-another out. However, as the object gets closer, it appears to expand more rapidly. This allows excitation to expand at a greater rate, while inhibition is still limited by the properties of the neurons that carry it. The result is that, without the restrictive effects of inhibition, the LGMD is strongly excited. We call this process a 'critical race' between excitation and inhibition and believe that it is responsible for the LGMD's preference for looming stimuli.

Figure 2. Locust watching 'Star Wars' in the cause of science.

(The) robot was able to successfully avoid collision in a simplified environment of coloured 'Duplo' bricks using only its LGMD-inspired collision detector.

To test this theory, a computational model of the proposed LGMD architecture was constructed, simulating the neurons that were known to exist in the locust's optic lobe. This model was challenged with a series of virtual looming stimuli that expanded in the same way as actual looming objects. The LGMD model responded in a similar way to the real LGMD — it was able to detect looming stimuli. Thus, this computational model was a plausible representation of the locust neuron and an effective collision detector. However, we needed to prove that it would work in the real world. To do this, we began collaborating with researchers at the Institute of Neuroinformatics, Zurich. Together we were able to connect the computational LGMD model, running on a PC, to a small mobile robot. The model received input from a miniature video camera mounted on the robot and, when its LGMD detected a potential collision, would send a command to the robot instructing it to take evasive action. This robot was able to successfully avoid collision in a simplified environment of coloured 'Duplo' bricks using only its LGMD-inspired collision detector. Although this work is still in its infancy and we have a long way to go before the sensor can be used in a complex natural environment, the results are encouraging. Within the experimental arena our LGMD model must cope with shadow and contrast effects whilst still avoiding potential collision, which supports the sensor's future use as a robust collision detector.

As biologists, the real draw has always been to understand how animals are able to function so effectively within their environment. We believe that our LGMD model represents the kinds of processing that occurs in the locust itself and detects potential collision in the same way. However, we're still not sure exactly how the complex information provided by the LGMD/DCMD system is used to instigate evasive behaviour. Our current research, supported by the Gatsby Charitable Foundation, is attempting to understand the behaviours that the locust uses to avoid collision with objects and predators. By understanding these behaviours, we aim to find out exactly how the LGMD and DCMD neurons trigger these behavioural reactions. In this way, we hope to gain a better understanding of how the complete collision detection pathway, from detection of a threatening stimulus to evasive behaviour, really functions. These findings can then be transferred back to our biomimetic work, taking us one step closer to a locust-inspired collision detector which will function effectively in the human world. Who knows, perhaps one day we will have a sensor that is reliable, quick and robust enough to compete with those found in Nature?

Tropical Neuroethology

Mark W. Miller (mmiller@neurobio.upr.clu.edu)
Univ. of Puerto Rico Medical Sciences Campus, USA

"Some of the most fascinating and pressing problems open to science concern the structure and function of the human brain, that exceedingly complex organ believed to be the site of our thoughts, the storeroom of our memories, and the source of all human achievements, including science itself. A number of avenues are open through which scientists can approach and explore this intricate organ. Perhaps one of the most fruitful is to study equivalent structures in simple primitive invertebrates such as those living in the tropical waters near the Laboratory of Neurobiology."

Professor José del Castillo, 1978

All of the research conducted in our lab benefits from the vision and legacy of Professor José del Castillo (1916-2002), who founded the Institute of Neurobiology in 1968. Although Prof. del Castillo's recognition and eminence are due largely to his pioneering work in synaptic physiology, his keen interest in animal behavior and its neural substrates are also reflected in his scientific accomplishments and contributions. Some would argue that del Castillo's collaborative efforts with Graham Hoyle to identify the missing link between the annelids and the arthropods by studying the neuromuscular physiology of *Peripatus* should be required reading for any card-carrying student of Neuroethology. The image of Hoyle and del Castillo sloshing into the depths of the Puerto Rico rainforest in search of specimens provide inspiration to all members of the Society.

Our research focuses on several themes that lie close to the hearts of many neuroethologists: central pattern generators, sensory-motor integration, neuropeptides, neuromodulation, and cotransmitters. In the grand tradition of the discipline, we pursue experimentally advantageous preparations that are likely to disclose principles that are generalizable to more complex systems. This pursuit has led us to approach and cross the great Squishy-Crunchy divide that once separated the two great camps of Neuroethology.

The Squishies: Cotransmitters and the Regulation of Feeding Behavior in *Aplysia*.

The driving force behind this project is Manuel Diaz-Ríos, a graduate student who is nearing completion of his Ph.D. training. In 1999, Manuel published an article in which he used immunohistochemical and nerve backfill techniques to map the distribution of GABA-like immunoreactive neurons in the *Aplysia* nervous system (Díaz-Ríos et al., 1999). Interestingly, Manuel observed that the GABAergic system of *Aplysia* was confined to the CNS. He concluded that GABA has little or no direct role in motor control or in the transmission of sensory information to the brain of *Aplysia*. From a functional perspective, the GABAergic system of *Aplysia* appeared to have more in common with that of vertebrates than with other invertebrates, in which GABA plays a major role in peripheral control.

When Manuel showed his results to other *Aplysia*ologists, they were often struck by the similarity of certain GABA-immunoreactive neurons and cells that had previously been shown to contain dopamine (DA) using various histofluorescent techniques. One investigator who was particularly influential in prodding him toward exploring their possible colocalization was the late Professor Irving Kupfermann. As was the experience of so many neurobiologists, Manuel could have done far worse than to follow Irving's instincts and advice. He conducted a double labeling study in which he showed that GABA-like immunoreactivity (GABAli) colocalized with catecholamine histofluorescence and tyrosine-hydroxylase immunoreactivity (Thli) in five interneurons within the buccal feeding circuitry (Fig. 1; see Díaz-Ríos et al., 2002). In this study, he observed that this

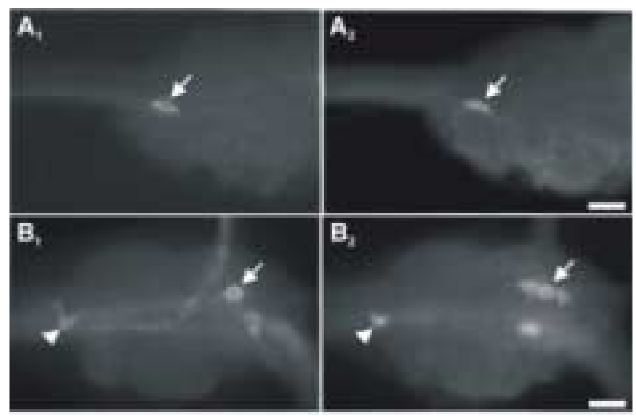

Figure 1. Colocalization of GABAli and Thli occurs in five neurons in the buccal ganglion. A1: Thli is present in the paired B20 cells (arrow, only left hemiganglion shown). A2: GABAli in the same preparation as A1. B20 is the only GABAli cell on the rostral surface of the ganglion. B1; Thli on the caudal surface buccal ganglion. Thli is found in the paired B65 neurons (only right hemiganglion shown, arrow) and in an unpaired cell near the commissure (arrowhead). B2; GABAli in the same preparation as B1. GABAli is present in B65 (arrow) and in the unpaired cell (arrowhead). The presence of additional Thli cells in B1 that are not GABAli, and GABAli cells in B2 that are not Thli support the specificity of these methods. From Díaz-Ríos et al., 2002.

colocalization was not obligatory. In fact, it was not detected in any additional neurons in the CNS.

Manuel's anatomical studies have enabled him to initiate physiological and pharmacological experiments aimed toward determining the contributions of GABA and DA to synaptic signaling by the five neurons in which they are colocalized. These interneurons exhibit substantial divergence and convergence and they are thought to play key roles in the initiation, selection, and phase relations of feeding motor programs. His experiments promise to increase our understanding of how these two colocalized 'conventional' or 'classical' neurotransmitters may act as cotransmitters in the regulation of the multifunctional circuitry that controls the consummatory behaviors of *Aplysia*.

The Crunchies: Modulation of an Integrated Central Pattern Generator – Effector System.

These experiments are led by Dr. Timothy J. Fort, who joined us after receiving his Ph.D. from the University of Rhode Island in 2000. Tim's experiments utilize a time-honored central pattern generator model, the crustacean cardiac ganglion, to examine interactions between 'central' and peripheral mechanisms of neuromodulation. In contrast to the myogenic heartbeat of the vertebrates, cardiac contractions in decapod crustaceans are controlled by a simple (nine neurons) ganglion that is embedded in the dorsal wall of the heart (recent review: Cooke, 2002).

Early workers, such as Alexandrowicz and Maynard, noted that the crustacean cardiac system exhibits numerous features, such as spontaneity, motor output, and sensory feedback, that make it an exceptional model for the brain. Tim's studies are influenced by this conception, as well as by more recent experimental and theoretical observations that emphasize the necessity for coordinated central and peripheral modulation of motor systems (Brezina et al., 2000). Tim is using a novel analytical approach known as the neuromuscular transform to examine relations between the patterned output of the ganglion and properties of the cardiac contractions that they produce. His work benefits substantially from the contributions of our collaborator Dr. Vladimir Brezina (Dept. of Physiology & Biophysics, Mount Sinai School of Medicine), originator of the neuromuscular transform.

Figure 2. Tim Fort and blue crabs in Puerto Rico.

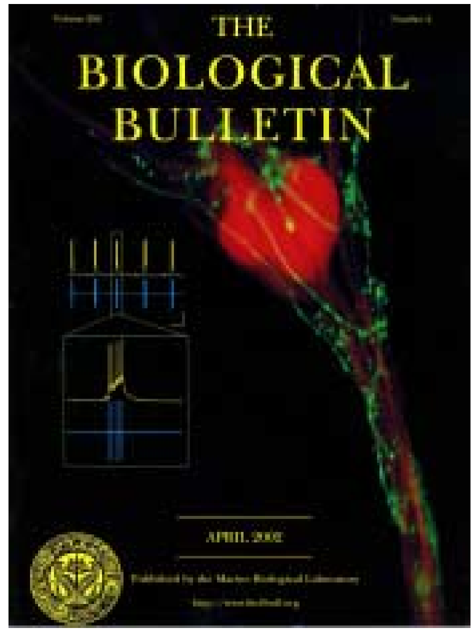

Figure 3. Cover of The Biological Bulletin featuring crab cardiac ganglion.

Tim uses the cardiac system of blue crabs (*Callinectes sapidus*) that he traps in local mangrove forests and lagoons (Fig. 2). This specific preparation was chosen because the impulses of its five motor neurons occur in precise synchrony. This peculiarity was originally demonstrated by Kenro Tazaki and Ian Cooke in crabs found in Hawaii (*Portunus sanguinolentus* and *Podophthalmus vigil*) and Tim's work suggests that it may be a common property of the portunids. It does not occur in closely related decapods, such as lobsters, where the five motor neurons fire in coordinated bursts, but with distinct, and sometimes multiple, sites of impulse initiation. Tim has developed a novel preparation, which he designates the semi-intact working heart, that enables him to simultaneously record the output of the ganglion and the muscle contractions that are produced. The simple impulse train that results from the synchronous motor neuron firing greatly facilitates his analyses of modulator actions. His present experiments focus on known modulators of crustacean cardiac activity [such as dopamine (Fig. 3), crustacean cardioactive peptide (CCAP), and the FMRFamide related crustacean neuropeptides] with an aim toward understanding how peripheral modulatory effects are coordinated with actions that occur at the level of the CPG.

Continued on next page →

Figure 4. Students in the Tropical Neuroethology course at the University of Puerto Rico.

Tropical Neuroethology – a Summer Program for Undergraduates

Undergraduate students play a key role in all aspects of our research program. From 1998 to 2001 we conducted a summer program in which undergraduate students (six per year; Fig. 4) were invited to Puerto Rico to participate in research and educational activities at the Institute of Neurobiology. This 5-week program, entitled *Tropical Neuroethology*, is modeled after the highly successful Neural Systems & Behavior course (at the Marine Biological laboratory, Woods Hole, Massachusetts, USA) that has had considerable influence on the ISN and on the field. Student participants receive an intensive 'hands on' introduction to research in the laboratory and in the field. Educational activities include: (1) daily introductory lectures; (2) workshops on modern neurobiological methods; (3) a weekly journal club; (4) a public seminar series; (5) weekly field trips and (6) a roundtable discussion of ethical issues in research. Students receive training in: sampling techniques in the field, underwater photography (Fig. 5), immunohistochemistry, nerve backfill methods, intracellular and extracellular electrophysiological recording, dye injection techniques, and fluorescence and confocal microscopy.

Tropical Neuroethology provides students with the opportunity to receive a comprehensive research training and educational experience. They are involved in all aspects of scientific research, ranging from the formulation of hypotheses and experimental design to the analysis and presentation of data. Finally, they have the opportunity to attend regional or national conferences to present their results to the scientific community. At least five publications have resulted from work initiated by students and faculty of the course (Díaz-Ríos et al., 1999, 2002; Delgado et al., 2000; Kirk et al., 2001; Robie et al., 2003). The significance of the *Tropical Neuroethology* program lies in its capability to expose students to opportunities that were previously unrecognized or inaccessible. Perhaps of equal consequence, it can promote a diversity and broader participation in Neuroethology that will ensure the continued vigor and vitality of the discipline for many years to come. ❖

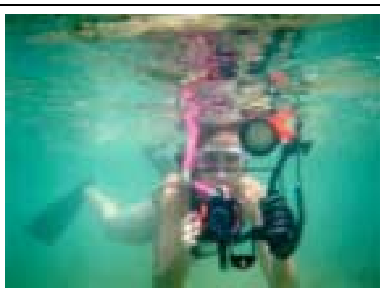

Figure 5. Photographing marine animal behavior in situ.

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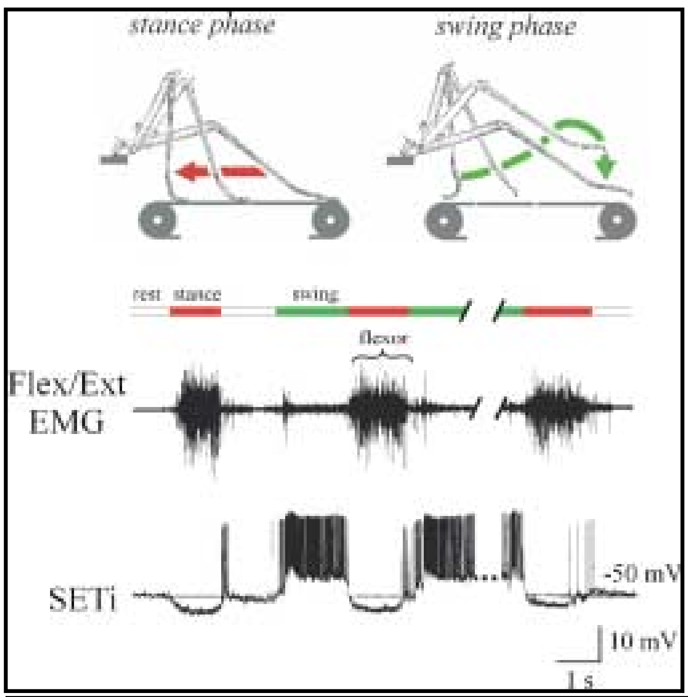
Recent Advances in Investigating the Complexity of Something Ordinary: Insect Walking

Ansgar Büschges (Ansgar.Bueschges@uni-koeln.de), Joachim Schmidt, Hans Scharstein and Tim Mentel
Universität zu Köln, Germany

The research of our group is aimed at understanding the neural control of locomotion. Most locomotor movements and their underlying motor patterns are rhythmic, being composed out of two main phases — a power stroke and a return stroke. In walking, these two phases are the stance phase, during which a leg is on the ground and contributes to moving the animal's trunk along the surface, and the swing phase, during which the leg returns to its starting position for generating the next stance phase. Despite the first impression, from a closer look it becomes clear that the generation of a functional locomotor program is quite complex. The complexity of a locomotor program increases with the versatility of the locomotor system and the complexity in the morphology of the locomotor organs. For example, in a multi-jointed insect leg the activities of more than a dozen muscles supplying the leg segments with differing phases of activity in the locomotor cycle have to be precisely coordinated for generating stance phase and swing phase for walking.

Today it is clear that a variety of principles in neural control of locomotor patterns for walking are common in vertebrates and invertebrates, regardless of the leg number being two, four or six. This offers the opportunity to choose the most appropriate system for getting answers to specific questions of general interest. We are studying walking in insects and we want to report here some recent findings from our lab on mechanisms for patterning and coordinating motoneuron activity in the multi-jointed stick insect leg. For assessing the significance of these findings a brief introduction into the current state of knowledge on walking pattern generation in the stick insect is necessary. The neural machinery of the walking system of the stick insect, and probably of other orthopteran insects as well, is composed of six individual walking pattern generators, so-called *leg controllers* (see also Orlovsky et al. 1999*; Oxford Univ. Press),* one for each leg. Each of those leg controllers

Figure 1. Rhythmic activity of the slow extensor tibiae motoneuron (SETi) during stepping movements of the middle leg (taken from Schmidt et al. 2001). The membrane potential of SETi is hyperpolarized below resting potential during flexor activity (Flex/Ext EMG) and depolarized during leg swing.



comprises central neural networks and sense organs on the leg. These days some, but still incomplete, evidence exists on the topology of these neural networks (for reviews see Bässler & Büschges 1998, *Brain Res. Rev*. **27**:65; Burrows 1996, *Oxford Univ. Press*). The activities of the leg controllers are coordinated by intersegmental influences. Each leg controller has a modular structure. It is composed of at least three central rhythm generating networks, one for each of the main leg joints. These networks are capable of generating alternating activity in the antagonistic motoneuron pools that can be strongly modified and modulated by sensory signals from the limb (for review see Bässler & Büschges, 1998).

…a special research group at the Institute for Advanced Study at Berlin…on 'Neural Control of Locomotion' brought together scientists with different backgrounds.

In order to investigate the segmental mechanisms of walking pattern generation in the individual leg we used the single-walking leg preparation, initially introduced by Ulrich Bässler. This preparation allows an investigation of the stepping motor program of the individual limb without sensory coordinating influences from the neighboring legs (Fig. 1; Fischer et al. 2001, *J. Neurophysiol*. **85**:241). We were able to verify a long-standing assumption: the activity pattern in insect leg motoneurons during actively-performed rhythmic leg movements, like walking, is based on the alternation of excitatory and inhibitory synaptic inputs (Schmidt et al. 2001, *J. Neurophysiol*. **85**:354). Recently we showed for the tibial motoneurons, i.e. extensor and flexor tibiae motoneurons, that the central rhythm generating networks contribute to the patterning of motoneuron activity by providing phasic inhibitory synaptic drive. Individual leg motoneurons express specific intrinsic properties, i.e., spike-frequency adaptation and repolarizing sag-potentials, that may be involved in shaping their activity in the locomotor cycle. From these results various lines of research emerge that we currently follow: (i) what is the function of the intrinsic properties of motoneurons in the generation of leg motoneuron activity? (ii) how is the recruitment of the different types of motoneurons, i.e., slow, semifast and fast motoneurons, within one pool regulated within the generation of the locomotor program?

A third question that we focused on since some time ago with a variety of experimental approaches is: what neural mechanisms exist that allow the coordination of activity in motoneuron pools, i.e., the activity of the joint controllers, in the locomotor cycle? By now, a detailed picture has emerged of how the action of the joint control networks is affected by influences of sensory signals from the leg and other adjacent leg joints. We found that sensory signals can pattern motoneuron activity by utilizing their access to the central rhythm generating networks of adjacent leg joints, the activity of which they can reset and entrain. Three examples: signals from the femoral chordotonal organ (fCO) related to extensions movements and/or extended position of the FT-joint

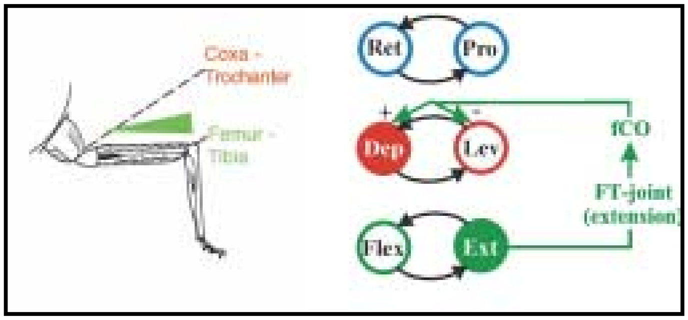


Figure 2. Schematic representation of an interjoint influence of proprioceptive signals from the FT-joint on the adjacent CT-joint. The circles together with the arrows interconnecting them denote for each of the three main leg joints (thoraco-coxal joint: Retractor/Protractor; coxa-trochanteral joint: Levator/Depressor; femur-tibia joint: Extensor/Flexor) an individual central rhythm generating network. Extension signals from the fCO can induce a transition in activity in the central rhythm generating network of the CT-joint by terminating levator trochanteris activity (-) and initiating depressor trochanteris activity (+).

facilitate the transition from activity in levator trochanteris to depressor trochanteris motoneurons. Thereby, they can contribute to the termination of leg swing (Fig. 2; Hess & Büschges, 1999, *J. Neurophysiol*. **81**:1856; Bucher et al. 2003, *J. Neurophysiol*. **89**:1245); load signals from the femoral campaniform sensillae (CS) assist ongoing flexor motoneuron activity during the stance phase of the leg by keeping the FT-joint network in the flexor phase (Akay et al. 2001, *J. Neurophysiol*. **85**:594); load signals from the trochanteral CS can initiate the transition from activity in protractor coxae to retractor coxae motoneurons. Thereby, signals from the trochanteral CS are used to couple the activity of the thoraco-coxal joint network to the walking motor program of the adjacent leg joints (Akay, Haehn, Ludwar, Schmitz & Büschges, in prep.). The latter results supplement the data on the role of strain signals that were collected by Sasha Zill and Josef Schmitz. Verification of the sensory influences mostly identified in very much reduced preparations was possible from lesion and stimulation experiments in 'semi'-intact preparations. Over the past couple of years we have unraveled what one could call a set of 'neural rules of sensory-central-interaction' for inter- as well as intrajoint control in a multi-jointed limb.

It became more and more clear that eventually a test of sufficiency of these 'neural rules of sensory-central-interaction' for generating a functional motor program in a stepping single stick insect leg on some kind of simulation platform would be desirable. By this time a similar situation existed for vertebrates, specifically for cat walking. We had this exciting opportunity as Ansgar had the chance to organize a special research group at the Institute for Advanced Study at Berlin during the academic year 2001-2002. The group on 'Neural Control of Locomotion' brought together scientists with different backgrounds: Ansgar Büschges (invertebrate neurobiology and locomotion), Volker Dürr (theoretical biology and neuroethology), Örjan Ekeberg (computer modeling), and Sten Grillner and Keir G. Pearson (vertebrate neurophysiology and locomotion). During the period at the Institute for Advanced Study — an ideal and supportive working environment to do theoretical oriented work — A. Büschges, V. Dürr, Ö. Ekeberg and K.G. Pearson created a framework for 3-dimensional dynamic simulations of walking in a tetrapod (cat) and a hexapod (stick insect). The simulation technique was based on the expertise of Örjan Ekeberg for calculating the movements of lamprey swimming in 2D and 3D. The primary advantage of the simulation scheme used, apart from the pure speed of the algorithm, is that additional motion constraints imposed on the joints as well as ground contacts can be added and removed dynamically as the simulation proceeds. On top of the numerical simulation platform, two different simulators were built: one for the stick insect and one for the cat. A graphical layer using the OpenGL industry standard graphics package makes it possible to see the resulting movements in the form of a walking animal on the screen.

Our biomechanical model of the stick insect was developed based on the species *Carausius morosus*. Morphological data, including sizes, weights, and center of gravity of each body segment, were taken either from published work, e.g., from Holk Cruse's work or collected in our laboratory. The head, thorax and abdomen are represented as one single segment, while each leg is simulated as three segments: coxa, femur and tibia (Fig. 3). The tarsal claws are currently not represented. Muscles were included in the form of torque generators

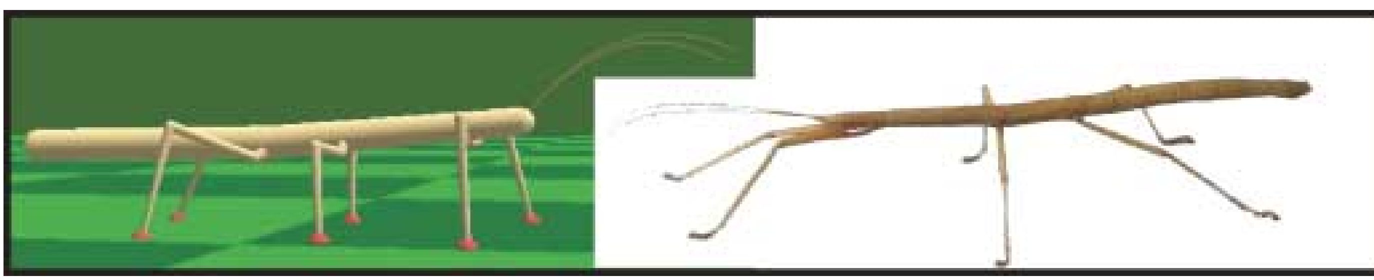


Figure 3. The stick insect (right) and its simulated companion (left; see text). The red dots in the simulation denote ground contact of a leg.

at the joints and realistic length-tension and velocity-tension characteristics can be used. The present muscle model in our simulation is rather simple. It is based on parameters indirectly calculated from data from Ulrich Bässler's lab and not yet as complete as the data of Ann Ahn and Bob Full from cockroach leg muscles. The neural control system for posture and movement in the simulator was encapsulated in a special 'plug-in' module using a high-level scripting language. This module receives information resembling true sensory signals, such as ground contact, joint angles, and load. The module is then responsible for setting up the muscle activation levels which enter the muscle model. At present, the neural control system uses two principles: (i) graded negative feedback from the position of the coxa-trochanteral joint (see also the work of Gernot Wendler) was used for height control in a way as described by Holk Cruse and coworkers; (ii) timing control for the individual leg joints is realized by a *finite-state* system in which sensory signals trigger transitions between the internal states. The timing controller is based on results from our experiments targeting the role of sensory signals in intra- and interjoint control with specific emphasis on sensory signals affecting the timing of individual joint controllers (see above). Although the stick insect simulation currently still bears substantial shortcomings, e.g., in using a very simple muscle model and lacking magnitude control of motor activity, the actual simulation verified the relevance of the recently identified 'neural rules of sensory-central-interaction' in intra- and interjoint control (see above) by generating coordinated stepping movements of the middle leg.

From getting a more and more detailed insight into the mechanisms that govern the generation of the motor program for locomotor movements in an individual insect multi-jointed limb, and from creating the simulation, we entered an area of research that we are currently pursuing with some focus: the neural basis for interleg coordination in the walking insect. ◆

Meetings and Courses

The third annual **Neural Coding Workshop** will be help at University of Chicago, USA, on Saturday, June 21, 2003. The topic of the workshop is 'Neural Coding of Behavior.' Speakers include Harold Zakon, Darcy Kelley, Gary Rose, Catherine Carr, Richard Mooney, Curtis Bell, Michael Brainard and Ofer Tchernichovski. We plan to leave considerable amount of time for discussions throughout the day, and following the workshop there will be a reception. If you are interested in attending the workshop please register online at cns.bsd.uchicago.edu. There is a modest fee to cover refreshments and lunch at the faculty Quadrangle Club. ◆

The Center for Comparative and Evolutionary Biology of Hearing (C-CEBH) at the University of Maryland, College Park, USA, and the Acoustical Society of America (ASA) have organized the first **International Conference on Acoustic Communication by Animals** to be held at the University of Maryland, from July 27 to 30, 2003. The emphasis of the Conference is to integrate information across animal taxa and to enable young investigators and students to meet and share ideas, data, and methods with more established investigators in this growing and exciting field of research. Keynote speakers include Donald Griffin, Jack Bradbury, and Darlene Ketten. Approximately 20 additional invited speakers from around the world will present talks, and there will also be contributed talks and posters. Further information on the meeting can be found at the meeting web site: http://asa.aip.org/communication.html. Deadline for submission of contributed papers is April 8, 2003. ◆

New Books by ISN Members

Sensors and Sensing in Biology and Engineering, edited by Friedrich G. Barth, Joseph A.C. Humphrey, & Timothy W. Secomb. Springer-Verlag, Wien - New York, 2003. ISBN 3-211-83771-X. EURO 85.60, sFr 133.00, US $99. 370 pages, 130 illus., hardcover. This book is designed to fill an urgent need for interdisciplinary exchange between biologists studying sensors in the natural world and engineers and physical scientists developing artificial sensors for scientific, industrial and commercial purposes. Among the topics covered by leading experts (26 chapters) are Mechanical Sensors; Visual Sensors and Vision; Chemosensors and Chemosensing; and The Embedding of Sensors. ◆

Positions available

Postdoctoral electrophysiologist for research on learning and memory, Zoology Department, Cambridge University, England. We are seeking a postdoctoral research associate with experience of *in vivo* electrophysiological recording. The project, supported by a BBSRC grant to Dr. Brian McCabe, Prof. Malcolm Brown and Prof. Sir Gabriel Horn, is for up to three years and will investigate mechanisms of learning and memory underlying imprinting, continuing a long-standing collaborative research programme [see Horn, G. (1998) *Trends Neurosci*. **21**:300; Horn, G. (2000), in *Brain, Perception, Memory*, Ed JJ Bolhuis, Oxford University Press, p. 329]. The Department is a lively and supportive research community, which has received the highest ratings in all Research Assessment Exercises. Starting salary up to £19,486 (RA1A spine point 6). Initial enquiries should be to Brian McCabe at bjm1@cam.ac.uk. Applications (including a PD18 form and three referees) should be sent to The Departmental Administrator, Dept. Zoology, Downing Street, Cambridge, CB2 3EJ, UK. Closing date for applications 28 February 2003. ◆

Position for a Ph.D. student available in project B1 of the SFB 'Theoretical Biology' at the Humboldt University, Germany. In a multidisciplinary program, combining electrophysiological and theoretical approaches, we investigate the recognition of acoustic communication signals in insects. The project focuses on the processing of temporal patterns in the auditory pathway of grasshoppers and possible modifications during evolution and speciation. Also of interest is how the neuronal implementation of signal recognition contributes to the robustness of these systems against external and intrinsic noise. Requirements: experience in electrophysiological techniques and an interest in theoretical approaches, modeling and behaviour. The Humboldt University is an equal opportunity employer and encourages applications from qualified female applicants. Applications of disabled persons will be considered preferentially in case of equivalent qualification. Send applications (CV, bibliography, summary of previous studies, names of two referees) to Prof. Dr. Bernd Ronacher, Institute of Biology, Humboldt-Universität zu Berlin, Invalidenstr. 43, 10115 Berlin. email: Bernhard.Ronacher@rz.hu-berlin.de. http://www.biologie.hu-berlin.de/~vhphys/index.htlm. Co-supervisor of the thesis will be Prof. Andreas Herz.

Two postdoctoral positions are available at the University of Washington in Seattle, USA, to study sensory processing in the central auditory system of echolocating bats. The focus of the research is to study processing of temporal patterns of sound in the lower brainstem (Position 1) and in the in the auditory midbrain (Position 2). The positions provide the opportunity to gain experience with a variety of neuroanatomical and electrophysiological techniques including extracellular and intracellular recording and neuropharmacology. Our research program emphasizes an integrative approach to studying the neural circuitry and mechanisms that operate in the mammalian central auditory system. Interested individuals should send letter describing long-term research interests and goals, a CV, and two letters of reference to: J.H. Casseday or Ellen Covey, Dept. of Psychology, Box 351525, University of Washington, Seattle, WA 98195, USA. E-mail inquiries: ecovey @u.washington.edu; casseday@u.washington.edu.

Postdoctoral position in birdsong learning. The Neural and Behavioral Dynamics Lab (Prof. Todd Troyer, P.I.) investigates the functional anatomy underlying sensorimotor learning in songbirds using a combination of high-density behavioral recording, computational models, and physiological manipulation of the song circuit (www.glud.umd.edu/~ttroyer). The University of Maryland, College Park, USA, has a large, highly interactive neuroethology community (see www.bsos.-umd.edu/psyc/neuroethology) and is located in the DC metro area (accessible by Metro). Experience with behavioral experiments and/or signal processing is a plus. Preferred starting time is fall 2003. Applicants should send a CV, a statement of research interest, representative reprints, and two or three letters of recommendation to Todd Troyer, Dept. of Psychology, University of Maryland, College Park, MD 20742, USA.

Postdoctoral and Ph.D. positions in cognitive neuroscience will be available to study the neuronal basis of numerical competence in behaving monkeys in the Primate NeuroCognition Laboratory, headed by Dr. Andreas Nieder, at the University Tübingen, Germany. Much effort will be directed at the prefrontal cortex, a brain region associated with the highest levels of cognitive function. A sophisticated behavioral methodology will be combined with techniques for examining the activity of groups of neurons. The independent junior research group (starting April 2003) will be funded by the German Research Council (DFG) within the Collaborative Research Center 550, and will be located at the Dept. of Cognitive Neurology. The laboratory will be housed in the brand new state-of-the-art Hertie-Institute for Clinical Brain Research. Candidates with a flair for animal training are particularly encouraged to apply. Experience in Matlab/C-programming and electrophysiological recordings from awake animals would be advantageous. Please send CV and the names of two or three referees to <nieder@mit.edu>.

Material for Future ISN Newsletters

We welcome material for future newsletters in a number of categories. Advertisements for positions are limited to 150 words. Announcements of new books (copyright 2002) *written or edited by ISN members* should include the full citation information (including ISBN) plus a 40-50 word description of the book (note: if an ISN member contributes only a chapter to a book it is not appropriate for inclusion in the newsletter).

We also welcome announcements of future meetings, reports on recent meetings, discussions of research areas or topics of interest to neuroethologists, laboratory profiles, editorials, and obituaries. Word limits depend on the type of article. Have an idea for an article that you or someone else would write? Contact the Secretary!

All material must be submitted electronically, preferably as a file attached to an e-mail message. Send queries or submissions to Janis Weeks (weeks@uoneuro.uoregon.edu). The deadline for the July issue is **June 1, 2003**.

International Society for Neuroethology
c/o Panacea Associates
744 Duparc Circle
Tallhassee, FL 32312 USA

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